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Potential Role of the Sterility Principle for Tsetse Fly Eradication

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In efforts to appraise the potential possibilities of the sterility principle for controlling or eradicating various kinds of insects, the writer has also given a great deal of attention to ways that this principle might be developed and applied for tsetse fly eradication. Advantage of every opportunity has been taken to discuss tsetse fly biology, ecology, and behavior with experts in the field and information in literature has been noted which might be useful in estimating the potential possibilities of this new approach for tsetse fly control or eradication. The experience and knowledge gained in the research conducted by various investigators with the Entomology Research Division on other insects relating to the sterility method of control has also been taken into consideration.

Scientists working on tsetse flies have obtained much valuable basic information on the biology, habits, and population dynamics of the various species in Africa. Additional information is needed, however, on pertinent aspects of the biology, ecology, behavior, population dynamics, and population densities of the various species before a full appraisal can be made of the potential value of the sterility principle. Information is needed on ways to produce sterility in various species. Methods of rearing or efficient methods of trapping the insects must be developed. However,

the writer is confident that the sterility method offers a procedure that through research can be developed so that it will be of great value in tsetse fly control and eradication programs. The purpose of this paper is to consider the basic principles of the sterility procedure and how it might be applied for tsetse fly eradication in various situations. It is hoped that this optimistic appraisal of the potentialities of the method will encourage a concerted research effort on the many aspects of the problem that are in urgent need of study. Following the successful application of the sterility method for screw-worm eradication, the writer appraised the potential possibilities of the sterility method for the control or eradication of various other insects, including tropical fruit fly species, cotton boll weevil, pink bollworm of cotton, codling moth, and tobacco hornworm moth. Hypothetical models were established to test the feasibility of the method for these insects. The models were established on the basis of the principles involved in relation to the available information on the biology, ecology, behavior, and population dynamics, and mass rearing possibilities for the insect species under consideration. In spite of major gaps in our knowledge about these insects, the calculations indicated that the sterility method could serve a useful purpose in the control or eradication of these insects. Intensive investigations are currently under way by the Entomology Research Division on all of these insects. In general, as the research progresses, the feasibility of utilizing the sterility method to help control or eliminate these insects in specified situations appears more and more promising and research information is not in wide variance with

the suppositions established in the hypothetical models. The same general approach has been followed in efforts to appraise the feasibility of utilizing the sterile male method for tsetse fly control or eradicatio in various situations. The line of reasoning followed in making this appraisal and the conclusions reached are discussed in this report.

No attempt will be made to review the literature on tsetse flies which has been noted in connection with this study. However, the writer has drawn heavily on the compilation by Buxton which discusses almost every aspect of the biology, ecology, and control of the tsetse flies. The writer also wishes to acknowledge with appreciation the opportunity to discuss or communicate on matters of tsetse fly biology, ecology, behavior, rearing methods, and on current control procedures with such authorities as J. Ford and his associates of the Department of Veterinary Services, Federation of Rhodesia and Nyasaland, Salisbury; W. H. Potts, Commonwealth Bureau of Entomology, London, England; P. E. Glover and W. P. Langridge, Kenya Veterinary Department, Kabete; K. S. Hocking, Tropical Pesticides Research Institute, Arusha, Tanganyika; and J. P. Bernacea, Uganda Department of Veterinary Services, Entebbe. The writer has likewise drawn on the wealth of information, much still unpublished, which has been obtained during recent years by various entomologists, chemists, and other scientists of the Entomology Research Division who are conducting research on chemosterilants, radiation sterility, rearing methods, and on various aspects of the biology and ecology of insects that are under study in connection with the possible application of the sterility method. No references will be made to

specific publications but a list of references that may be useful to the reader is appended to this report.

