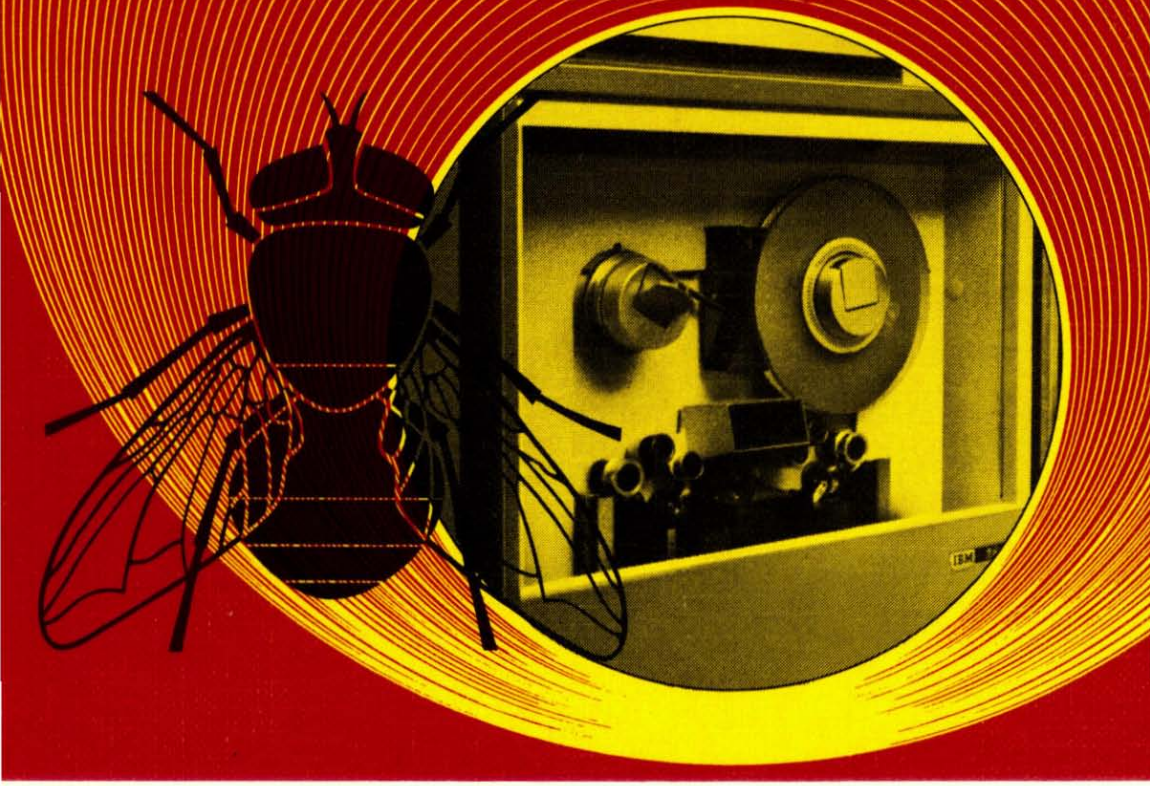
COMPUTER MODELS AND APPLICATION OF THE STERILE-MALE TECHNIQUE

PROCEEDINGS OF A PANEL VIENNA, 13-17 DECEMBER 1971 ORGANIZED BY THE JOINT FAO/IAEA DIVISION OF ATOMIC ENERGY IN FOOD AND AGRICULTURE



INTERNATIONAL ATOMIC ENERGY AGENCY, VIENNA, 1973

COMPUTER MODELS AND APPLICATION OF THE STERILE-MALE TECHNIQUE

PANEL PROCEEDINGS SERIES

COMPUTER MODELS AND APPLICATION OF THE STERILE-MALE TECHNIQUE

PROCEEDINGS OF A PANEL
ORGANIZED BY THE
JOINT FAO/IAEA DIVISION OF ATOMIC ENERGY
IN FOOD AND AGRICULTURE
HELD IN VIENNA, 13 - 17 DECEMBER 1971

INTERNATIONAL ATOMIC ENERGY AGENCY
VIENNA, 1973

COMPUTER MODELS AND APPLICATION OF THE
STERILE-MALE TECHNIQUE
IAEA, VIENNA, 1973
STI/PUB/340

Printed by the IAEA in Austria
June 1973

FOREWORD

The sterile-male technique is a species-specific non-polluting method of insect control which has proved effective against a number of noxious species of insects. With the increased application of this technique that is expected in the future, it is essential that computerized programs be developed to assist the entomologists who are conducting the insect control projects. With the aid of computer simulation, the costs of implementing and successfully carrying out these plans will be reduced. An additional advantage of the skilful use of computer simulation is that mistakes in applying the technique can be corrected before irreparable damage is done. In the development of the sterile-male technique, the work on computer simulation will help to indicate which phases of the research are most important, thus making for a more effective use of available resources.

A panel convened by the Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture at the IAEA Headquarters in Vienna from 13 to 17 December 1971 was the first specifically held to discuss the problems of computer simulation applied to the sterile-male technique. As well as the various papers presented, the present book includes the recommendations of the Panel, which included several experts from the computer sciences.

It is hoped that this publication will assist in guiding research administrators and workers in the application of the sterile-male technique for control of noxious insects and will stimulate them to provide the necessary data to computer experts so that computer simulation can be fully utilized. Similarly, it is hoped that computer experts will seek out entomologists with whom to cooperate.

CONTENTS

GLOSSARY OF COMPUTER TERMS

MODELLING, Computer:

A means of describing a real or proposed situation by use of programming to form a model. Qualitative factors in the real case must be resolved to quantitative factors in the model.

MODEL, Mathematical:

The characterization of a process, object or concept in mathematical terms as a series of equations. The variables may then repeatedly be assigned values and adjusted to see how the model behaves in different situations.

MODEL, Deterministic:

Each independent variable in the model may be assigned a predetermined value to observe its effect on other variables.

MODEL, Stochastic:

Each independent variable in the model may be assigned a range of values, which will be random, but which will generally correspond to a statistical distribution.

SUBMODEL:

A distinct part of a model, which is in itself a model.

SUBROUTINE:

A distinct, separate part of one or more computer programs, which usually performs a unique function upon request of the main, or driving, routine. The implementation of an algorithm. For example, to obtain a square root of a certain value one uses a previously written subroutine, to which one supplies the value and from which one receives the result. This precludes the need always to program similar instructions, since the subroutine is sufficiently generalized to be able to deal with a variety of particular cases.

LANGUAGE, Computer:

A set of characters used to form a rigidly defined set of symbols or words. These are used in conjunction with strict rules to communicate meaningfully with the computer. In general, a compiler program will be needed to translate or interpret the language to those instructions understood by a particular machine.

PROBABILITY distribution:

A table showing the relative frequencies of each subset into which the total observations are divided. The table may be read to show the probability of occurrence of each subset value.

