STERILE INSECT AND PARASITE AUGMENTATION TECHNIQUES: UNEXPLOITED SOLUTIONS FOR MANY INSECT PEST PROBLEMS[1]

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The Florida Entomological Society is to be commended for selecting The Screwworm Research Team as the recipient of your Pioneer Award. The selection of this team for the award will not only be an honor for this pioneering group of scientists, it will also enhance the prestige of the new awards program. I feel doubly honored to have been invited to deliver the Pioneer Lecture for this special occasion.

It is regretted that several members of the team are no longer with us. I am sure that if they were here today they would be as proud and would feel as honored as those of us who have had the good fortune to survive the years that have gone by.

I wish to pay special tribute to the deceased members of the team. I would like to acknowledge one of my most respected colleagues and a special friend of the family, Dr. Raymond C. Bushland. Dr. Bushland and his assistant D. A. Hopkins, who is also deceased, demonstrated in the laboratory that the sterile insect technique was a viable concept. They participated in the field studies that proved that the sterile flies would perform under natural conditions. Dr. Bushland was a technical advisor to the pest mangers who conducted the suppression programs.

I also wish to pay tribute to another highly respected colleague, an able and dedicated scientist and a special friend of the family, Dr. Arthur W. Lindquist. He had confidence in the sterile insect technique from the beginning. As chief of the section on Insects Affecting Man and Animals, he did all that he could to support the efforts of those who were conducting the laboratory and field investigations.

Another key member of the team who made the technique work in practice was Chet Husman. Mr. Husman was the engineer who designed the machinery for the mass rearing of the flies. He designed and supervised the construction of the first screwworm rearing facility that was located at Sebring, Florida, and the larger facility that was later constructed in Texas. Every aspect of the engineering work required innovation on the part of Chet Husman because never before had insects been reared on the scale of 50 to 100 million per week.

I want also to acknowledge the members of the team who have had the good fortune to survive the many years that have passed. A key member of the team who was directly in charge of the field release experiments was Al Baumhover. He made the first sterile fly releases on the Island of Sanibal which is not far from here. That experiment demonstrated that the sterile males would perform their mission in a natural environment. He was also in charge of the experiment conducted on the island of Curacao, Netherlands Antilles. This classic experiment was of great importance. It demonstrated that the technique could eradicate an isolated screwworm population. In the conduct of this experiment he had the cooperation and support of Dr. B. A. Bitter, the veterinary officer for the island.

I hope that Al will have the opportunity to describe the details of the pioneering experiment. I recall the great satisfaction that Drs. Bushland, Lindquist, and I had in receiving Mr. Baumhover's favorable report each week for the first 9 weeks after the

[1]This is a more detailed version of the lecture that was presented to the society members August 5, 1997.

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sterile fly releases began. The proportion of the sterile egg masses deposited by the wild female flies increased each screwworm cycle, while the number of egg masses deposited decreased. The results confirmed the type of suppressive action predicted by the model I had developed. Within a period equal to four generations of the fly no more egg masses, either fertile or sterile, were collected.

There were other key members of the team. They included A. J. Graham, F. H. Dudley, W. D. New and G. W. Eddy. All these individuals played important roles in the research that led to the eradication of the screwworm from Florida and the southeastern states and later in the Southwestern United States and Mexico.

During my long career I observed important research in progress by many able and dedicated scientists. No research team has ever performed more diligently or accomplished as much as did the team you are honoring today.

It would be a serious omission, however, if I did not acknowledge the contributions of the many able and dedicated pest managers and workmen with the United States Department of Agriculture and the cooperating state agencies who put the research findings into practice - first in Florida and the Southeast and later in the Southwest and Mexico. Virtually every aspect of those unique programs required ingenuity, perseverance and innovations by those who conducted them. They involved the production and handling of millions of insects per week and the distribution of the flies by aircraft on several hundred thousand square miles of all types of terrain. They dealt with thousands of livestock producers in the United States and Mexico who were involved in one way or another with the program.

Many people have asked me how I got the idea of controlling the screwworm fly by the sterility technique? The answer to this question involved a number of other developments. The discovery by Cushing and Patton (1933) that the screwworm was a true parasite and differed from the common and very abundant scavenger blow fly, *Cochliomyia macellariia*, was an important factor. This meant that the pest existed in relatively few numbers in the natural population. Also, Melvin and Bushland (1936) had developed an artificial medium for rearing the fly. These two factors suggested that it might be feasible to rear more flies than existed in the natural population.

For years, research effort had been focused on controlling the worms in the animal wounds and on protecting the animals from reattack by the flies. But I kept thinking of possible ways to control the pests before most of the damage had been done to livestock and wild animals. This suggested the possibility of control by rearing and releasing flies that were sterile or that had genetic deficiencies that could be transmitted to the natural population.

It was not possible for any of us to undertake research on the idea of sterility releases for a number of years. During the 1940's we were assigned to other projects, including the research conducted at Orlando, Florida to develop means to control insect pests and disease vectors of military importance. But I kept thinking of ways that screwworm might be controlled before it caused damage to the livestock and wild animals. I discussed the feasibility of the genetic approach with a number of scientists. Most expressed skepticism that this would be successful. It was not until after the war that active research was started on the sterility procedure.

I wish I could say that all aspects of the operational programs that followed went smoothly. But this would not be correct. Those responsible for the control programs encountered and had to resolve many operational problems. There was skepticism by many; there were critics. After the programs in the southwest were initiated some scientists tried to discredit the work. Self-proclaimed authorities on the screwworm and the sterility technique grew in numbers. Some even went so far as to advocate that the program be discontinued.

I am happy to say, however, that all the obstacles were eventually overcome. The rewards by the dedicated people who executed the program have been very great. The savings for the livestock economy in the United States and Mexico have amounted to many billions of dollars during the past 40 years. Those benefits will continue to accrue by a half billion dollars each year so long as measures are taken to prevent the reestablishment of the pest in its former range. One of the greatest satisfactions from the success of the programs is the knowledge that one of nature's most cruel and obnoxious pests can be brought under control. Only those who have witnessed the trauma and suffering that helpless domestic and wild animals experience when they are literally eaten alive by thousands of maggots can fully appreciate the full benefits of this achievement.

It was a privilege for me to be associated in one way or another with various aspects of the research and control programs from the time of their inception until they became a reality. When I see the difficulty today of gaining the support needed to undertake other new approaches to insect pest control and think of the many obstacles that people can throw in the paths, I consider it miraculous that the screwworm programs ever materialized and that they proved to be so successful.

I wish time would permit a more detailed discussion of some of the aspects of the research and operations that became involved in the development and execution of the sterile insect technique for screwworm control. This is not feasible here. However, I would like to call attention to some of the publications that deal with the early research and the control program that followed. They include those by Bushland and Hopkins (1951 and 1953), Baumhover et al. (1955), Lindquist (1955), Knipling (1955 and 1959), O. H. Graham (1985), Scruggs (1975) and Meyer and Simpson (1996).

MERITS AND LIMITATIONS OF THE STERILE INSECT TECHNIQUE

The sterile insect technique (SIT) represented a new principle of insect population suppression. The type of suppressive action that follows the release of sterile insects is generally well understood. However, I have developed a model to demonstrate how a pest population will respond to the release of sterile insects throughout its ecosystem.

A basic model that depicts the demographics and dynamics of an uncontrolled insect pest is first needed to show how a pest population grows in the absence of control. Such model is shown in Table 1. Authorities on various pests could make appropriate modifications to such a model so that it would be reasonably representative of the demographics and dynamics of a wide range of insect pests. I have developed hypothetical models of this nature for many of our important insect pests (Knipling 1979, 1992). The degree of accuracy of some of the models may be questioned. Nevertheless, they have proved to be very valuable for analyzing the principles and for estimating the influence of various methods of control.

The hypothetical pest is assumed to exist at its normal low density level at the beginning of a season. It will grow to its normal high level as the season advances. Each generation the rate of population growth diminishes as the population increases. It will eventually stabilize due to the action of various density dependent suppression factors. By season's end this hypothetical population has increased by about 20 fold. Then, due to the high mortality that generally occurs during the winter months the population at the beginning of the next year will be similar to the population at the start of the first year. Populations of most insects are extremely variable from habitat to habitat, generation to generation, and from year to year. But they establish a steady density level that when averaged over a period of years tends to remain rather constant. This is a fundamental characteristic of all animal populations.