An Estimate of the Potential Effects of Sterile Male Releases on Tsetse Fly Populations

In discussing the potential possibilities of sterile male releases for tsetse fly control or eradication, no attempt will be made to consider the many variations in life history, behavior, preferred ecological environments, or other aspects that would of course have to be taken into account for a full appraisal of the method for the control of specific kinds of tsetse flies. Instead, a hypothetical species and hypothetical conditions will be established which are assumed to be reasonably representative of the various species. Although the subject will be discussed in some detail later, the assumption for the present is made that feasible and sufficiently economical ways of mass rearing the insect can be developed. It is also assumed that it will be possible to induce complete and irreversible sterility in the males without serious adverse effects on the ability of the released sterile males to compete with normal wild males in mating with the natural wild females. The advances made on other insects in methods of producing sterility are discussed elsewhere in this report. A period of three months is regarded as the time required for one complete generation. The maximum net increase potential of a tsetse fly population is assumed to be 50 percent per generation, regardless of the natural population density. In efforts to make an appraisal of the conditions where the sterile male release method might prove to be feasible and practical, tsetse fly populations are classified into 4 categories as discussed below:

1. High density population, averaging over 1,000 flies per square mile for the area as a whole. Variations in abundance in different parts of the total environment would, of course, occur, but for a large area an average population exceeding 1,000 flies per square mile would no doubt be regarded as a high density area.

2. Moderate population density levels, averaging between 200 and 1,000 flies per square mile in the total area of infestation.

3. Low density population, averaging 200 flies or less per square mile in the total infested area. Although higher densities may occur in localized parts of the total environment, the average population would not exceed 200 flies per square mile in the area requiring treatment. The writer had occasion to visit the Ankole District in Uganda where an eradication program is under way against Glossina morsitans, under the direction of the Department of Veterinary Services and supported in part by the Agency for International Development. Although no precise information is available on the natural population density, the average fly population in the approximately 1,000 square mile area under treatment may not exceed several hundred flies per square mile, and a large portion of the area to be treated probably has density levels below 200 flies per square mile.

4. Minimum survival populations levels, averaging 10 flies or less per square mile. Such areas are regarded as representative of fringe infestations where tsetse flies are spreading or areas that are being reinvaded from adjacent infested areas following an eradication program. This is also regarded as representative of areas where eradication measures have been undertaken but where low residual populations have survived within the eradication area and will gradually increase following termination of eradication efforts.

In such extremely low population situations, establishing the presence of an infestation may be difficult and costly because of limitations in methods of detection for very low level populations. Population density levels in this category are often the most difficult

to deal with in insect eradication efforts.

From the standpoint of control or eradication, it is assumed that for selective residual spraying, airplane application of mist sprays, brush clearing or game destruction, the cost per unit area to achieve eradication will likely be essentially the same whether the average tsetse fly populations are high, moderate, or low.

From the standpoint of eradication by the release of sterile males, however, the assumption is made that the cost of eradication will be in inverse proportion to the natural population density. This is the chief advantage of the sterile male method that remains to be fully exploited in connection with the eradication or control of tsetse flies as well as certain other insects. It represents a feature that may permit practical use of the sterile male method alone as the primary and most practical means of control or eradication in some situations, but perhaps more often prior reduction of high or moderate populations by the use of insecticides or other methods would first be necessary or advantageous. The use of sterile males may then become more economical than continued use of insecticides until eradication is achieved.

In order to estimate the possible effect of sterile male releases on tsetse fly population trends, a mathematical model has been established on the basis of the various assumptions made in the foregoing discussion. A low level population averaging 200 flies per square mile has been chosen as the natural population density for the model. The calculations are shown in table 1. If the natural male population is outnumbered by 3:1 during the first period or generation, a downward trend in the

population would theoretically result, permitting a reduction in the number released each period until elimination is achieved by the end of a year. It is the assumption in this model that the releases are reduced by half each period. Since the theoretical rate of decline in the natural population is greater than the reduction in sterile males released, the ratio of sterile to fertile males will gradually increase. It is recognized that in actual practice many factors would have to be taken into account and release rates in different areas would depend on natural population densities in various parts of the environment under treatment. Actually, on the basis of the population dynamics of tsetse flies in general, we could expect an initial release rate as low as 2:1 to start a marked downward trend in the natural population. However, the 3:1 ratio was selected so that the estimates will be as conservative as possible. A point that should be mentioned is that older females already mated before sterile males are released would not be affected if monogamous mating by females is the rule. Therefore, male releases could only begin exerting effects on the over-all reproductive potential of the population as new virgin flies emerge from pupae. Thus, the full impact of the releases will not begin to be felt until older previously mated females decline due to normal environmental resistance factors. In actual practice, therefore, the effect on population trends may be somewhat delayed in the beginning. Theoretically, however, the effects of the releases should extend beyond the period indicated by virtue of some survival of released males beyond the time indicated. From a practical standpoint these should be compensating factors so far