POPULATION:

The total collection of all observations and events associated with a given experiment.

BINOMIAL probability distribution:

A type of probability distribution applied to situations which may have one of two possible outcomes. If the probability of an event having result A is p, then the probability of the same event having result B is 1-p, or q. Therefore the probability that x out of n events have result A is:

$$p(x) = \binom{n}{x} p^x q^{n-x}$$

GAUSSIAN distribution:

A "random error of sampling" is a variation due to chance alone. If the sample is truly random, small errors will be more numerous than large errors and positive errors will be as likely as negative errors, thus giving rise to a symmetrical, bell-shaped normal curve of errors.

POISSON probability distribution:

A specific binomial probability distribution often used when a large number of independent events each have a small probability of occurrence. The probability that exactly x number of occurrences will happen is:

$$p(x) = \frac{\mu^x e^{-\mu}}{x!}$$

where μ is the "true" or population mean.

FACTOR analysis:

A statistical technique for reducing a large number of correlated variables to terms of a small number of uncorrelated variables, thereby learning something of an overall effect by combining many constituent parts.

ALGORITHM:

(1) A fixed step-by-step procedure for accomplishing a given result; usually a simplified procedure for solving a complex problem.
(2) A defined process or set of rules that leads to and assures development of a desired output from a given input.

FINITE difference equation model:

A deterministic model using equations comprised of finite differences.

FINITE differences:

A tabulated function and its differences are used as the numerical equivalents of the true function and its successive derivatives. First differences are obtained by subtracting each value of the function from that for the following argument. Second differences are formed in a similar manner using the first differences. Third and higher-order differences are formed in the same way.

PARAMETER:

(1) In a subroutine, a quantity which may be given different values when the subroutine is used on different occasions. (2) An argument of a mathematical formula which may be assigned any arbitrary value.

A VIEW OF COMPUTER SIMULATION IN STERILE MALE EXPERIMENTS

C.B. CUELLAR
Ross Institute of Tropical Hygiene,
London School of Hygiene and Tropical Medicine,
University of London,
London,
United Kingdom

Abstract

A VIEW OF COMPUTER SIMULATION IN STERILE MALE EXPERIMENTS.

A brief historical introduction is followed by a discussion of two models of sterile male releases into an insect population. The importance of biological parameters is emphasized by the apparently diverging results. In the specific case of tropical anopheline vectors of malaria some theoretical possibilities are mentioned and a hypothesis put forward that in some instances, for purely biological or logistic reasons, simultaneous releases of sterile males and females in the same area might be more efficient than sterile males alone, or sterile males and females in separate areas.

1. INTRODUCTION

In the letter announcing this meeting it was stated that its purpose was to exchange ideas between entomologists and computer programming experts. This is a bold but necessary undertaking, because of the increasing importance of computer simulation in the research and development of the sterile male and allied techniques.

The first mathematical treatment of the role of an insect vector of disease was published in 1911 by Sir Ronald Ross [1], the discoverer of the transmission of malaria by anopheline mosquitoes. Until the early 1950s malaria mathematical models did not give much prominence to entomological aspects. However, the importance of entomological parameters was stressed by the late Professor George Macdonald, who made substantial contributions to the epidomiology of this disease [2]. Under his direction a library of computer malaria programs was created in 1966-67 [3], followed by an extension into the simulation of a sterile male system. This latter development originated from the discovery by G. Davidson, of Professor Macdonald's department, that Anopheles gambiae, the notorious malaria vector of tropical Africa, was in fact a complex of at least 5 species [4]. The F_1 generations from crosses between the complex members exhibited the phenomenon of hybrid male sterility, which could be used as a biologically produced sterility system to eradicate a suitable wild population [5].

Until now many biologists have felt uncomfortable with mathematics, however elementary, and for this reason perhaps it is preferable to express principles and ideas in non-mathematical terms. For this old-fashioned biological approach apologies are given to the initiated.

The proliferation of computers has significantly contributed to today's information explosion in the sciences. In regard to bio-ecological systems a valuable outline has been described by Holling [6, 7] and Watt [8]. These authors have built models with many variables and a high degree of

complexity from originally elementary concepts. Their Experimental Components Approach illustrates a methodology of close integration between computers and biology from the very beginning of a research project. This contrasts with the humble origins and original modesty of biomathematics.

The application of mathematics to biology is older than the computer and is indissolubly linked to the basic concept of a mathematical model. Definitions are very difficult and probably for this reason many mathematical developments follow from a series of statements assumed true in order to avoid the quagmire of proving essentials beyond doubt or ambiguity.

In a broad sense, a model could be defined as an abstraction, usually simplified, of reality. Its origins are hazy and humble, inevitably related to the evolution of a nervous system with a capacity for memory. We use models all the time in our thinking, and a model becomes mathematical when associated with quantities, numbers, or even notions of less and more. However, the 1964 edition of the Encyclopaedia Britannica devotes almost five pages to the entry, "Mathematical Model", and describes exclusively geometric models. This is the traditional meaning of the term.

2. A HISTORICAL VIEW

The first historical records of calculations can be traced to the period of intense mercantile activity carried out by the Babylonians during the third millenium B.C. They used a sexegesimal number system still surviving in the division of hours and degrees by 60. The last remnant in Europe in the commercial sense proper was removed by decree in 1971 when Britain decimalized its currency (an English Crown used to be worth 60 pence).

Besides the use of mathematical tables, of which the earliest surviving are found in Ptolemy's Almagest, calculating aids were seemingly restricted for centuries to the ubiquitous abacus, a device still surviving in many countries.

The golden century of mathematics, the seventeenth century, witnessed the invention by Blaise Pascal of a machine which could perform the four fundamental operations. Leibnitz, the vigorous philosopher who, searching for a general pathway to knowledge, discovered the fundamental principle of the calculus at about the same time as Newton (thus participating willingly or unwillingly in a famous scientific priority controversy), either improved Pascal's machine or invented a better one and wrote [9]: "For it is unworthy of excellent men to lose hours like slaves in the labour of calculation, which could be safely regarded to someone else if the machine were used". However, the nineteenth century had to dawn on mankind before another serious (and recorded) attempt was made to construct a calculating machine. Charles Babbage was confronted with the sad fact that mathematical tables had a proportion of misprints and errors very resilient to correction because of the modicum of human error involved in typesetting and proofreading, let alone the calculation itself. Endowed with both a clear, logical mind and a considerable fortune he conceived making a machine which could calculate the tables and print them automatically, thus bypassing human error in perceptual or repetitive tasks. An alternative approach, that of changing the visual format of the table to improve perception and eliminate minor printing errors, has only recently been used in statistical tables [10].