TABLE 1. THE DEMOGRAPHICS AND DYNAMICS OF A TYPICAL INSECT PEST POPULATION AS IT DEVELOPS DURING A CROP GROWING SEASON.*

	Generation			
Parameters	1	2	3	4
Normal females	1,000	4,000	10,498	19,415
Normal males	1,000	4,000	10,498	19,415
Eggs deposited per female	200	180	162	146
Total eggs deposited	200,000	720,000	1,700,676	2,834,590
Survival of eggs to small established larvae, percent	40	36	32	29
Total small larvae	80,000	259,200	544,216	822,031
Survival of small to large larvae, percent	40	36	32	29
Total large larvae	32,000	93,312	174,149	238,389
Survival large larvae to adults, percent	25	22.5	20	18
Adult progeny, next generation, both sexes	8,000	20,995	38,830	42,910**
Increase rate	4.0	2.6	1.7	1.1

*The density-independent control factors such as weather conditions are assumed to be normal and favorable. The density-dependent control factors such as biological agents are assumed to intensify by 10 percent each generation as the population grows.

**The progeny of the fourth generation are assumed to be the overwintering population. If the probability of winter survival is 5 percent, the population the next spring would again be near 1,000 adults of each sex. The model is considered representative of a steady density population.

The actual number of insects in natural populations and the growth rates of the population are not of much importance when the pests are to be controlled by the application of insecticides or other methods that have suppressive action independent of the pest density. But if the objective is to regulate or eliminate populations by the use of control measures that have pest density dependent suppressive action such as the sterile insect and parasite augmentation techniques, the number of insects in the natural population and their growth rates are key parameters. Obtaining such information has been one of the most neglected aspects of insect population ecology. Therefore, I have used indirect procedures to make realistic estimates for these parameters.

Nearly all insect populations have the potential of increasing by a hundred fold or more during a single generation. However, all of their life stages are subjected to many hazards even when conditions for reproduction are favorable. This restricts the reproductive rate to a low level. The population shown has an increase rate of 4 fold during the first generation. If the species has the potential of producing 1,000 progeny per female, which would be typical of a number of our major pests, then less than 1 percent of the potential progeny will normally survive even under favorable conditions.

This suggests that if a new pest specific hazard is superimposed on existing hazards, it will not require a high degree of control to cause a marked decline in a pest population. But, if in the process of achieving control a high proportion of the natural biological agents are also destroyed, the potential rate of increase of the surviving pests and coexisting non-targeted pests that are normally held in check by natural biological control agents may increase by 10 fold or more per generation. This in essence is what we have been doing to many insects during the past 50 years because of the use of broad-spectrum insecticides.

The model in table 2 depicts the influence of the release of sterile insects into a pest population of the nature shown in table 1. If enough fully competitive sterile insects are released *throughout* the pest population to achieve a sterile to fertile ratio of 9:1, only 10 percent of the normal females will mate with normal males and the reproductive success of the population will be reduced by 90 percent. If the reproducing females produce an average of 10 adult progeny the population will decrease by 50 percent. The release of the same number of sterile insects will then result in a sterile to fertile ratio of 18:1, and reproduction will be inhibited by about 95 percent. This in turn will cause an even sharper decline in the pest population and the release of the same number of sterile insects during generation 3 will then inhibit reproduction by more than 98 percent. By generation 4 the natural population will be so low that the release of relatively few insects will reduce the probability of a fertile female mating to less than one. The model shown is representative of a classic sterile insect suppression model I first described in 1955 (Knipling 1955). In theory all reproduction will cease by the fourth generation. This is what happened to the screwworm on Curacao.

The success of the sterile insect technique against the screw worm prompted scientists to investigate the feasibility of using the technique for dealing with other insect pests.

The first intensive research effort on other insects involved tropical fruit fly species. As a complex these are the world's most important fruit insect pests. Early research on the technique was led by L. F. Steiner, Director of the Agricultural Research Service Laboratory in Hawaii. He and his associates demonstrated that the technique could be used to suppress and eliminate isolated populations of the melon fly, *Bactrocera cucurbitae*, and the oriental fruit fly, *Bactrocera dorsalis*, (Steiner et al. 1965 and Steiner 1970). Japanese scientists further developed the technique in order to eradicate the melon fly from the Okinawa islands (Kakinohama *et.al.* 1997). This virtually

TABLE 2. THE INFLUENCE OF STERILE INSECT RELEASES ON THE DYNAMICS OF A PEST POPULATION OF THE NATURE SHOWN IN TABLE 1.

	Generations			
Parameters	1	2	3	4
Normal females	1,000	500	132	10
Normal males	1,000	500	132	10
Sterile insects released, both sexes	18,000	18,000	18,000	400
Sterile-to-fertile ratio	9:1	18:1	68:1	20:1
Normal females mated with normal males	100	26.3	2	0
Expected adult progeny per normal mated female	10	10	10	—
Adult progeny, next generation, both sexes	1,000	263	20	—

doubled the vegetable economy of the islands. The technique also played a role in the elimination of the oriental fruit fly from Japan, which was accomplished largely by the use of the male attractant, methyl eugenol (Koyama *et al.* 1984).

The SIT is playing a major role in dealing with the Mediterranean fruit fly, *Ceratitis capitata*, (medfly) in various parts of the world. This is the most important of the tropical fruit fly species. Scientists in several countries have contributed to the development of the technique for controlling or eradicating this pest. Much of the research effort has been sponsored by the International Atomic Energy Agency (IAEA). Scientists with the U.S. Department of Agriculture (USDA) Laboratory in Hawaii in cooperation with the University of Hawaii and the University of California conducted much of the early research that led to use of the technique as a key component in eradication and containment programs for the medfly in the United States, Mexico and other countries.

There have been numerous introductions and establishments of medfly populations in the United States during the past half century. Until the SIT came into use control agencies relied largely on insecticide applications and drastic host removal to eliminate them. However, there is strong public opposition to the use of non-selective insecticides for eradicating insect pests, especially in urban areas where medfly introductions are most likely to become established. Relying on SIT for dealing with such introductions was slow to be accepted. The technique is not very effective when the pest populations are high and its suppressive action is slow compared with the use of insecticides. But limited use of insecticides followed by the release of sterile flies to complete eradication or to prevent the reestablishment of populations is now an accepted practices.

SIT has also had a rather slow history of development for the eradication of tsetse fly populations, *Glossina spp*. Tsetse flies are probably the most important insect pests in the world. The IAEA assumed leadership in developing and promoting the use of SIT for eradicating these disease vectors. Because of the difficulty and high cost of rearing tsetse flies these insects would seem to be poor candidates for eradication by SIT. However, by using insecticides when the pest populations are high and then releasing sterile flies against the reduced populations, this pest management strategy has been used successfully.

Sterile pink boll worm moths have also been used for some years to prevent the establishment of this cotton pest in the San Jauquin Valley of California. This important cotton growing area has been kept free of the pink boll worm for about two decades by the use of the technique (Bartlett and Staten 1996). Canadian scientists are using the technique in efforts to eradicate the codling moth from Western Canada.

Thus the SIT is playing an increasing role in dealing with several important insect pest problems. It is my opinion, however, that the technique has not been developed and put into use to the extent that it should have been. There are a dozen or more major insect pests in the United States and in other parts of the world that would be good candidates for management on a year by year basis by the sterility technique, or for eradication when this is a feasible option. The pests I have in mind would include all of the tropical fruit fly species; European corn borer, *Ostrinia nubilalis*; sugarcane borer, *Diatraea succharalis*; and even the widespread and costly Helicoverpa/Heliothis complex. However, development and use of the technique has lagged for a number of reasons. Technology must be developed and made available to mass produce large numbers of insects. This has not yet been done for a number of candidate species. Some insects are very susceptible to irradiation damage and thus are not sexually competitive with wild rivals. This is the case for the boll weevil, *Anthonomus grandis*.

However, one of the main reasons for the limited use of the technique has been the lack of support from and even opposition by much of the pest management community to the holistic approach to insect pest management. This makes it difficult to obtain the public and political support for areawide insect pest management programs. As time goes on there will be increasing concern over the use of potentially hazardous insecticides. It will also become increasingly apparent that a defensive reactive pest management procedure based largely on the use of insecticides will not provide satisfactory solutions for many pest problems. SIT has some important limitations, but it also has merits not possessed by other methods of control. With greater recognition of the advantages of the holistic approach to insect pest problems there will be more interest in feasible ways to achieve this objective.

Merits and Limitations of the Use of Insecticides

Control of insects by the use of insecticides has always appealed to agriculturists. The availability of many effective synthetic insecticides has made it possible for farmers to control most insects of agricultural importance. Their intensive use worldwide is one of the reasons that agriculture has been able to meet the food requirements for the expanding world population. Also their availability for the control of arthropod vectors of human diseases has prevented illness or the death by hundreds of millions of people each year during the past 50 years.

Insecticides have a number of advantages over other methods of insect control. They are rapid and positive in action. Insect outbreaks can be controlled in a matter of days and disease transmission can be halted within hours by the application of insecticides. They are readily available to consumers and equipment for their application is also readily available. Society should be mindful of the important contributions that insecticides have made to human welfare. People should also be mindful of the continuing need for these chemical insecticides for the indefinite future.