as the number of insects required is concerned. The time required for eliminating the natural population may be extended for a month or so beyond that indicated in the model. In connection with this point, the reader is referred to the section of this report which discusses the possible use of sterile males following a single application of a mist spray to destroy the accumulated adult population.

Cost of Rearing Tsetse Flies as a Factor in Estimating the Circumstances Where Sterile Male Releases Would be Practica

If the foregoing is a realistic appraisal of the potential effect of sterile male releases on tsetse fly population trends, it then becomes a matter of economics to determine the relative advantage of the sterile male method over existing methods in various situations. There could, of course, be other advantages in that the sterile male method should avoid the upsets in the balance of the other natural fauna that can result from the use of insecticides, brush clearing and game destruction methods. However, for this discussion, the relative merits of the sterility system and chemical control methods will be considered primarily from the standpoint of cost.

On the basis of available information it is assumed that a cost of $500 per square mile is necessary to achieve tsetse fly eradication by the application of selective residual insecticide to the vegetation in the tsetse fly environment or for the cost of applying airplane mist sprays at required intervals. Actual costs will no doubt vary greatly depending on a number of factors, and further research and experience may lead to reductions in cost of eradication by the use of insecticides.

However, current information indicates that this cost factor should be reasonably valid as a basis for estimating allowable costs for rearing and releasing sterile flies.

The difficulties and assumed high cost of rearing tsetse flies are regarded as the major obstacle to the practical utilization of the sterile male release method for tsetse fly control. The reproductive potential of tsetse flies is extremely low. There is no doubt about the importance of this inherent limitation to the production of large numbers of tsetse flies. However, the writer is of the opinion that the importance of this factor has been overemphasized and that there is every reason to believe that through a concerted research effort with a view to the development of economical mass production methods, it would be possible to rear the insects at a cost that would fall well within the range of practicability. Based on information supplied the writer by J. Ford of the Department of Veterinary Services, Salisbury, Southern Rhodesia, it may even be feasible to collect pupae from high density areas at a cost that would be practical for limited use of sterile flies. The possibility of collecting male flies from high density areas for subsequent sterilization and release may also be feasible.

If a rearing factor of 5¢ per male could be attained, and if, as indicated in the model, only about 1,700 sterile males would be required to eliminate populations averaging 200 flies or less per square mile in the total area requiring treatment, the cost for the flies would amount to only $85.00 per square mile for such situations. This cost plus all other costs, including the distribution of the insects, probably would

not exceed $125.00 per square mile, a highly favorable figure in relation to costs for chemical control. If the estimates are realistic, the sterility method may actually be competitive in cost with chemical control in some situations at natural population density levels up to 1,000 tsetse flies per square mile.

For minimum survival population levels of the order of 10 tsetse flies per square mile, a rearing cost factor of 5¢ per male would probably permit the release of sterile males more economically than it would be to carry out intensive and continuing surveys. However, if sterile males cost as much as $1.00 each, their use might still be favorable in relation to chemical control procedures in some situations having very low population densities. This estimate is made on the assumption that for fly density levels of 10 or less per square mile, a 4 to 1 ratio of sterile to fertile males would be adequate to eliminate or prevent establishment of tsetse fly infestations. If releases were made at the rate of 20 sterile males per square mile per month for 1 year, the total number of flies required would be 240, or $240.00 when costs are calculated at $1.00 for each fly. Such high cost per sterile males, however, hardly needs to be considered, but the matter of allowable cost per sterile fly for use under some circumstances is brought out to emphasize the potential possibilities of the sterile male release method from an economic standpoint, if the method can be developed to approximate the effects estimated. A cost factor of 5¢ per male at the release rate proposed would amount to only $12.00 per year for the males required for one square mile. The use of sterile males should be especially useful

and practical as a means of preventing the spread of tsetse flies into new areas or to prevent reintroductions into areas where eradication has been achieved.