Babbage managed to obtain a research and development grant from the British Treasury and started work. Dissatisfied with his engineers he plunged into engineering himself, making original contributions as a side-line. His fertile mind could not rest and in 1834 invented the principle of a modern computer as an "analytical engine", a grandiose design exceeding that of many modern machines [9]. This "engine" would be more automatic than the previous one and would be directed by perforated cards, which were already in use in Jacquard silk looms in France for about a century. However, against the advice of the Royal Society, the British Government withdrew its support, writing off some £17 000, and his first design was never finished. Nevertheless, machines based on his ideas were completed considerably later. Babbage, unruffled, used his private fortune and devoted years to his second design, dying unnoticed in 1871, a bitter and disappointed man, surrounded by fragments of machinery. Perhaps it is not a coincidence that this seminar is held one century after his death.

The linking of biology and mathematics in a modern sense can be traced to the work of G.A. Borelli, a disciple of Galileo, who in the seventeenth century published a book on muscular mechanics. Many years later, S. Hales, a botanist, calculated the rate of rise of water in stems and measured the water taken in by the roots and given off by the leaves. The eighteenth century however was the century of Linnaeus, the great Swedish naturalist, who influenced generations of biologists with his emphasis on observation and classification, thus diverting attention from quantitative biology. To redress the balance this century has seen enormous expansion in this field and it has even been said with justice that the American biologist, Chapman, who wrote about biotic potential and environmental resistance, would have been the inventor of the analogue-computer "had (he) been more successful in the logical development of this electrical analogy" [11, 12].

3. COMPUTER AND MODELS IN BIOLOGY

Until the popularization of computers, applied mathematics had to rely on what was called by mathematicians "mathematical maturity" and by non-mathematicians "a bag of tricks", a speciality in itself of something which has as an important component an array of labour-saving, short-cut computational methods. This situation has been changed by the computer with its incredible capacity for speedy calculations. Computers have been called electronic brains, an unfortunate misnomer because no machine has ever approached human perception, discrimination and ability for analysis and synthesis. For a computer to decide, it is necessary not to go beyond yes-no or equal-more-less steps. Yet computers have an advantage over humans because routine, boring, repetitive calculations can be performed effortlessly at high speed. These activities invariably induce errors in human performance. In summary, computers have aptly been named TOMS (Totally Obedient Morons) [13], and possess only a very limited capability for mathematical operations, but these can be repeated thousands of times and the results printed automatically.

A very convenient development has been the creeping into the literature of descriptive strings of computer language statements [8, 14] which many workers find easier to follow than orthodox descriptions of models. Flow diagrams are also very informative and some versions (Table I) do not

TABLE I. SIMPLIFIED FLOW DIAGRAM OF ANOPHELINE MOCK TRIAL PROGRAM

START

Read

(a) Sequence of natural daily yields of the area
(b) Probabilities of daily survival for males and females
(c) Maximum value of the probability of aquatic survival
(d) Number of sterile adults to be released daily, their sex-ratio, competitiveness and other factors
(e) Mating behaviour variables
(f) Aquatic stages interval
(g) Oviposition intervals
(h) Size of clutch, egg sex-ratio
(i) Others

(1) Compute initial load of males and females

(2) Compute today's emergence from eggs laid one aquatic interval ago

(3) Have releases started? YES, go to (5); NO, go to (4)

(4) Compute normal fertilization, then go to (6)

(5) Compute fractional fertilization considering all relevant input variables

(6) Add today's contribution to the array of ovipositing females

(7) Add today's contribution to the total of males

(8) Add today's contribution to the total of females

(9) Print the relevant figures for today

(10) Compute survivors for tomorrow

(11) Any fertile ovipositing female surviving? YES, go to (13); NO, go to (12)

(12) Were fertile eggs laid one aquatic interval ago? YES, go to (13); NO, then STOP

(13) Has the time allocated for this mock trial been used up? YES, then STOP; NO, go to (2)

require the knowledge of a computer language for the reader. However, demands for conciseness have increased the temptation to concentrate on the results of modelling rather than on the detailed description of the model itself, quite apart from the fact that a happy balance is always difficult to achieve. It is a herculean task to outline even superficially the literature on mathematical models in population biology and ecology. This approach has revolutionized both the concepts and the methods of these branches of biology. Ecological and life-system models started earlier than sterile male models and thus we have much to learn from the writings of the many distinguished scientists in that field. The Experimental Components Approach of Holling and Watt has already been mentioned and emphasis should also be given to population dynamics and life-systems studies in the manner outlined by Solomon [11, 15] and by Clark and co-workers [16].

4. STERILE MALE MODELS

In the sterile male field the father of modelling is Knipling [17] who, in a series of tabular models easily understood by biologists and simple enough to be worked by hand with a minimum of arithmetic, illustrated convincingly the potential value of the sterile-male and associated techniques.

Knipling's work can only be challenged by resorting to complexity, as Table II shows. In Table II the added complexity or refinement of Geier's model [19] is clearly seen: A changing rate of increase which he obtains from an "Allee-type" curve (see Fig.1) which simply depicts the rate of increase of a population as a function of the total number of individuals of that population. The essence of this type of curve is that it shows graphically that there is an "optimum" population size in which the rate of increase is at its maximum. Either very few individuals or "excessive" numbers will be associated with low rates of increase. The curve shown in his paper [19] is already descending, touching the 20x level when the individuals reach a total of 1000. In the last column of Table II the 9000 sterile adults released into the population are considered fully fledged members of the horizontal axis of the curve, bringing down the rate of increase from 20x to 5-6x and producing "eradication" in a manner similar to Knipling's model. Figure 1 shows the same curves but the second has the biological assumption of the last column of Table II, namely that the rate of increase depends on the number of both wild and released adults. Perhaps at this stage it could be fruitful to consider whether the "Allee-type" curve holds for the case in question in terms of the adults only or of the immature stages or of both. The above exercise illustrates an ever-recurring theme in which answers and queries from a model depend mostly on the biological input assumptions or data fed into it.

5. SEXED versus UNSEXED STERILE ANOPHELINES

The biologically produced sterile male system for Anopheles gambiae already mentioned has the advantage of having a distorted sex-ratio in favour of the males. However, it is logistically cumbersome since it involves the independent rearing of two parent colonies, followed by perfect sexing (since the hybrid is produced by placing together the males of one species and the females of another) and the final rearing of the eggs of this cross. Furthermore, the hybrid females are fertile and capable of laying fertile eggs when mated to a fertile male (unless the target species is not one of the parents of the hybrid). A more orthodox technique of sterilization (e.g. gamma irradiation) would involve only one rearing and the females could be sterilized as well. A satisfactory automatic sexing device has not been found, so far, for Anopheles gambiae s.l. and for all these reasons it is justified to explore the possibility of releasing sterile males and females.

A sophisticated model with many input variables, overlapping generations and elastic aquatic mortality would be unnecessary and even confusing in the early exploration of this problem.