At the same time, however, the extensive use of the insecticides, most of which have broad-spectrum activity, has created many complex environmental problems. Residues of the chemicals in or on agricultural products pose potential hazards to people and animals. The welfare of fish and wildlife in environments treated for insect pest control can be jeopardized. The balance between destructive and beneficial insects can be so seriously disrupted that natural biological control agents cannot perform their normal function. In my opinion, the ecological disruptions resulting from the use of broad-spectrum insecticides is the most serious of the environmental hazard problems associated with the use of insecticides. I can say without qualification that ecologically sound insect pest management will not be possible so long as the use of broad-spectrum insecticides is a major component in pest management systems.

Pest management scientists are aware of this, and accordingly have devoted much effort to the development of safer ways to control insects. Major efforts have been made to find new and better insect attractants; insect pathologists have discovered a wide range of insect pathogens and microbial agents that offer promise as safe alternatives to chemical insecticides. More emphasis has been placed on classical biological control and the use of entomophagous insects for augmentation purposes. Plant breeders and entomologists have intensified investigations on host plant resistance, including resistance by biotechnology.

Good progress has been made on all of these approaches for insect control. But when viewed from a broad perspective very little of the new technology has been put into practice. Agriculture still depends largely on insecticides for the control of insects (U.S. Congress 1995).

In the efforts to reduce the amount of insecticides used, a supervised system of insect control evolved that is broadly defined as Insect Pest Management (IPM). To minimize the use of environmentally hazardous insecticides and to reduce costs farmers are urged to rely as much as possible on natural control agents before applying insecticides. They are also encouraged to use supplemental control measures such as cultural procedures and to grow pest resistant crop varieties. As a guide for growers, economic treatment levels have been established by pest managers for various insects on different crops.

IPM has achieved some important objectives. It has virtually eliminated the indiscriminate use of insecticides. It has been profitable for growers because it minimizes expenditures for insecticides yet prevents the heavy losses that can occur if control measures are not applied. However, it has not reduced primary reliance on pesticides to control pests.

After intensive efforts to develop alternative ways to control insects, we must ask ourselves why is agriculture still so dependent on insecticides? The answer involves a number of complex factors. But the basic reasons are clear. Most of the possible alternative methods of control are not as effective or as practical as insecticides after insect pest populations have already reached economic treatment levels. They also lack the fast and positive action that growers desire for protecting their crops when insect pest populations reach such levels. Moreover, the alternative methods of control are usually not available to individual growers. Therefore, agriculture has continued to depend largely on fast-acting insecticides for controlling insect pests for a half century. And when broad-spectrum insecticides are applied it defeats one of the primary objectives of IPM programs: to obtain optimum benefits from natural biological agents.

Despite all that has been said about the benefits of IPM, when we analyze the dynamics of insect pest populations and the kinds of suppressive action that is achieved by the use of insecticides, the defensive reactive method of insect control that has evolved is not a sound insect pest management system. It gives insect pest populations the opportunity to increase virtually unhampered from their normal low to their normal high levels each year. And when they reach the economic treatment levels about the only option that growers have is to apply fast-acting, broad-spectrum insecticides. Then, the reproductive success of the proportion of the target pest population not controlled is higher than normal leading to possible resistance and the serious depletion of the total complex of natural control agents will permit normally minor or secondary pests to become important pests. The method also concedes to insects the losses they cause below the economic threshold levels. For some of our important insect pests such as the corn earworm on corn and the European corn borer, these losses amount to about $500 million per year for either pest. What the total damage is that falls below the economic pest control level is difficult to determine, but it probably amounts to several billion dollars annually. The losses that fall below current economic threshold levels give us a good perspective of the amount that agriculture could afford to spend on alternate ways to deal with specific pest problems that would be less costly and more acceptable from environmental standpoints.

This is the current status of insect pest management. While the methods of control that have evolved are profitable for the growers, they have not reduced the overall threat that insects pose for agriculture. In support of this conclusion, if a list were made of the insect pests that were of major concern to agriculture before the new insecticides came into being and such list were also drawn up today most of the same pests would be on both lists—except that the current list would be longer. Only two important insect pests would not be on the current list: the screwworm and the boll weevil in the southeastern cotton growing region. It is significant that these are the only insect pest problems that have been subjected to organized suppression programs that are designed to eliminate or maintain total populations below damage levels.

The limitations of the largely defensive systems of insect control have prompted me to continue theoretical appraisals of other techniques and strategies for controlling insects. My efforts have been focused on the possibility of making use of entomophagous insects to regulate total pest populations as a preventative measure. As the investigations have progressed and with the promising results obtained on several of the major insect pests by research entomologists who are investigating area wide management by the release of biological agents, I have gained more and more confidence in the holistic approach to insect pest control.

The Holistic Approach to Insect Pest Management by the Parasite Augmentation Technique

The possibility of controlling insect pests by the release of reared insect parasitoids or insect predators into pest habitats is not a new concept. Indeed, biologists have devoted as much or more research efforts to this method of control than to any other method besides the use of insecticides. Much of this effort has been on Trichogramma parasitoids. While the use of these parasitoids is reportedly successful in some countries for controlling certain lepidopterous pests (Ridgway and Vinson 1977), it has not been very successful in other countries. The results obtained with other parasitoids or predators have been largely unsatisfactory. This is reflected in the limited use of reared biological agents for controlling insect pests. While a number of such biological agents are being produced and sold by small private industries (Hunter 1994), probably less than one percent of the agricultural insect pests are currently controlled by the release of insect parasitoids or predators into insect pest habitats.

There are several reasons for such limited use of the technique. It is a technique that is not very effective, practical or reliable when used on a farm-by-farm basis and only as the need arises. But when used as a preventative measure to regulate total insect pest populations it has very important advantages over all other methods of control.

Until recent years the possibility of rigidly regulating total insect pest populations as a preventative measure by the release of selected parasitoids or predators throughout pest ecosystems has been given little consideration by biologists. Very few insect pests have been subjected to such releases. The use of natural enemies to control insect pests in greenhouses would be an exception to this generalization. Releases of insect predators or parasitoids are often quite successful because the total pest populations are subjected to the releases.

Notwithstanding the poor record of certain insect parasitoids both in nature or when spot released, I undertook a detailed study of parasitism processes and the influence that parasitoids have on the dynamics of insect pests (Knipling 1992). The study was conducted largely by theoretical means, but I reached the conclusion that the parasite release technique offers almost unlimited possibilities for regulating populations of many of the nation's and world's major insect pests if selected species can be mass produced at reasonable costs and appropriate numbers of the parasitoids are distributed *throughout* pest ecosystems at strategic times during the seasonal or periodic cycles of the pests. I emphasize the term *throughout*. Like sterile insects, parasitoid releases are not effective when releases are made in small, unisolated habitats.

The results of the investigation I conducted have been published in a handbook entitled *Principles of Insect Parasitism Analyzed from New Perspectives: Practical Implications for Regulating Insect Populations by Biological Mean*. U.S. Department of Agriculture, Agricultural Research Service. Handbook No. 693, (1992).

The publication explains how parasitism works in natural environments and how biological actions evolved under nature's natural balancing mechanisms to maintain the relative number of parasites and hosts within safe limits. Simple rationalizations tell us that the numerical relationships between parasites and hosts must be maintained within certain limits for the welfare of the hosts as well as for the parasitoids that are dependent on specific hosts or host complexes for reproduction and survival. It is nature's objective to maintain a safe balance between associated organisms, and it is very successful in achieving that objective. But this objective can be in conflict with agriculture's needs. It permits too many insect pests to cause excessive damage to crops and livestock. Also, intensive agriculture favors many insect pests. So, the implications are clear. To achieve satisfactory management of insect pest populations by the use of insect parasitoids it will be necessary to increase the ratio of parasitoids to hosts in coexisting populations in all parts of the ecosystem they cohabitate. About the only way this can be done will be to augment the natural populations by artificial means.

To determine if it is feasible to regulate total populations of various insect pests by use of the parasite release technique, it is necessary to have reasonably good information on the actual number of parasitoids that must be produced and maintained in the pest ecosystems to achieve various rates of parasitism. Such information is not now available for any of our parasitoids. However, largely by deductive procedures and by the use of hypothetical models of the nature already described, I feel that I have been very successful in making realistic estimates of the *relative* number of parasitoids and hosts that normally coexist in natural populations for a wide range of our pests. This in turn makes it possible to estimate the *actual* number of parasitoids that will have to be produced and released in pest ecosystems to achieve satisfactory control.