Some Factors to Consider in Estimating the Feasibility of Rearing Tsetse Flies in Numbers Adequate for Practical Use in Eradication Program

Because of the low reproduction potential of tsetse flies, there is the tendency by many to question the feasibility of mass production in the numbers required for practical use in tsetse fly eradication. However there are certain compensating factors, which in the final analysis may place tsetse flies in a category comparable to that of other insects as favorable subjects for the practical application of the sterile male technique.

Although the inherently low reproductive potential of tsetse flies is a disadvantage in mass rearing, it is also a factor favoring full impact of sterile fly releases on the reproduction potential of the natural population. In considering the release of sterile males for insect species having a high reproductive potential, the writer estimates that the initial natural populations of males must be exceeded by a factor of at least 10 to 1 by sterile males to expect to cause a downward trend in the natural population. For tsetse flies, due to the low reproductive potential under natural conditions, an initial matching population of sterile males may be adequate to start a downward trend in the population. In the model presented in table 1, the initial ratio was established at 3:1 to provide a safety factor that in all probability would be necessary. Several students of tsetse fly population dynamics have pointed out,

however, that these insects are generally highly stable in terms of population densities so that there is relatively little fluctuation in average abundance from year to year. For an insect having such low net increase potential, irrespective of population density, a matching population of sterile males may be equally as drastic in affecting reproduction in tsetse flies as a 10 to 1 ratio would be for such insects as the screw-worm fly, fruit flies, and other species. If this should prove to be a valid assumption, then we have, in relation to other insects, a factor of 10 in favor of the method for tsetse flies, which would offset to a great extent the inherently low reproductive capacity of these insects.

Another factor that could be of major significance in the mass production of tsetse flies would be the economic feasibility of utilizing all of the reared females for reproduction purposes. The cost of manually separating males from females probably would not exceed 0.1¢ per male. A cost factor of this magnitude for each individual insect is not now regarded practical in connection with the sterility program for such insects as the screw-worm and tropical fruit flies. For tsetse flies, however, this cost factor would be minor in relation to the total production cost that may be practical. Moreover, it is possible, if not probable, that the release of males only would result in greater efficiency of the sterile insects released than to release both sexes. It may also be desirable or even necessary to not release females in certain situations so as to minimize the extra hazard large sterile fly releases may create.

Thus, in a mass tsetse fly production program, it can be assumed

that all of the females produced would be available for reproduction. Since the males of most insects have the capacity to inseminate many females, it seems probable that a low male to female ratio in the brood colony would be satisfactory. In effect, therefore, if a simple and relatively low cost technique for feeding and maintaining tsetse flies with only moderate production efficiency can be developed, adequate numbers of females should automatically be available at all times to meet the need for males. If the females would only average slightly more than 2 progeny during their life, the number of males required for release and the number of females required to maintain adequate production automatically would become properly balanced provided a low ratio of males would insure fertilization of the females. Therefore, if elaborate or costly procedures are necessary to assure high yields per female, the objective in research should be to develop the most economical way to maintain an adult colony on essentially a self-sustaining basis with enough surplus males to insure adequate fertilization of the females. The writer has been in communication with Mr. J. Ford of the Department of Veterinary Services, Salisbury, Southern Rhodesia, to obtain his views regarding the feasibility of rearing tsetse flies in a natural high population environment suitably modified for maximum production.