Table III presents simple probability models of fertilization of an anopheline population. Rows 1 and 2 are self-explanatory. Row 3 shows the case where males have an unlimited ability for sequential mating and Row 4 illustrates the concept mentioned by Whitten and Taylor [20]

TABLE II[a]. STUDY OF TWO MODELS[b] AND THE RESULT OF INCORPORATING A BIOLOGICAL ASSUMPTION INTO THE SECOND MODEL. Treatment means that 9000 sterile adults are released per generation

Generation	Knipling				Geier				Geier	
	No treatment		Treatment		No treatment		Treatment		Modified treatment	
	N[c]	R[d]	N	R	N	R	N	R	N	R
1	1000	5x	1000	5x	1000	20x	1000	20x	1000	5x
2	5000	5x	500	5x	20000	3x	2000	11x	500	5.5x
3	25000	5x	132	5x	60000	1.5x	4000	7x	145	5.9x
4	125000	1x	10	irrelevant	90000	1.04x	8615	5.3x	14	irrelevant
5	125000	1x	0		94000	1.03x	22124	2.8x	0	
6					96400	1.01x	44034	1.9x		
7					97800	1.01x	69100	1.3x		
8					99000	1.01x	80090	1.1x		
9					100000	1x	82079	1.1x		
10					100000	1x	82846	1.1x		
11							82948	1.1x		
12							83000	1.1x		

[a] Based on Geier [19].
[b] Knipling [18] and Geier [19].
[c] N = number of insects.
[d] R = rate of population increase.

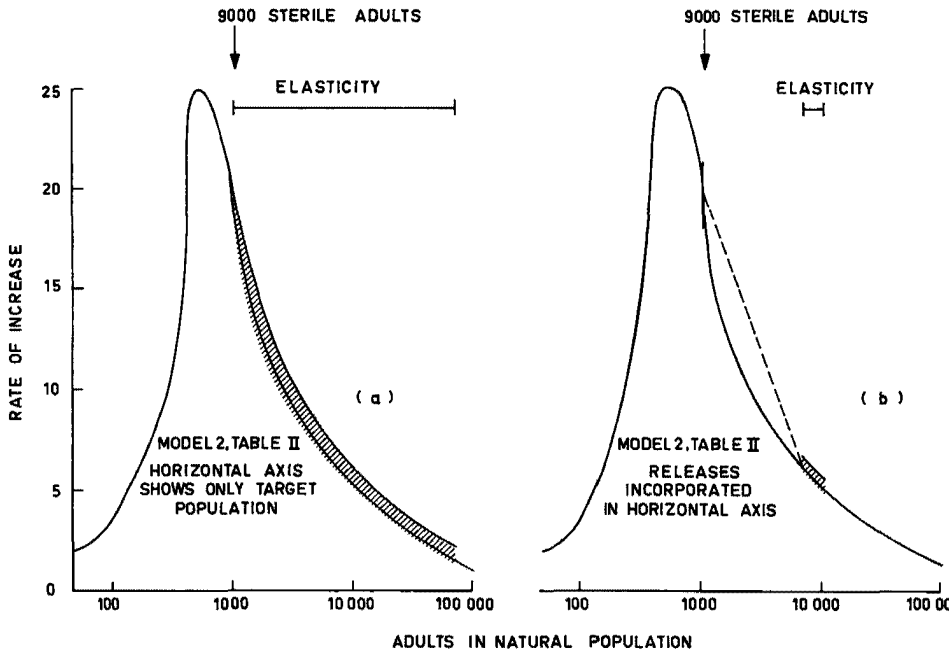


FIG. 1. Assumed rate of population increase over density range: (a) after Geier [19]; (b) modification of (a) by inclusion of 9000 sterile males in the population of the horizontal axis.

suggesting the release of sterilized females in a separate area to enhance the efficiency of the sterile insect factory. These authors, working with the Australian sheep blow-fly Lucilia cuprina found that males have a limited mating capacity restricted to an average of 10 matings per male, and logically proposed that the release of masses of sterile females could erode the surplus mating ability of the wild male population, eventually reducing the fertility of the wild females. All this would occur while the sterile males were being released in the target area proper. Successful selection experiments were mentioned in which the normal 1 - 5% of polygamous females increased to 30%. As an example, Row 4 shows the case where the upper limit of male multiple mating is 5 (5 matings per average male). This system requires the erosion of male fertility to be the reciprocal of the "upper limit" before any movement of the wild female fertility could be detected, and thus sterile females can be considered less efficient than sterile males, since one sterile male can eliminate one female from the mating pool, if they mate, while a fertile male is eliminated only after 5 matings with sterile females.

TABLE III. PROBABILITY OF A WILD FEMALE BEING FERTILIZED. (Equal competitiveness of released sterile individuals is assumed as well as perfect mixing in all instances except in Row 6, where the explanation might be imperfect mixing)

Row	Males		Females		Probability, $\hat{P}$, of a wild female being fertilized	Comments
	Wild	Sterile	Wild	Sterile		
1	1000		1000		1.0	Ideal conditions, full fertilization.
2	1000	9000	1000		0.1	Sterile males only are released.
3	1000		1000	9000	1.0	Mating depends only on the males. Unlimited ability for sequential mating.
4	1000		1000	9000	0.5	Males have an upper limit of 5 for multiple mating.
5	1000	9000	1000	9000	0.1	Same results as Row 2. Explanation same as that for Row 3.
6	1000	9000	1000	9000	$0.1 < P < 1.0$	Sterile females reduce the efficiency of the sterile males. Imperfect mixing or dispersal factors may reduce the available mating potential of the sterile males.
7	1000	9000	1000	9000	$P < 0.1$	It is assumed that the sterile females have an adverse effect on the probability of a fertile mating (possible "interference" effect).

Rows 5, 6 and 7 of Table III could be explained as follows:

M_s = Number of sterile males
M_f = Number of fertile males
F_s = Number of sterile females
F_f = Number of fertile females
W = Number of matings in the system
R = Number of fertile females mated with a fertile male

The subscripts of W and R are

1, when no sterile insects are released
2, when sterile males only are released
3, when sterile insects of both sexes are released.

In normal conditions in anopheline populations the female is monogamous, thus:

$$W_1 = F_f = R_1$$

(Adult females are considered to be fertilized soon after emergence from the aquatic pupal stage.)

Mating in ordinary models of sterile male systems are simulated in the manner illustrated by Row 2, Table III, i.e.

$$R_2 = \frac{M_f W_2}{M_f + M_s} \quad (1)$$

and it is generally assumed that $W_1 = W_2$ (mating continues undisturbed as sterile males are pumped into the target population).

G. Conway of Imperial College, London has constructed a theoretical model in which large numbers of sterile males interfere with each other in the mating process leaving some fertile females unmated (i.e. $W_1 > W_2$). He logically postulated that if in subsequent generations or farther along in time fertile males emerge or immigrate into the area, these females (which were assumed to have mated with the sterile males) could in fact be fertilized, compensating, at least partially, for the "sterilizing" effect of the releases.