For solitary parasite species, the proportion of the host population that is normally parasitized provides a good clue to the normal parasitoid to host ratio that occurs in natural populations. It is a good clue because the probability of survival of the immature parasitoids in the host to the adult parasitoid stage and the probability of survival of the hosts that are not parasitized to the adult host stage are very closely linked at all host and parasite density levels. Biologists have obtained considerable information on the usual rates of parasitism caused by virtually all of the better known parasitoid species of our major insect pests. While such data are usually variable because of agricultural practices and other factors, including inadequate sampling, they nevertheless give us a good indication of the normal ratio of parasitoids to hosts in natural populations and a good indication of the rate of parasitism to expect from different ratios. Recognition and adoption of this logical theory has made it possible to gain a good understanding of virtually all aspects of insect parasitism. It has shed new light on what we can and cannot expect from insect parasitoids.

If a parasitoid species causes an average of about 10 percent parasitism, which would be typical of some parasite species, the normal ratio of adult parasites to adult hosts will be near 10:90 or 1:9. If the average rate of parasitism is near 20 percent, which would be typical of many other species, the ratio will be near 20:80 or 1:4 and so forth. Those approximate numerical relationships will hold regardless of the biology and behavior of the parasitoid and regardless of the host stage parasitized. Most importantly such numerical relationships and rates of parasitism hold regardless of the density of the host and parasitoid populations. The practical implications of this theory are clear when pest populations exist at low levels.

Another very important conclusion reached from the investigation is that, contrary to popular opinions, differences in the rates of parasitism caused by different parasite species are due to differences in the ratio of parasites to hosts that can coexist because of the constraints imposed by nature's natural balancing mechanisms.

Many biologists assume that differences in the rates of parasitism caused by various parasite species are due to differences in their host-searching and host-finding ability. Parasitoids are often categorized as good or poor host-finders based on the rates of parasitism they achieve. But we can accept with complete assurance that *all parasite species are diligent host-searchers and highly efficient host-finders and at all host density levels.* Otherwise they would not exist.

The way parasitism works has very great practical implications. It means that the usually low rates of parasitism that occur naturally can be overcome by the simple procedure of mass producing and liberating appropriate numbers of key parasitoid species *throughout* pest ecosystems. This may not be easy to accomplish, but there will be few if any barriers to the attainment of the objective if insect rearing experts are given even modest support for conducting research on parasitoid and host rearing procedures. I am confident that scientists and engineers can, by in vivo or in vitro procedures, mass produce any parasitoid species in unlimited numbers and at reasonable costs if given such support.

If the approximate rate of parasitism caused by a given parasitoid to host ratio is known it is possible by extrapolation to calculate the approximate rate of parasitism that will be achieved by increasing the parasitoid to host ratio. If a ratio of 1:4 causes 20 percent parasitism, a ratio of 2:4 will cause 20 + .20 (100-20) or 36 percent parasitism. A ratio of 4:4 or 1:1 will in theory cause 36 + .36 (1000-36) = 59 percent parasitism. This procedure makes allowances for the intraspecific competition factor. It does not, however, make allowances for the probable shorter life span and the lower average host-finding ability of the female parasitoids when the populations exist at abnormally high levels. But adequate allowances can also be made for this factor.

When allowances are made for both factors, I estimate that an adult parasitoid to adult host ratio of 1:1 will cause about 50 percent parasitism; a ratio of 2:1 will cause about 75 percent parasitism; and a ratio of 5:1 will cause about 95 percent parasitism. If these estimates are accepted as realistic, we have a good idea of the influence that various rates of parasitism will have on the dynamics of different insect pests. We have already noted that natural control factors greatly limit the growth rate of insect populations. I believe that most of our major insect pests would be of minor importance if an additional 50 percent control were superimposed on all natural hazards that each pest faces and if this occurred *throughout* the pest ecosystem. Again, I emphasize that such additional mortality must be achieved against the total population.

One might ask how realistic are these assumptions? I believe that most biologists would agree that if a new biological agent were introduced that achieved 50 percent parasitism every cycle, most of our major insect pests would become minor pests. If this is true, there is every reason to assume that 75 percent mortality above normal hazards would assure virtually complete control of nearly all of the major insect pests. It would seem almost certain that 95 percent control superimposed on all natural control factors would within a few cycles result in complete elimination of a pest population—and keep in mind that the lower the pest density the fewer the number of parasitoids that will be required to achieve high parasitoid to host ratios.

If we accept these hypotheses as reasonable expectations—and I firmly believe that they are—the practical question is whether there are any feasible ways to superimpose such levels of control with reasonable consistency and uniformity throughout pest ecosystems each pest cycle. In my opinion, the most feasible way to accomplish this will be by the release of mobile parasitoids that have the instincts and the *capability* of finding the precise location of the hosts.

We have already estimated the rate of parasitism to expect from different parasitoid to host ratios. But, we must consider how pest populations will respond to different rates of parasitism. We will use a hypothetical pest population to estimate the influence as we did for the sterile insect technique.

Influence of Parasitoid Releases on Pest Host Populations

To estimate the influence of the release of parasitoids in pest host ecosystems, we need information on the rates of parasitism to expect from different parasitoids to host ratios as well as information on the average host-finding efficiency of the parasites to be released. I have indicated the rates of parasitism to expect from different parasitoid to host ratios, but we also need to quantify the actual numerical relationships and rates of parasitism.

The basic host population model shown in table 1 can be used to postulate the relative and actual number of parasitoids and hosts that will normally coexist in natural populations and also estimate the average number of host larvae that the female parasitoids will parasitize during their lifetimes if the normal rate of parasitism is known. The model shown in table 3 depicts the coexistence pattern of a pest an associated parasitoid species. The hypothetical parasitoid is a solitary species that averages between 15 to 20 percent parasitism. For this model an average of 17 percent parasitism is assumed. Therefore, based on the comparable survival theory, the normal ratio of adult parasitoids to adult hosts will be near 17:83 or about 1:5. If the host population numbers 1,000 females, as we have assumed, this would mean that 200 female parasitoids will normally coexist with 1,000 female hosts. It will also mean that if the rate of parasitism averages 17 percent, the female parasitoids will parasitize 13,600 of the 80,000 host larvae presumed to be present. It follows that each female parasitoid will on average parasitize 68 hosts during their lifetime during the first generation. Thus, by indirect procedures we have established approximate values for all the parameters needed to calculate the influence a known number of parasitoids will have on the dynamics of a host population having a known number of hosts.

The model depicted in table 4 shows the theoretical results to expect if enough parasitoids of the nature depicted in table 3 are released during generation 1 to achieve an adult parasitoid to adult host ratio of 3:1. This would require the release of 3,000 female parasitoids (6,000 of both sexes.) It should be kept in mind that a 3:1 ratio would be *15 times* the 1:5 ratio that is estimated to cause 17 percent parasitism of the host larvae. Thus, the pest population would be subjected to a very high parasitoid population. We have estimated that at normal densities each female parasitoid will parasitize 68 host larvae. But because of the high parasitoid density I assume, rather arbitrarily, that the average host finding ability of the female parasitoids will be 25 percent lower or 51 per female. However, this will permit 3,000 females to find and parasitize 153,000 host larvae.

Since only 80,000 host larvae are available to be parasitized, the ratio of hosts encountered to hosts available will be about 1.9:1. According to the formula described for table 1 in the publication by Knipling (1992), approximately 15 percent of the host larvae will escape parasitism by chance and 85 percent will be parasitized one or more times when the ratio of total hosts parasitized to hosts present is 1.9:1. Therefore 12,000 host larvae will escape parasitism by chance and 68,000 will be parasitized one or more times. Being a solitary species only one immature parasitoid can develop successfully in one parasitized host.

According to the basic model, table 3, the survival rate of the unparasitized larvae to the adult host stage and the survival rate of the parasitized host larvae to the adult parasitoid stage will be 12 percent during the first generation. Therefore, in generation 2 the adult host population will number 720 females, and the adult parasitoid population will number 4,088. This would be a 28 percent decrease in the host population but a 32 percent increase in the parasitoid population. Therefore, the ratio of adult parasitoids to adult hosts during generation 2 would increase substantially. There are only slight changes in the average number of host larvae produced per female host and the average number found per female parasitoid so the ratio of hosts encountered to hosts present will increase to 3.3:1. This in theory will cause 96 percent parasitism.

Such high rate of parasitism would cause a marked decline in the pest population for generation 3, but, significantly, the parasitoid population would not decline as

TABLE 3. THE ESTIMATED COEXISTENCE PATTERN OF A LARVAL PARASITOID WITH A HOST POPULATION OF THE NATURE SHOWN IN TABLE 1.