The possibility of rearing tsetse flies in large fly-proof enclosures several acres in size, if necessary, should not be ruled out as a practical procedure. Natural highly favorable environmental conditions might be maintained or simulated in such cages and large animals exposed

as required so that the flies could feed without special handling and where reproduction could take place under natural or simulated natural conditions. Very rough estimates indicate that production costs as low as 1¢ per male might be possible if females plus a low ratio of males could be crowded in 10 acre cages at a level of about 500,000 females and if each female under such circumstances would produce an average of slightly over 2 progeny during its life span. If rearing methods could be developed that would permit male production at a cost level of the order of 1 or 2¢ per male, sterile male releases alone might be the most economical procedure for eradication in all moderate to low density areas. A natural population density of 1,000 flies per square mile, on the basis of the calculations for a 200 fly density level, would require 8,500 sterile males. At 1¢ each the rearing cost would be $85.00

The Use of Sterile Males as an Adjunct to Other Tsetse Fly Control Methods

Under conditions where the population density of tsetse flies is high, the sterile male release method should still prove useful as an adjunct to chemical control procedures or chemical control might be regarded as an adjunct to the sterility method. The research by K. S. Hocking and associates of the Tropical Pesticide Research Institute, Arusha, Tanganyika, have shown that 2 or 3 airplane sprays will drastically reduce natural population densities, even though 6-8 treatments may be required for eradication. Under circumstances where the natural population of tsetse flies in an area are too high to manage

economically with sterile male releases, the prior application of 2 or 3 airplane sprays should reduce the natural population to levels that could then be readily handled with sterile males. If a natural population averaging 2,000 flies per square mile is reduced to a level of about 200 flies per square mile with 3 mist spray treatments, it may then be more economical and desirable to complete eradication by the release of sterile males than to apply from 3 - 5 additional spray treatments.

For many moderate or even high density situations, a single non-residual mist spray treatment might be used as the first step in an eradication effort involving the use of sterile males. A single thorough spray treatment of this kind should kill virtually all of the adults that have accumulated during a period of 2 months or longer. Most of the females in such case would have already mated and could not be affected by sterile males. However, if all of the flies present in the environment were destroyed, sterile males subsequently released would not only have fewer competing fertile males, but the virgin females emerging from pupae would then be subjected immediately to the influence of sterile males which should be released as soon as possible after the insecticide treatment. If substantial numbers of sterile males are released, the ratio of sterile to fertile could be at a very high level during the early part of the post-treatment period. As the fertile males accumulate by emergence from pupae already present, the ratio would drop but the impact on the over-all reproduction potential would be rapid and very great with continued release of sterile males.

In other situations, limited selective spraying of residual insecticides

might be the most practical in a tsetse fly infested area where high fly concentrations exist in a relatively small part of the environment, and the release of sterile males might be the most practical procedure for low density fly environments surrounding the areas of high density.

Status of Knowledge on Ways to Produce Sterility in Insects

Published information available on ways to produce sterility in tsetse flies is limited. However, W. H. Potts of the Commonwealth Bureau of Entomology, London, has shown that gamma radiation can be used to produce sterility in tsetse flies, and that males so sterilized are reasonably competitive in mating. The Entomology Research Division has obtained a great deal of information on the effects of gamma radiation on a wide range of insect species. While there is good reason to believe that gamma radiation applied to pupae or adults could be employed as a satisfactory way to produce sterility in tsetse flies, the advances made in the development of chemosterilants for various insects suggests that this method of inducing sterility might be more efficient and more practical.

Much of the information obtained by the Entomology Research Division on the effects of chemosterilants on insects has not been published. However, great progress has been made in developing chemosterilants which are highly effective against such insects as the house fly, *Anopheles*, and culicine mosquitoes, tropical fruit flies, the stable fly, *Drosophila* fruit flies, the pink bollworm, the boll weevil, as well as other species. Most of the research on chemosterilants has been conducted by the Orlando,

Florida, Kerrville, Texas, and Corvallis, Oregon, laboratories of the Insects Affecting Man and Animals Research Branch; the Beltsville, Maryland, laboratories of the Pesticide Chemicals Research Branch; the Mexico City Fruit Fly Laboratory, and the Beltsville, Maryland, laboratory of the Fruit and Vegetable Insects Research Branch; and by the College Station, Texas, Brownsville, Texas, and State College, Mississippi, laboratories of the Cotton Insects Research Branch.

Insects respond to the action of chemosterilants when the chemicals are administered orally or by contact. For most species there appears to be little or no adverse effects by certain chemosterilants on the mating competitiveness of the sterilized males. There is some indication that the vigor of the sterilized males is actually greater than normal males in the house fly and the Mexican fruit fly.