When sterile adults of both sexes are released, the number of fertile females mated with fertile males would be

$$R_3 = \frac{M_f \ F_f \ W_3}{(M_f + M_s)\ (F_f + F_s)} \quad (2)$$

The case of Row 5, Table III, is where $R_3 = R_2$. Row 6 in Table III is the situation described by Proverbs [21]: Sterile males alone "suppressed reproduction somewhat more effectively than the addition of sterile moths of both sexes" ($R_3 > R_2 > R_1$). This occurred in laboratory and field cage experiments with Laspeyresia pomonella. A plausible explanation is that there is probably a "wastage" of the sterile males mating capacity since they are likely to mate first with sterile females on account of dispersal

factors. This drawback could be compensated for by the increased logistical capacities of a sterile insect factory when a cumbersome operation (sexing) is eliminated.

Row 7, Table III, presents the case where $R_3 < R_2$. This could be a possibility with tropical anopheline mosquitoes since their daily mating period is restricted in time. A delay in mating, falling equally on all females (fertile and sterile), could have a snow-balling effect. Under these conditions the next mating period (if daily releases of sterile adults are sustained) will have a larger " mating pool", thus producing further delays.

In regard to anopheline mosquitoes important considerations, such as increase in biting nuisance or in the transmission level of malaria or other diseases, may preclude the use of sterile females, either alone or in combination with sterile males. However, the possibility of population reduction or eradication may outweigh the difficulties of the period of primary releases. More sophisticated refinements, such as short-lived females incapable of being vectors, could overcome objections.

Perhaps it is fitting to mention that the releases of tsetse-fly sterile males (Glossina sp.) is just as objectionable since they are blood feeders and vectors, too, while male mosquitoes have vegetarian diets. In any case the model necessary to aid in the planning and operational evaluation of a field experiment will require a minimum of flexibility and complexity. Ideally all factors bearing on the test parameters should be considered as realistically as possible but it is difficult to achieve or even to approximate this goal satisfactorily. However, the very process of attempting to construct a computer model helps in the clarification of thinking and the categorization of processes. A greatly simplified flow diagram of an anopheline model appears in Table I.

6. CONCLUSION

Computer simulation holds its own in pure research and development, generating ideas and building up theories, but operates at best in the form of a feedback system, in combination with competent biologists, even from the planning stage of problem-orientated activities. The computer is undoubtedly an essential part of today' s research and field experiments and will likely remain so.

ACKNOWLEDGEMENTS

The generous support of the United Kingdom Medical Research Council and of the National Autonomous University of Mexico is gratefully acknowledged.

REFERENCES

[1] ROSS, R., The Prevention of Malaria, 2nd Edn, John Murray, London (1911).
[2] MACDONALD, G., The Epidemiology and Control of Malaria, Oxford University Press, London (1957).
[3] LONDON SCHOOL OF HYGIENE AND TROPICAL MEDICINE, Report on the work of the School, 1966-67, University of London Press (1967).
[4] DAVIDSON, G., The five mating types in the Anopheles gambiae complex, Riv. Malar. 43 (1964) 167.

[5] WORLD HEALTH ORGANIZATION, Annex 2, Technical Report Series No. 268, Genetics of Vectors and Insecticide Resistance, WHO, Geneva (1964).
[6] HOLLING, C.S., Principles of insect predation, Annu. Rev. Entomol. 6 (1961) 163.
[7] HOLLING, C.S., The Functional Response of Predators to Prey Density and its Role in Mimicry and Population Regulation, Mem. Entomol. Soc. Can. No. 45 (1965).
[8] WATT, K.E.F., Ecology and Resource Management, McGraw-Hill, New York (1968).
[9] LAVER, F.J.M., Introducing Computers, H.M. Stationary Office, London (1965).
[10] FISHER, G.H., The New Form Statistical Tables, University of London Press (1964).
[11] SOLOMON, M.E., Population Dynamics, Institute of Biology Studies in Biology, No. 18, Arnold, London (1969).
[12] CHAPMAN, R.N., Animal Ecology with Special Reference to Insects, McGraw-Hill, New York (1931).
[13] BBC: Mathematics in Action, Spring 1966, British Broadcasting Corporation, London (1965).
[14] CONWAY, G.R., Computer simulation as an aid to developing strategies for anopheline control, Misc. Publs Entomol. Soc. Amer. 7 (1970) 181.
[15] SOLOMON, M.E., "Investigating the regulatory aspect of insect population dynamics", Insect Ecology and the Sterile-Male Technique (Proc. Panel Vienna, 1967), IAEA, Vienna (1969) 87.
[16] CLARK, L.R., GEIER, P.W., HUGHES, R.D., MORRIS, R.F., The Ecology of Insect Populations in Theory and Practice, Methuen, London (1967).
[17] KNIPLING, E.F., The Potential Role of the Sterility Method for Insect Population Control with Special Reference to Combining this Method with Conventional Methods, Agricultural Research Service, USDA, Rep. ARS 33-98, Washington, D.C. (1964).
[18] KNIPLING, E.F., Opportunities for developing alternate ways to control insects, Amer. J. Public Health 55 Pt. 2 Supplement, (1965) 20.
[19] GEIER, P.W., "Demographic models of population response to sterile-release procedures for pest control", Insect Ecology and the Sterile-Male Technique (Proc. Panel Vienna, 1967), IAEA, Vienna (1969) 33.
[20] WHITTEN, M.J., TAYLOR, W.C., A role for sterile females in insect control, J. Econ. Entomol. 63 (1970) 169.
[21] PROVERBS, M.D., "Orchard assessment of radiation-sterilized moths for control of Laspeyresia pomonella (L.) in British Columbia, Application of Induced Sterility for Control of Lepidopterous Populations (Proc. Panel Vienna, 1970), IAEA, Vienna (1971) 117.

PRINCIPLES OF THE STERILE MALE TECHNIQUE WITH EMPHASIS ON ECOLOGY

D.E. WEIDHAAS
Entomology Research Division,
United States Department of Agriculture,
Agricultural Research Service,
Gainesville, Fla.,
United States of America

Abstract

PRINCIPLES OF THE STERILE MALE TECHNIQUE WITH EMPHASIS ON ECOLOGY.

The principles and models developed by E.F. Knipling for the sterile male release technique are reviewed in detail with examples to illustrate the basic concepts involved, i.e., that ratios of sterile to fertile insects that cause levels of sterility high enough to balance or overcome the reproductive success of the existing population can limit the increase in density of such populations or result in extremely high levels of control or actual elimination. Requirements for the technique are reviewed. Simplified equations for the technique are presented. Particular emphasis is given to the usefulness of the models for the sterile male release technique as a concept for total population suppression by other methods of control and as a biological tool for studying population dynamics and ecology. Specific examples are presented. Sterility itself is an extremely useful means of tagging insects. Since valid results depend upon sterile insects dispersing and mating, this type of tagging system could be extremely useful in determining absolute population density and reproductive success under natural field environments. Data on population dynamics and ecology obtained from sterile insect releases could be used to confirm similar information obtained by other ecological methods. Problems associated with the use of insect sterility as a biological tag are reviewed. Finally, the relative efficiency of the sterile male release technique at high and low density levels is reviewed in the light of the need for integrating this technique with other methods of control.