Parameters	Generation 1	2	3
Female hosts	1,000	3,984	10,668
Small larvae produced per female	80	72	65
Total small larvae	80,000	286,848	693,420
Coexisting female parasitoids, natural population	200	816	2,240
Adult parasitoid-to-adult host ratio	1:5	1:4.9	1:4.8
Larvae parasitized per female parasitoid	68	61	55
Total host larvae parasitized	13,600	49,776	123,200
Percent parasitism	17	17.3	17.7
Host larvae not parasitized	66,400	237,072	570,220
Survival, unparasitized host larvae to adult hosts, percent	12	9	6.75
Adult hosts, next generation, both sexes	7,968	21,336	38,490
Survival, parasitized host larvae to adult parasitoids percent	12	9	6.75
Adult parasitoids next generation, both sexes	1,632	4,480	8,316
Increase rate of host population	4.0	2.7	1.8
Increase rate of parasitoid population	4.0	2.7	1.8

much. Therefore, the ratio of adult parasitoids to adult hosts during generation 3 would increase dramatically to a ratio of 96;4 or 24:1. This ratio of parasitoids to hosts would be about *120 times* higher than the ratio that is estimated to exist in natural populations which is assumed to cause 17 percent parasitism. While the host population has declined sharply during generation 3, enough hosts should be present for the female parasitoids to find their normal quota of hosts. This will mean that the ratio of hosts found and presumably parasitized to host present will exceed 13:1. Therefore the rate of parasitism during generation 3 should be near 100 percent. Near complete collapse of the host population could be expected for generation 4. In all probability a few adult hosts would still be present during generation 4. Some adult survivors can be expected to overlap into generation 4 and a few adult progeny might be expected from larvae that escaped parasitism during generation 3. But the ratio of parasitoids to hosts would remain very high until the parasitoid population also collapses due to the lack of hosts.

It is possible that certain biological actions of which we are not aware might occur that would not permit the degree of suppressive action that is shown in the model. However, it is difficult to envision how any host population could maintain a damaging level or even survive if subjected to the dramatic changes in the numerical relationships between parasitoid and host populations that would be brought about by the type of release procedures proposed. It is certain that no insects in all of their evolutionary history have ever come close to experiencing such dramatic changes in para-

TABLE 4. INFLUENCE ON THE DYNAMICS OF A HOST POPULATION WHEN ENOUGH LARVAL PARASITOIDS ARE RELEASED IN THE HOST ECOSYSTEM TO ACHIEVE AN ADULT PARASITOID-TO-ADULT HOST RATIO OF 3:1.

	Generation		
Parameters	1	2	3
Female hosts	1,000	720	154
Host larvae produced per female*	80	82	86
Total host larvae	80,000	59,040	13,244
Female parasitoids released generation 1 only	3,000	4,080	3,684
Adult parasitoid-to-adult-host ratio	3:1	5.7:1	24:1
Host larvae parasitized per female**	51	48	49
Host larvae parasitized	153,000	195,840	180,516
Ratio, host parasitized to hosts present***	1.9:1	3.3:1	13.6:1
Percent parasitism	85	96	99+
Host larvae parasitized, number	68,000	56,678	13,112
Host larvae not parasitized, number	12,000	2,362	132-
Survival, unparasitized host larvae to adult hosts, percent*	12	13	14
Adult hosts next generation, both sexes	1,440	307	18-
Survival, parasitized hosts to adult parasitoids, percent*	12	13	14
Adult parasitoids, next generation, both sexes	8,160	7,368	1,836+

*Some changes in parameter values are made because of changes in parasitoid and host densities.

**Females in a natural population as shown in Table 3 are estimated to parasitize an average of 68 larvae. However, because of the high density the average has been reduced by 25 percent to 51 per female.

***The rates of parasitism at different ratios of hosts parasitized to hosts present are based on data in Table 1 of USDA Handbook, Number 693, "Principles of Insect Parasitism Analyzed from New Perspectives; Practical Implications for Regulating Insect Populations by Biological Means" published in 1992.

sitoid-host relationships. And, since no insect pest, to my knowledge, has ever been subjected to the release of such large numbers of reared parasitoids *throughout* its ecosystem we have no direct information on the results to expect. Therefore, until this is done for a number of species, we will not know for certain how much influence parasitoid releases will have on the dynamics of pest host populations. But, in my opinion, the probability is near 100 percent that the suppression model reasonably reflects the results that can be expected from the parasitoid augmentation technique. Keep in mind that all such actions have remained obscured for years because parasitoid releases have never been made *throughout* a pest ecosystem in the manner proposed and the theoretical effect has never before been calculated in the manner I have used.

The release of 6,000 parasitoids during one pest generation would achieve about the same results that can be expected from the release of about 54,000 sterile insects during 4 generations as shown in table 2. This would be a 9 fold difference in numbers of insects required. It should be kept in mind that this assumes that the sterile insects are completely competitive. For many insects some loss in competition is likely to occur because of radiation damage. Therefore, there could be an even greater difference in the relative efficiency of parasitoids and sterile insects than is indicated by this study. Also, the higher the parasitoid to host ratio the greater will be the advantage of parasitoids over sterile insects.

I have developed and critically analyzed similar models involving known parasitoids of a number of our major pests including the boll weevil, *Anthonomus grandis*; corn earworm, *Heliothis zea*; tobacco budworm, *Heliothis virescens*; European corn borer, *Ostrinia nubilas*; sugarcane borer, *Diatraea saccharalis*; Colorado potato beetle, *Leptinotarsa decimlineata*; Mediterranean fruit fly, *Ceratitis capitata*, tsetse flies, *Glossina spp.* and a dozen other parasitoid-host associations. In every case, the parasitoid population will, in theory, so dominate the host population within a few cycles that the elimination of completely isolated host populations would seem to be inevitable. But until we subject completely isolated populations to parasitoid releases in the manner proposed we will not know for certain to what level augmented parasitoid populations can suppress their host populations. However, the same question confronted researchers on the sterile insect technique. But the question no longer exists for the sterile insect technique. Sterile insects have been shown to be capable of eliminating populations of several different pests on numerous occasions. I feel certain that host specific or primary parasitoids will be much more effective than sterile insects for the management or elimination of pest populations. This assumption is of such great importance from both economic and environmental standpoints that it will be critically analyzed in greater detail.

A Comparison of the Suppression Characteristics of the Parasitoid Augmentation and Sterile Insect Techniques When Used for Regulating Total Populations

We have shown by hypothetical population models how insect pest populations will respond to sterile insect and parasitoid releases. The suppression characteristics of the two techniques have also been discussed to some extent. However, a full understanding of the suppression characteristics of both techniques is vital to the total pest management concept and to the role that the two techniques can be made to play in future insect pest management systems. Therefore a critical comparison will be made of the suppression characteristics of the two techniques with some comments on how they differ from other insect control methods. There is increasing interest in the areawide approach to insect pest management. However, it is very important to have a good understanding of the suppression characteristics of different methods of control because they differ in their effectiveness for areawide management.

Target Pest Specificity

The chief goal of insect pest management scientists for several decades has been to develop ways of controlling insects that will permit natural biological agents to perform their normal functions. We noted previously how important this is and why ecologically sound insect pest management will not be possible so long as the use of broad-spectrum insecticides is a major component in pest management systems. Yet, most agricultural insect pests are now being controlled by the use of broad-spectrum insecticides. Fortunately, most alternative methods of control that scientists are investigating have a high degree of pest specificity. The parasitoid release technique using host specific or primary parasitoids would be about as pest specific as is possible to achieve. The sterile insect technique is also highly pest specific although when the adult stage causes harm to plants or animals the technique may not be acceptable. For some insects this is not a matter of great importance because when the pest populations are very low the number of sterile insects that will be required will usually cause little damage. But no harm to people, animals or plants will occur when parasitoids are released in pest ecosystems.

Pest Density Dependent Suppressive Action

The suppressive action of all methods of insect control can be placed in two categories: those that achieve about the same degree of control whether the pests are abundant or scarce; and those that have low effectiveness and efficiency when the pest populations are high but which become increasingly effective and efficient against declining pest populations. The sterile insect technique, the parasitoid augmentation technique and the use of sex pheromones have pest density dependent suppressive action. This is a negative characteristic when pest populations are high, but it is a very positive characteristic when the pest populations are low.

The suppressive action of all other methods of control is independent of the pest density. A given chemical or biological insecticide formula will kill about the same proportion of a pest population whether the insect population are high or low. It is a favorable characteristic when the pest populations have reached high levels. However, there may be little or no advantage to the use of insecticides against low pest populations in areawide insect management programs. But, it should be kept in mind that there can be a great advantage to the integration of density independent and density dependent methods of control when the objective is to manage total populations on an areawide basis. This is a principle of insect pest management that has not been adequately exploited.

Mobility Factors

The excessive movement of released parasitoids and their progeny out of small unisolated pest habitats and the excessive movement of the pests into habitats where parasitoids have been released has probably done more to obscure the true efficiency of the parasitoid release technique than any other factor. This can also be said for the sterile insect technique and probably also for the sex pheromone control technique. However, when the objective is to manage insect pests on an areawide basis, the ability of the organisms to disperse and achieve control in all of the pest habitats becomes one of the most favorable characteristics of the parasitoid release and the sterile insect techniques.