On the basis of progress to date on other insects, there is every reason for optimism that chemicals among those already known or which might be developed in the future could be used by simple techniques for sterilizing male tsetse flies without serious adverse effects on their competitiveness.

Research Needed

The major purpose of this report is to advance the hypothesis that the sterility principle, involving the production and release of sterile male tsetse flies offers a new and highly practical approach to tsetse fly eradication. However, much research on many aspects of the problem will be required to appraise and develop this concept of insect control or eradication. Although information gained in the past by the many

research workers on tsetse flies will prove invaluable, full appraisal of the potential possibilities and eventual efficient practical application of the technique will require special biological and ecological investigations on many aspects that have not been considered to be of special significance in the past. In addition, research is needed to investigate ways to induce sterility in various species of tsetse flies, taking full advantage of progress that has been made on other insects. Of equal importance is adequate research on methods of mass rearing of the more important species of tsetse flies. Various agencies including the U. S. Agency for International Development, the World Health Organization, and the International Atomic Energy Agency have indicated interest in supporting research on tsetse flies. A number of African nations have research under way on tsetse flies and on the over-all trypanosomiasis problem as it relates to man and animals. On the basis of this appraisal of the potential value of the sterility principle of insect populations and how it might be applied for the control or eradication of tsetse flies, the writer feels that there is every justification for major research support on the many aspects that need investigation for a full exploration of this new and desirable approach for the elimination of these important insects in various areas of Africa where eradication can be economically justified.

Although a discussion of the sterility principle in this report is limited primarily to its possible use by the production and release of sterile males, the sterility principle may eventually be developed for use in other ways. For example, if highly effective means of trapping tsetse flies can be developed through the use of attractants, the natural

population of tsetse flies might be utilized for their own destruction by exposing the insects to chemosterilants and then returning them into the environment. This would obviate the necessity of rearing the insects. Recent progress in the development of attractants is indicated by the research of Langridge of the Kenya Department of Veterinary Services.

By studying the mating behavior of various species of tsetse flies and through the use of chemosterilants, it may also be possible by appropriate treatment of females to induce sterility in the natural population of males which attempt to mate with the treated females. The Orlando, Florida, laboratory of the Entomology Research Division has demonstrated in cages that male house flies can be sterilized in this manner. Finally, effective and safe chemosterilants may be developed that could be used as space or residual sprays to produce sterility in tsetse flies. As brought out by the writer in several publications, sterilizing a high proportion of an insect population without serious adverse effects on mating behavior offers a much more effective system for reducing the reproductive potential of the population than can be achieved by killing a like number of the insects. Tsetse flies, as vectors of trypanosomiasis in both man and animals, represent one of the most important obstacles to the economic development of vast and potentially productive areas in Africa. Research on the sterility principle and how it might be utilized to help meet tsetse fly problems deserve major attention and support.

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Table 1. Showing the theoretical trend of a low density tsetse fly population averaging 200 flies per square mile, when subjected to sterile male releases at the rates and periods indicated.

Period of release	Natural population density at beginning of each period	Number of sterile males released each period	Estimated average ratio of sterile to fertile males	Assumed natural population density at the end of each period 1/
0-3 months	200 (100 males + 100 females)	900 (300 per month)	3:1	75
4-6 months	75 (37 males + 37 females)	450 (150 per month)	4:1	22
7-9 months	22 (11 males + 11 females)	225 (75 per month)	7:1	4
10-12 months	4 (2 males + 2 females)	112 (37 per month)	16.5:1	< 1
		1687 Total		

1/ In calculating the theoretical effect of the sterile male releases, it is assumed as explained in the text, that the released males are fully competitive with normal wild males and exert full effect in reducing the reproductive potential of the total population. The assumption is also made that in the absence of control efforts the natural population from a low level would increase by 50 percent each 3-month period (each generation). Thus, in the absence of sterile male releases the population trend would be as follows: First period, 200 flies per square mile; 2nd period, 300 flies per square mile; 3rd period, 450 flies per square mile; 4th period, 675 flies per square mile.