The principles developed by Knipling for the sterile male release technique [1, 2] are relatively easy to demonstrate in theory with simplified models. However, the requirements for the successful application of this technique under practical situations indicate the difficulties which will be encountered in the development of this technique, the advantages and limitations of the method itself, and the need for computerized analysis of field data to indicate the feasibility of the technique alone or in combination with other methods.

Research on the development of the method itself along with other developments in the field of entomology have clearly demonstrated our lack of quantitative knowledge on total populations and their dynamics as they exist under actual field conditions. The fields of entomology and insect control are moving further into the development of integrated control techniques, the evaluation of the feasibility of new approaches to control and the attempt to manage or eliminate total populations of insects over time, rather than simply reduce them when high densities become economically important. Thus, the lack of quantitative data on total populations and population dynamics has become both more obvious and more important and limits our ability to predict the feasibility, effectiveness and cost of any given method of control or combinations of control techniques.

Knipling's principles for the sterile male release technique have been particularly interesting to researchers at the Insects Affecting Man and Animals Research Laboratory at Gainesville, since they offer potential solutions to the problems cited above. As is obvious to all, the method offers a new approach to insect control which may make available yet another control weapon in addition to those already at hand. One of the problems has been to determine what role it can play with what insects in what types of integrated control programs. I think two other important aspects of Knipling's principles for the sterile male release technique have not been emphasized.

First, these principles offer simplified concepts and models to deal with the management of total populations of insects if one is considering control over extended periods of time or elimination from certain areas or eradication. Any method of control — be it insecticides, sterility, genetic manipulations, attractants, biological control or other methods — may (such as with insecticides) or may not (such as with sterility or genetic manipulation) reduce density immediately at the time of application of the method (one might call this an effect on the existing or "parent" generations). To date most control programs have been based on immediate kill of high-density populations. However, to be effective in reducing or controlling populations over time or generations a method of control must limit the reproductive success of the population by some means of controlling reproduction. Knipling has proposed with his sterile male release technique that one deals with populations over time in terms of generations. His models relate: (1) total or relative numbers of individuals per generation, (2) rates of increase from generation to generation (actual reproductive success) and (3) reduction in reproduction caused by artificial, man-made control techniques per generation. These models will be illustrated with formulas; however, for now I want simply to make the point that the models provide simplified concepts to deal with total population dynamics under stress of artificial control techniques and stress or favour of existing environmental conditions and therefore will be useful to entomologists primarily interested in control.

Second, insect sterility provides a highly efficient and useful tool or tag in the study of the biology of insects and dynamics of populations [3]. For example, once it is determined that an insect can be sterilized by radiation, one generally proceeds immediately to use the tag of sterility to determine the mating competitiveness of males by competing sterile males against normal males in mating females. One needs no other marker because sterility itself is the tag. The number of times a female can be fertilized by males has been determined using sterility as a tag. Behavioural differences in mating between strains of the same species of insects have been demonstrated in house flies and mosquitoes using sterility as a tag. Total numbers of individuals in an isolated population of mosquitoes along with reproductive success of the population has also been determined by the use of sterility as a tag with the mosquito, Culex pipiens quinquefasciatus Say.

A review of Knipling's classic example of the principles behind the sterile male release technique would be helpful in illustrating these remarks concerning the sterile male release technique as (1) an approach to insect control, (2) a concept for working with pest management or eradication and (3) a useful biological tool or tag.

Knipling gave a theoretical example of the elimination of an initial population of 1×10^6 individuals (referred to hereafter as P) with the release of 9×10^6 sterile individuals (referred to hereafter as N) and a rate of increase of 5x (referred to hereafter as RI). F_1 will be used to denote the number of individuals expected in each subsequent generation. The example is not reviewed in detail since it is familiar to many people. Simply stated, the degree of sterility caused initially by the ratio of sterile to fertile insects must be sufficiently high to overcome the rate of increase (reproductive success) of the number of individuals present, to obtain a reduction in density. If this requirement is met and density is reduced, then the continued release of sterile insects results in increasing ratios of sterile to fertile insects, increasing degrees of sterility and decreasing density to the point of elimination in isolated areas. Thus, the sterile male release technique is the only demonstrated method of population control whereby efficiency increases theoretically as population density decreases.

To demonstrate the usefulness of Knipling's model as a concept in population management and as a biological tool in population dynamics, it would be helpful to illustrate the model with simple formulas using the above-mentioned notations. For example:

$$F_1 = P \left[1 - \frac{N}{N+P} \right] RI$$

Thus, the degree of sterility, S, is simply $N/N+P$ and one can consider that the degree of fertility, F_e, of the population is simply $1 - S$.

In practical control situations one will be interested in maintaining the condition $(F_1/P)=1$ to keep populations at low levels without increases in density, or making $(F_1/P)<1$ to cause reductions in populations. Since $F_1/P = (1 - S)(RI) = F_e (RI)$, the product of the rate of increase times the remaining fertility of the population must be equal to one to prevent a population from increasing and less than one to reduce it. This is a handy "rule of thumb" for entomologists interested in population management.

As one works with these models and attempts to relate them to practical field usage, one's lack of quantitative data becomes apparent immediately. What are the total numbers of insects of a given species in a given area at a given time? Is this a single population? What are the relative or absolute densities of all stages of a given species of insect on a monthly basis throughout a full year including both maximum and minimum density levels? What rates of increase do insect populations attain from time to time or from generation to generation under actual field conditions? What is a generation time for a given species of insect? How much does it vary in duration at different times of the year? What levels of control of reproduction must be maintained from generation to generation to prevent a population from increasing or to reduce its density? What is the maximum rate of increase of a population under stress of environmental factors and artificial, man-made control procedures? What influence does migration have on total populations and the attempts to understand their dynamics and manage their densities?

The concepts behind the sterile male release technique and sterility itself offer the opportunity to answer many of these questions. For

example, the release of a known number of sterile males, a knowledge of the sex-ratio of the species and the determination of the degree of sterility produced in wild females allows a calculation of the number of males and females in the population, since, using previous notations

$$S = \frac{N}{N+P} \qquad \text{and} \qquad P = \frac{N - SN}{S}$$

Also one would be able to study rates of increase of populations under stress or favour of environmental factors, since

$$RI = F_1 / P$$

or under stress of both environmental factors and artificial man-made control procedures, since

$$F_1 = P(1 - S)(RI) \qquad \text{or} \qquad RI = \frac{F_1}{P(1 - S)}$$

Studying rates of increase under stress of artificial control procedures will be particularly valuable since it will provide data for populations as they are being controlled. The requirements are that one must be able to measure relative densities of populations from time to time or generation to generation and measure the degree of sterility produced in the wild population by the release of sterile insects. If this is possible, and I believe it is, one can simply calculate the rates of increase that occur at different levels of population reduction. If population reduction occurs with 50, 80, 90 or 99% sterility, then one knows rates of increase were limited to less than 2x, 5x, 10x, or 20x, respectively. When population density is reduced to very low levels, one should be able to estimate maximum rates of increase that can occur with a given population at a given time and place.