One of the major disadvantages of the use of control methods that lack mobile action is that it will require much greater precision in their application than will the release of mobile parasitoids or sterile insects. Treatment intervals of 100 feet or less will probably be required for highly effective control by non-mobile biological organisms, such as insect pathogens and immature insect predators, whereas release intervals ranging between one half to one mile (approximately 2,500 to 5,000 feet) should be adequate for most parasitoid species and sterile insects. Therefore there can be as much as a 25 fold difference in the cost of applying mobile versus non-mobile control procedures when the objective is areawide pest management.

Pest Guidance Factor

When host-specific parasitoids are released in pest ecosystems, the released organisms will tend to disperse into all of the pest habitats in their search for the hosts.

These highly specialized organisms by nature have the ability to find their hosts with a high degree of efficiency (Nordlund et al. 1981) even when the host populations are very low. Their highly developed host-detection mechanisms, plus their mobility and instincts for host-finding give real meaning to the often used phrase: "You can run, but you can't hide." One could characterize insect parasitoids as "biological guided missiles." I am sure that they can find pest targets with much greater precision than can the most sophisticated guided missiles for detecting military targets. Sterile insects also have the mobility factor, but when both sexes are released the sterile males or females are no more likely to search specifically for wild mates than for their sterile siblings. If it is feasible to release males only the pest guidance factor should also apply to the sterile insect technique.

The pest guidance factor is a characteristic of immense practical significance for insect pest management or eradication programs. The parasitoid release procedure and the release of males only in sterile insect programs are the only techniques that possess these characteristics.

Self-Perpetuating Parasite Populations

The frequency that the control procedure must be applied can be a very important factor in selecting the way to deal with insect pest problems. Long residual action of insecticides can be a desirable characteristic in controlling certain pests. However, when an insecticide has broad-spectrum activity long lasting effects can also be very objectionable because of ecological reasons. New plant growth can nullify insecticide residual action under certain circumstances.

The ability of released parasitoids to maintain self-perpetuating populations and achieve control from cycle to cycle throughout a pest ecosystem is without a doubt one of the most important characteristics of the parasitoid release technique. This is an inherent characteristic of both classical and augmentative biological control. However, in natural populations, as we have already noted, there are constraints imposed by nature's natural balancing mechanisms which tends to maintain the relative number and the rate of parasitism within certain limits. This natural barrier can be overcome by augmented populations. If enough parasitoids are released throughout a pest ecosystem to achieve an adult parasitoid to adult host ratio higher than 1:1 this can, in theory, induce a progressive increase in the rate of parasitism from cycle to cycle without the release of additional parasitoids. This theoretically will continue until the host population is eliminated. For some parasitoid-host associations, there seem to be mechanisms that will prevent this progressive increase, as described by Knipling (1992). For others, however, such mechanisms seem not to exist. The self-increasing effect cannot be triggered so long as the rate of parasitism remains below 50 percent. It can occur only when the parasitoid progeny will exceed the host progeny that are produced throughout coexisting populations. If such increasing action can be confirmed for any parasitoid species until the host population is eliminated it would be a biological action new to science.

The self-perpetuating characteristic is one of the most important advantages of the parasitoid release technique over the sterile insect technique and most other control methods. There is some persistent suppressive action when lepidopterous insects that receive substerilizing dosages of irradiation are released in pest ecosystems (Carpenter, et al. 1987), but such action does not persist for more than about one generation. Growing pest resistant host plants, whether developed by genetic selection or by biotechnology, is perhaps the most persistent suppressive action that can be achieved. But host resistance is not applicable for some pests and has limited action for others.

General Discussion

Thus, when the objective is total population management, no method of control has as many desirable characteristics as does the parasitoid augmentation technique. However, the full potential of this technique for dealing with insect pest problems has long remained obscured because the science of insect pest management has not considered or tested its use to manage total pest populations. The effort that have been made in the past to use the technique has generally been patterned after the way insecticides are employed. However, it is my opinion that neither the parasite augmentation or sterile insect techniques will ever play prominent roles in future insect pest management systems if they are intended for use against high pest populations on a farm by farm basis as a substitute for insecticides. Their density dependent suppressive action, the propensity for the organisms to move out of small size habitats, plus their slow action will make these two method of control unacceptable for growers no matter how much they might be encouraged to use such biological control procedures.

However, one or the other of the two techniques has characteristics which are of special importance for regulating total pest populations. They offer almost unlimited potential for dealing with many insect pest populations in an effective, low-cost and environmentally safe manner. The only requirement will be the technology for mass producing the organisms in large numbers and at reasonable costs. Considering the progress that insect rearing experts have achieved in rearing a variety of insects on a large scale (King and Leppla 1984) (Anderson and Leppla 1992) there are reasons to believe that rearing insects for augmentation purposes or for autocidal control will pose no serious problems.

A few examples can be cited. Excellent progress has been made on rearing several parasitoids of tropical fruit fly species, Harris and Okamoto Cyo 1991, (Wong and Ramadan 1992, Burns 1993). A tachinid parasitoid of the corn earworm *Archytas marmoratus* can be readily reared under laboratory conditions, Gross and Johnson 1985 as can be the tachinid *Lixophaga diatraeae*, a parasitoid of the sugarcane borer.

It might be necessary to rear most insect parasitoids on their hosts or a surrogate host, but excellent progress is being made in rearing parasitoid species by in vitro procedures. This has been accomplished for the boll weevil parasitoid *Catolaccus grandis* by Royas et al. (1996). Carpenter and Greany, (1997), report progress in rearing a pupal parasitoid of the corn earworm on artificial media. Also, Cohan (1997) has developed in vitro procedures for rearing two well known insect predators, *Geocoris punctipes* and *Chrysoperla carnea*.

An important obstacle to overcome before making wider use of the parasitoid augmentation technique to manage insect pests on an areawide basis is the need to demonstrate that the techniques will in fact be highly effective and practical. This is the same problem that has handicapped researchers developing the sterile insect technique.

It is not possible to obtain a high degree of suppression or to achieve eradication of insect pest populations by the release of parasitoids unless the releases are made against isolated populations or in large areas. Research scientists have not had the opportunity to conduct such experiments for any parasitoid species. Until this is done we will not know the full potential of the parasitoid release technique for rigidly managing total pest populations or if the technique can be used to eradicate isolated pest host populations.

To demonstrate that mobile biological organisms are capable of suppressing pest populations to very low levels or to achieve eradication of isolated populations will require carefully planned and well executed experiments. Each trial is likely to cost several million dollars. However, this would be a very small investment in research on methods of insect management that could eventually benefit agriculture by several billion dollars per year and also make a major contribution to reducing the need for ecologically disruptive insecticides.

Synergistic Suppressive Action When Different Insect Control Methods are Integrated

In appraising the influence of the integration of different methods of insect control, I recognized a suppression mechanism that I call *mutual synergistic suppressive action*. The concurrent release of sterile insects and parasitoids produces this type of action.

This previously unrecognized type of suppressive action can add a new dimension to insect pest management methodology. It offers the science of insect pest management the opportunity to achieve extraordinary effectiveness and efficiency when it is feasible to integrate two or more control techniques that have this characteristic.

The model shown in table 5 depicts the theoretical influence of the concurrent release of enough sterile insects and parasitoids during the first generation to achieve ratios of 2:1 for each organism.

The sterile insects are assumed to be fully competitive. The release of 4,000 sterile insects of both sexes would achieve a sterile-to-fertile ratio of 2:1 during generation 1. Therefore only 33.3 percent or 333 of the 1,000 normal females will mate with fertile males. The concurrent presence of 2,000 female parasitoids would mean a parasitoid to host ratio of 6:1. This will have an effect equal to the release of 12,000 female parasitoids alone. A ratio of 2,000 female parasitoids to 333 reproducing female hosts is estimated to cause about 98 percent parasitism. Thus the combined influence would be 67 +.98 (100-67) = 99.3 control.

To inhibit reproduction by 99.3 percent by the release of sterile insects alone the sterile to fertile ratio would have to be about 130:1. This would require the release about 260,000 sterile insects of both sexes. To achieve 99.3 percent parasitism by the release of parasitoids alone, I estimate that it would be necessary to release about 16,000 parasitoids of both sexes.

The advantage of the release of both organisms is not limited to the action during generation 1. Even if no sterile insects were released during generation 2, enough parasitoid progeny would in theory be present to achieve an adult parasitoid-to-host ratio of 49:1 during generation 2. Thus, releases would be necessary for only one pest generation. Earlier we noted that it has not yet been demonstrated that parasitoids alone are capable of eliminating pest populations. But, if even a few sterile insects were released along with parasitoids this would ensure the use of a method of suppression that can lead to eradication of isolated populations.