Field research of this type will not be easy. Isolated populations will have to be used or the extent of migration known. Sterility, alone or in combination with other methods of tagging, will be a useful tool in studying migration as well as survival. Such information can be developed by the use of tagging methods other than sterility and should be encouraged. The development of population data by more than one method would be extremely useful in increasing confidence in the results obtained. Sterility itself should be an excellent tag in such field studies, because its effective use depends upon the fact that released sterile insects disperse and mate with naturally occurring insects and behave as do insects in the naturally occurring population. If this requirement seems too demanding, then one would have to conclude that the development of population management techniques, the study of total populations and the successful development of the sterile male technique should be left to empirical approaches of evaluation and chance. The least one can do is to attempt to design studies on the release of sterile insects to provide both an estimate of the feasibility and economics of a method and the dynamics of the populations with which one is dealing. For some insects this information may already be available or the data awaiting further analysis. In a second presentation

I plan to review some of the detailed data obtained with mosquitoes, house flies and stable flies at the Insects Affecting Man and Animals Research Laboratory. These are only preliminary studies but have given an insight into the dynamics of populations of these insects.

It was with a great deal of pleasure that I learned of this panel on computer models for the sterile male technique because the need exists for organized collection of data and interpretation and analysis of such data. It can serve not only as a means of determining the feasibility of the sterile male release approach to insect control and its most appropriate use with other methods of control, but also as a means of developing basic information on population dynamics useful in predicting the feasibility of any method of control. One needs more and more to be able to estimate and compare costs of control technologies. Knowledge of the dynamics of populations will help to make this more meaningful.

Finally, a few words on terminology and concepts used in the sterile male release technique and pest management. The term generation is useful in studying populations from time to time. Where populations occur in discrete generations the concept is straightforward. When insect populations occur in overlapping generations with some or all stages present at the same time, the concept is more difficult. A generation is considered to be that time equivalent to the life cycle, i. e. the median time required for egg hatch, larval development and pupal development plus the time from adult emergence to the time for deposition of the median number of eggs. This generation time may vary from season to season depending upon temperature and other environmental factors. The preoviposition time for the median number of eggs may not be available for actual field conditions. Females that survive to oviposit for a period of time longer than the generation time may tend to make interpretation of data more difficult. As one develops new information and analyses current data, the concept of a generation time should become clearer. Further, one may need more precise definitions for such terms as rates of increase. For example, with no artificial control on populations, the rate of increase is simply a comparison of the relative or absolute numbers of individuals from one generation to the next. Stable populations would have a rate of increase of 1x, populations increasing in density from generation to generation would have rates greater than 1x and populations decreasing in density would have rates less than 1x. However, when populations are subjected to total population control by a method such as the sterile male release technique, populations that are stable or decreasing in density may have rates of increase greater than 1x. It would be helpful to coin a term for the reproductive success of a population under stress of total population control and a term for the maximum reproductive success of a population under actual field conditions. These values may well vary from time to time and place to place.

It is indeed a pleasure to have been present at this particular panel, and I look forward to interesting conclusions and recommendations on the application of the sterile male release technique to population control and research on the ecology and dynamics of insect populations. All of my remarks have been made on the basis of experience with insects of medical and veterinary importance. Some of the problems and questions that are pertinent to this panel discussion may already have been answered in studies with other insects.

REFERENCES

[1] KNIPLING, E.F., The Potential Role of the Sterility Method for Insect Population Control with Special Reference to Combining this Method with Conventional Methods, USDA Publication ARS 33-98, U.S. Government Printing Office, Washington, D.C. (1964).

[2] KNIPLING, E.F., "The potential role of sterility for pest control", Principles of Insect Chemosterilization (LaBRECQUE, C.C., SMITH, C.N., Eds), Appleton-Century-Crofts, New York (1968) 7.

[3] WEIDHAAS, D.E., "Field development and evaluation of chemosterilants", ibid., p.295.

COMPUTER MODELLING OF THE DYNAMICS OF INSECT POPULATIONS

M.J. FRISSEL, K.J.A. WIJNANDS-STÄB
Association Euratom-ITAL
Institute for Atomic Sciences in Agriculture,
Wageningen,
The Netherlands

Abstract

COMPUTER MODELLING OF THE DYNAMICS OF INSECT POPULATIONS.

To develop a model of an ecosystem, such as the dynamics of an insect population after the release of sterile and/or translocation insects, several aspects are of main importance: (a) Careful selection of processes and parameters which have to be included in the model, so that maximum insight is guaranteed. Therefore a team of entomologists and model builders should evaluate the available knowledge and the possibility of combining the information in a simulation model in close cooperation. (b) The model structure should be flexible and should easily allow modifications. Therefore it has to be divided into submodels, each one describing a separate part of the overall model. (c) Selection of the language which will be used to reach the proposed aims. At present a combination of CSMP and FORTRAN seems to be the best choice.

1. INTRODUCTION

For the model builder the concept "model" has a particular meaning, though his ideas are certainly not contradictory to the general meaning of the word. In his eyes, a model is a schematic representation of the real world. Its primary purpose is communication, because it provides a way of developing ideas and of describing them; Fig. 1 may be regarded as such a discussion scheme [1].

2. EVALUATION OF PROCESSES

The ideal way to obtain a good simulation model is by cooperation within a team of specialists; some of them should be experienced entomologists, whereas others must be skilled model builders. Only intense communication between these specialists will obtain both the maximum from the computer and the maximum from the available knowledge.

In the beginning the description is verbal and qualitative, but this still-vague description should quickly be replaced by quantitative statements. The entomologists will have to explain their problem by equations, graphs and decision statements.

Equations can be used if well-defined mathematical expressions are available. Unnecessary simplifications should be avoided.

The graphs may represent relationships between variables if no mathematical relationship is present. In biological models this is often the case, examples being: the influence of the temperature on the emerging of pupae, the growth capacity as a function of the host, etc. An example of the use of graphs is shown in Fig. 2.