The degree of enhanced suppressive action depends on the size of the initial ratios of released parasitoids to the natural populations. The higher the ratios, the greater will be the enhanced suppressive action. At ratios as high as 3:1 for each organism - or an overall ratio of 6:1 - the combined suppressive action during the first and second generations would be so high it would be difficult to even calculate. It would require the release of about 2,000,000 sterile insects alone to achieve a ratio of 1,000:1 to equal the effect of a ratio of 6:1 of both organisms. When pest populations are very low due to natural causes or are first suppressed to a very low level by other means, it would not require the production and release of many organisms of both kinds to achieve ratios as high as 10:1 or even 100:1.

In areas subject to the invasion of only a few insects by long distance flight or by way of imported infested commodities the routine release of only a few insects per unit

TABLE 5. INFLUENCE OF THE CONCURRENT RELEASE OF ENOUGH STERILE INSECTS AND PARASITOIDS TO ACHIEVE RATIOS OF 2:1 DURING GENERATION 1 OF A PEST POPULATION OF THE NATURE SHOWN IN TABLE 1.

Parameters	Generation 1	Generation 2
Normal males	1,000	32
Normal females	1,000	32
Sterile insects, both sexes	4,000	none
Sterile-to-fertile ratio	2:1	—
Females reproducing	333	32
Small larvae per female	80	86
Total small larvae	26,640	2,752
Female parasitoids released, generation 1 only	2,000	1,567
Ratio, female parasitoids to reproducing female hosts	6:1	49:1
Host larvae parasitized per female	52	52
Total larvae parasitized	104,000	29,484
Ratio, larvae parasitized to larvae present	3.9:1	10.7:1
Percent parasitism	98	99+
Larvae parasitized, number	26,107	2,724+
Larvae not parasitized, number	533	27
Survival larvae to adults, percent	12	—
Adult hosts next generation, both sexes	64	—
Adult parasitoids, next generation both sexes	3,133	—

area might ensure overwhelming ratios and protect the area from the establishment of invading pests. This would be a new procedure for preventing the establishment of invading insect pests.

The examples described are merely an indication of the potential benefits that can be realized by combining different insect control methods that have density dependent and mobile suppressive action. In theory, similar enhanced suppressive action can be realized by releasing two parasitoid species that parasitize and complete development in different life stages of the host. The concurrent release of a parasitoid species that parasitizes and completes development in the host eggs and another species that parasitizes and completes development in the host larvae or pupae would be examples of such parasitoids. The concurrent release of a larval and puparia parasitoid would be another example. The use of insect sex pheromones in traps or as attracticides that have long range attraction power plus the release of parasitoids would be another example of the integration of two suppression techniques that could lead to mutually enhanced suppressive action.

It is difficult to anticipate just what this potentially powerful mechanism of suppression can mean to insect pest management if it is exploited and applied for the regulation and eradication of insect pests. When the pest populations are very low for any reason and if relatively few insects would have to be released to achieve high ratios the cost can be very low. The release of biological organisms that have density dependent suppressive action and which also have mobility and pest detection mechanisms would combine several characteristics that can result in a very powerful method of insect control and eradication. And we should keep in mind that we would be using methods of control that would be highly pest specific and would permit all other natural control factors to operate in a near normal manner. If these principles are confirmed and exploited it could dramatically alter future insect pest management and eradication programs with great economic and environmental benefits.

PRACTICAL IMPLICATIONS FOR SPECIFIC INSECT PESTS

I have described various mechanisms and principles of insect control and the results to expect from different control procedures. However, what agricultural executives and farmers want to know is what does all this mean in terms of dealing with specific insect pest problems and what will be the costs and benefits compared with current control procedures.

Any one of a dozen insect pests could be selected to make such analysis. However, I will describe in a general way the procedure that could be followed in making use of insect parasitoids and sterile insects for regulating total populations of two of our most important insect pest species; the corn earworm, *Helicoverpa zea*, and the tobacco bud worm, *Heliothis virescens*.

The two pests differ somewhat in their biology and host plant preferences, but they will be regarded as one pest entity. To relate the theoretical results we have presented to practical utilization several estimates and assumptions must be made. The released organisms will be directed against the insects that emerge from the overwintering pupae. Most of the reproduction by this first generation normally occurs on wild host plants. But most of the wild hosts are in cultivated areas.

A vitally important parameter that will determine the feasibility of regulating populations of the two pests is the number of insects that emerge from the overwintering population. I have, with the help of some of my colleagues, made estimates of the number of adults that are likely to emerge from the overwintering puparia. I estimate that the overwintering population will normally consist of about 1 billion moths of both sexes. Emergence and reproduction by the overwintered population are assumed to occur primarily in cultivated areas comprising about 75,000 square miles or about 50 million acres of cultivated lands. The suppressive measures will be applied in the United States and northern Mexico where most overwintering occurs. Biologists have obtained information which suggests that many of the insects that reproduce early in Mexico will emigrate to the United States. Therefore, international cooperation would be necessary.

Thorough surveys and monitoring of the pest populations will be an essential aspect of such a program. The biological organisms should be released at the proper time and in appropriate numbers as emergence of the natural population occurs. It no doubt would be advantageous to release more than one parasitoid species. Promising parasitoids would include the hymenopterous larval parasitoid, *Microplitis croceipes* and the tachinid larval-pupal parasitoids, *Archytas marmoratus* and *Eucelatoria bryani*. As depicted in table 5, good control will result if sufficient numbers of a parasitoid are released for one generation to achieve an adult parasitoid to adult host ratio of 3:1. Thus the release of 3 billion parasitoids is proposed. Releases in the different regions would begin, perhaps in February in Mexico. Then as the season advances the parasitoids would be released to coincide with the emergence of the pests from the overwintering pupae.

I assume that the parasitoids will be released in each area at 1 mile intervals every five days for 40 days or about 8 releases. If reproduction of the first generation is largely inhibited this would minimize the number of immigrant moths that normally disperse for several hundred miles to supplement the overwintering populations. While such program may seem to be of unprecedented scope, it would not be much larger than the screwworm program that has been conducted in the United States and Mexico for the past 25 years.

As depicted in table 4, an adult parasitoid to adult host ratio of 3:1 is estimated to cause virtually complete control within several cycles. A high degree of control of the overwintering population could be expected in the United States and northern Mexico the first year. If so, very few moths should be available to migrate into the agricultural areas north of the normal overwintering areas and thereby avoid the heavy losses the pests cause each year in the northern states.

Obviously we are dealing with rough estimates and assumptions that would have to be investigated intensely. However, for the purpose of this gross analysis I estimate that the eventual cost of rearing suitable parasitoids will average $10 per 1,000 or $10 million per billion. The cost for distributing the organisms is estimated to be $2 per mile of flight for the aircraft. It is assumed that the biological agents will be distributed at 1 mile intervals in about 75,000 square miles of territory. The cost for distributing the organisms each release period would amount to only about $150,000 or $1.2 million for 8 releases. Based on a rearing cost estimate of $10 million per billion parasitoids, the cost for 3 billion parasitoids would be $30 million. Other costs including thorough surveys, general supervision and other costs are assumed to increase the cost during the first year to about $35 million. This is about what the screwworm programs have cost during the past 25 years.

Recognizing that there are unavoidable inefficiencies in such operations, it would seem more rational to assume the need for producing and distributing 6 billion parasitoids rather than 3 billion during year 1. Other costs would be about the same regardless of the number of parasites released. Therefore, we might assume that the costs during year 1 would be about $65 million. *This would be less than 10 percent of the losses the pests now cause under current management procedures.*

In dealing with insect pest populations from a total population perspective using control methods that have pest density dependent suppressive action the major benefits should be realized after the first year. The elimination of the population is out of the question. Some adults of both species no doubt can immigrate several hundred miles from other regions. Some of the insects will be present in the management areas each year even though most of the reproduction is inhibited. However, if we assume that the normal overwintering and immigrating population will be as low as 100 million as few as one billion parasitoids should achieve a parasitoid to host ratio as high as 10:1. In that event the annual cost for management of the pests might be below $25 million.

In considering the feasibility of dealing with the corn earworm and the tobacco budworm by the procedure described it should be kept in mind that under current control procedures the two pests are estimated to cost agriculture in the United States more than $1 billion per year (King et al. 1989). They are also responsible for much of the insecticides required for agricultural purposes.

Some or all of the estimates I have made may be too liberal. The normal overwintering population might be higher than 1 billion and the parasitoid-to-host ratio may have to be higher than 6:1 to achieve adequate control. On the other hand, it is also possible that one or more of my estimates are too high. If the overwintering population is normally as low as 667 million and the parasitoids could eventually be reared at a cost as low as $5 million per billion, the estimates I have made for the first year would be too high even if the parasitoid to host ratio would have to be as high as 10:1. The continuing annual cost might be less than half the cost during the first year.

From a national and worldwide standpoint, it is probable that no insect pest complex has been investigated as intensively as has the Helicoverpa/Heliothis complex. In my opinion about all of the basic technology needed has already been developed. No new discoveries are necessary. Nature has created the organisms. However, scientists and agriculturalists must accept the holistic approach and focus on making the transition from basic information to practical application. I see no obstacle to making this transition other than failure of our agriculture executives in both the public and private sectors to accept the concept and unwillingness of our scientists to undertake the research challenges that would be involved in perfecting the technology and proving its performance.

The same principles and the same techniques of control should apply for many other insect pests. Other important species that I consider good candidates for total population management in a similar cost effective manner include such major pests as the bollweevil, *Anthonomus grandis*; European corn borer, *Ostrinia nubilalis*; sugarcane borer, *Diatraea saccharalis*; the medfly, *Ceratitis capitata*, and other tropical fruit fly species; Colorado potato beetle, *Leptinotarsa decimlineata*; codling moth, *Laspeyresia pomonella*; and numerous other species. For some of the species the costs during year 1 might be quite high and other methods of control may be needed to reduce the normally high natural populations to a level that can be managed by parasitoids and/or sterile insects.

Much research will have to be conducted to obtain the needed ecological information and to perfect the technology. Research on managing or eradicating total insect pest populations will be costly and demanding. It will be necessary to demonstrate that the proposed procedure will perform as expected. It might cost several million dollars to conduct one trial experiment involving a single pest. But we are dealing with techniques and strategies that have the potential of benefitting agriculture by several billion dollars per year and also make a major contribution to the goals of greatly reducing the need for costly and ecologically disruptive insecticides. Considering these large potential benefits, an expenditure of $25 million per year for research and development focused on the holistic approach to insect control by biological procedures would be very small. It could be one of the best research investments that agriculture could make. I cannot envision any alternative techniques and strategies that would even approach the economic and environmental benefits that could be realized by the holistic approach using mobile biological organisms.

Insect Pest Problems Especially Relevant For the State of Florida

The principles and mechanisms of suppression that I have described in this lecture are basic and fundamental. They will apply for a wide range of insect pests. Entomologists in Florida could do a great deal to advance the principles and concepts that have been discussed. Your state is a well isolated ecosystem. It could take unilateral action and benefit more than could other states that are not as well isolated from long range insect immigration.

The probability is high that at least two of your important pest problems could be readily resolved by the parasitoid release technique especially if supplemented by the release of sterile insects. I refer to the Caribbean fruit fly, *Anastrepha suspensa*, and the sugarcane borer. Excellent parasitoids of both of the pests are known and efficient mass rearing procedures have been developed for them. Also considerable research has been conducted on parasitoid releases that have given promising results against the sugarcane borer, (Summers et al. 1976). The sterile insect technique has been shown to be an effective means of suppressing several tropical fruit fly and lepidopterous pests. Parasitoid releases have also shown promise for suppressing tropical fruit flies, (Wong, et al. 1992 and Sivinski 1996). I can see no reasons for permitting the Caribbean fruit fly to continue to exist in your state and cause the problems it does for your fruit industry. Also, I can see no reason why the sugarcane borer should be costing sugarcane growers $25 to $50 per acre or more in losses year by year. The first year costs might be considerably higher, but I am confident that after sugarcane borer populations have been reduced to very low levels, they could be maintained below the level of damage at a cost of $2 to $3 per acre per year by the release of relatively few parasitoids per acre perhaps supplemented by the release of some sterile moths.

However, there are a number of other insect pests in your state that are of national significance and which find refuge in your state during the winter months. Each spring and summer enough of the pests spread northward into other agricultural regions and cause damage to a variety of crops before season's end. Those pests include the fall armyworm, *Spodoptera frugiperda*; the beet armyworm, *Spodoptera exigua*; cabbage looper, *Trichoplusia ni*; and diamondback moth, *Plutella tylostella*.

The number of insects of these species that reproduce only in Florida during the winter months has not been determined. But there is little question that the populations that emigrate from your state can increase by 25 to 50 fold during the growing season and threaten losses on perhaps 25 times the crop acreage in other states before season's end.

What the total losses due to these pests amount to per year in the states north of Florida is difficult to say, but they probably aggregate several hundred million dollars per year. I am greatly indebted to Dr. F. A. Johnston who made a special effort to obtain information on the annual cost of control and losses caused by the fall armyworm, beet armyworm, corn earworm, diamondback moth and cabbage looper in Florida. Insecticides now provide the only way to control these pests. I was amazed at the amount that growers spend per year controlling these pests. On most crops it amounts to as much as $100 per acre or more.

From time to time I have discussed with various scientists the feasibility of rigidly controlling such pests during the winter months in Florida to avoid the losses the pests cause other states after they spread northward. But research programs to investigate the feasibility of dealing with the pests during the winter in Florida have not yet materialized.

Since I have been interested primarily in the possible use of the sterile insect and parasitoid release techniques I have made gross estimates of the probable size of the overwintering populations in Florida. It is difficult to say how accurate they are, but I feel confident that it would be feasible to rigidly manage populations of the pests mentioned during the winter primarily by the use of parasitoids at costs of only a fraction of the losses they cause under present methods of control. Mandatory cultural measures such as the destruction of host plants within a certain period after the host crops are harvested should be integrated into a total population management system. This would cost farmers very little, but it can be of major importance in an integrated program. This alone might reduce the number of parasitoids or sterile insects required by half and still result in a more effective program.

The feasibility of managing these pests in the winter by the release of parasitoids and/or sterile insects will depend on the number of the pests that reproduce in your state during the winter and early spring. In my opinion, research to determine as accurately as possible the actual number of the different species that exist in the natural population would be of the highest priority. Certainly through joint efforts by the state and federal scientists, it should be possible to obtain good information on the actual number of the different pests that reproduce in Florida during that period and the source of the reproduction. Until such information is obtained, there is likely to be little that anyone can or will do to develop and make use of the proposed biological techniques for dealing with these pest problems.

I raise the question, however, whether agriculture can afford to be so dogmatic and intransigent in meeting its insect pest problems. Is there any justification for or does it make any sense to continue to rely year by year on costly and ecologically disruptive insect control methods when the prospects are so favorable for dealing with the pest problems at very low cost and in an environmentally safe manner? Will the time come when society will demand the use of environmentally safe ways to deal with pest problems especially if it will also greatly benefit producers and consumers? What can we do as entomologists to gain the interest and support needed to achieve these goals.

Looking to the Future

The world's leading scientific institutions are projecting that agriculture within 30 years must produce two times as much food as it now produces to meet the demand of an expanding world population and economy. This will require that agriculture worldwide become more efficient in a number of ways. Protecting crops and livestock from insect damage will be one of the ways to meet the monumental tasks that agriculture faces within the short span of a few decades. People will and *should* demand that the food that is produced be safe and that the quality of the environment in which we live will not be jeopardized.

The methods of insect control that have evolved during the past 50 years have contributed to the highly productive agriculture that we now enjoy. However, this in part has been accomplished by relying primarily on costly and ecologically disruptive insecticides for insect control. The prospects seem dim to me that our present defensive system of management can be greatly improved, if at all. Insects continue to develop resistance to insecticides. People continue to be concerned over the environmental hazards insecticides can produce and more restrictions are being placed on their use. Agriculturists are beginning to wonder if we can maintain the standards of control that have been achieved in the past.

A study of the dynamics of many of our major insect pests and an analysis of the suppression characteristics of various methods of control clearly indicate to me that the preventative measures applied against total insect pest populations would be a much more rational way to deal with many of our major insect pests than to rely on the largely defensive procedures that have been followed for half a century. Two biological control procedures involving mobile organisms offer the best hopes of accomplishing this objective in an effective, economical and environmentally safe manner: the mass-rearing of key parasitoid species and their release throughout the pest ecosystem in adequate numbers and at strategic times in the pest's seasonal cycle; and the release of sterile or genetically altered insects in the same way.

The holistic approach to the management of insect pests by these two biological procedures offers almost unlimited potential for dealing with insect pest problems in an environmentally safe manner and at very low cost. Mass producing the biological organisms should pose no serious technical problems in view of the outstanding progress that insect-rearing scientists and engineers have made in rearing many kinds of insects in large numbers.

The time will come, and sooner than we realize, when it will be necessary for agriculture worldwide to produce the maximum amount of food on diminishing agricultural lands and water for irrigation. This will require greater efficiency and productivity from every aspect of agriculture. Better protection of crops and livestock from insect attack will be one of the ways to achieve these objectives. This will be the responsibility of entomologists and our associated scientists.

I am confident that we already have or could readily develop the technology that will be needed to deal with most of our major insect pest problems in a much less costly and a more ecologically acceptable manner during the next half century than we have done during the last few decades. But it will require that our agricultural leaders in both the public and private sectors make provisions for developing and implementing the type of technology that will permit maximum efficiency and yields and which will also be environmentally acceptable.

We need more positive decisions and bold actions by our scientists and agricultural leaderships in both the public and private sectors that will lead to many other programs as successful and practical as the screwworm program that your society has honored today.

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