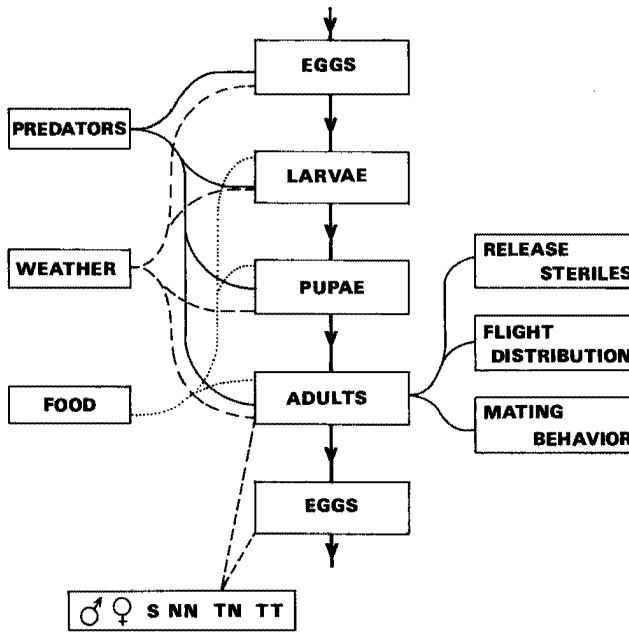


FIG.1. Example of a model as a base for calculations. The model explains that the quantities of each of the stages – eggs, larvae, pupae and adults – are calculated for each generation. The left hand side shows that the influence of the weather, predators and available food is considered in most of these calculations. On the right hand side some processes which are typical for release calculations are shown, which only need to be considered for adults. The bottom shows that it might be necessary to split the population into males, females and steriles and, in the case of translocation insects being used, into heterozygotes and two types of homozygotes. The authors realize that almost no one will agree with all the details of the model; indeed for each particular insect it will have to be modified by simplifications and/or additions.

The decision statements describe verbal expressions such as: if a chemical treatment is used and at the same time the temperature is higher than ..., then something will happen, and if the conditions are not met, it will not happen.

Such a development guarantees that a rather complete list of the required data is obtained. It also shows the form in which the data have to be collected: as tables, as functions or as coefficients.

2.1. Responsibility of the model builder

The model builder should understand why the problem is presented in a certain way and use his experience and intuition to develop a model which has a clear structure and yet contains enough possibilities for the further modification of the model, but which can also be simplified in the course of the development. He must take care that the various parts of the model can be interrelated so that a completely balanced overall model is obtained. He has to watch the accuracy of the various parts; there is no sense in increasing the accuracy of a certain part (at the price of a considerable amount of computer time) if the other parts are still rather inaccurate.

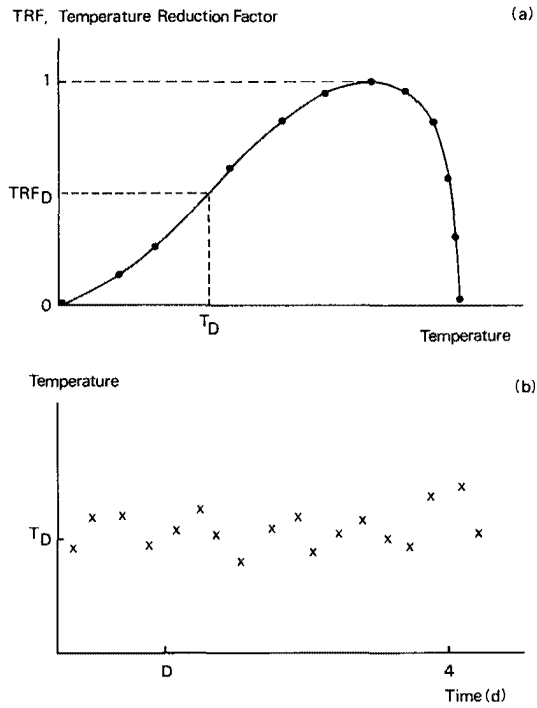


FIG.2. Use of non-linear relationships in a computer model. A certain process, e.g. the development of an egg, is considerably influenced by temperature. This influence can be described by a temperature reduction factor TRF which varies between 0 and 1 (see Fig.2a). The observed temperature is shown in Fig.2b; the observation points can be fed directly to the computer. The actual temperature for each moment can then be found by interpolation by the computer (e.g. temperature T_D for time D). In this example it is assumed that the curve for the temperature reduction factors is obtained from the literature. To feed such a curve to the computer it is necessary to characterize the curve by a set of co-ordinates (the 12 black dots in Fig.2a). The temperature reduction factor is then once more found by interpolation (TRF_D for T_D). The advantage of using curves or observations in this manner is that the curves and observations can be used in a straightforward way; it is unnecessary to fit the observation points first in a mathematical expression. (Note: The interpolation is not limited to linear interpolation; quadratic or other interpolation methods may be used as well).

2.2. Parameter selection

From the beginning one should consider each parameter carefully [2]:

(a) Is it really necessary to include the parameter in the model?
(b) Is this parameter constant, at least in the range used? (If a parameter is a variable of which only one value is known, it is still a variable and should be introduced as such. Otherwise new information invalidates a whole program).
(c) Is the parameter a function of time?
(d) Does the parameter depend on other variables? (For both (c) and (d) the same reasoning as for (b) is valid); if a parameter depends on time or other variables, it should be introduced as such, even when the information is limited).

2.3. Statistical fluctuations

In all biological processes fluctuations occur frequently. Such fluctuations can easily be simulated by a computer. It is not recommended, however, to start with such a stochastic model; it is better to begin with a deterministic model and begin by checking all parts of the program carefully. Only if there is no reason to mistrust any part of the program should one introduce fluctuations. Too early an introduction might easily cover up errors.

2.4. Test of the model

It is stressed that a model cannot be used for predictions or decisions without thorough experimental verification. Just several reasonable results of a few calculations are no proof of the correctness of the model. Unfortunately, there is no general rule as to how a model can be tested, it depends on the situation.

2.5. Errors which are often made

It is not recommended that a biologist, working on a large ecological system and having no experience in model building, should work out a mathematical description of his problem and bring it to a programmer. There is a good chance that the biologist has simplified part of the mathematics, which would have given no difficulty to the programmer, and so has unnecessarily neglected part of the available information. The assumption that a certain relationship is linear, although it is known that the relation in fact is non-linear, belongs to these type of errors. The use of a homogeneous system instead of a heterogeneous one can also lead to serious errors.

Another disadvantage might be that the programmer did not completely understand the scope of the problem and has chosen a program structure which, in a later stage of the investigations, causes difficulties if the program has to be modified or adapted to other programs or situations.

3. SUBMODELS

A program on eradication of insect populations should of course take into consideration all of the well-known topics, these being: population density, distribution, flight range, mating places, mating behaviour, host preference, release strategy, etc. [3]. Besides these purely technical topics it is possible to include economics in the program.

To maintain overall insight into such a program, a well-thought-out structure is necessary. It may be worthwhile, therefore, to split the model into submodels, each submodel describing a certain aspect.

The model of Bogyo, Berryman and Sweeney [4] may be regarded as a good example of such a submodel. It has well-defined input variables and a well-defined output. To include such a submodel in the program presented here by Mrs. Wijnands is indeed a simple procedure.

The possibility of exchanging submodels greatly facilitates the general use of a program. It can be adapted in this way to a particular insect.

Exchange of submodels provides a possibility for improving the program gradually. It might, for instance, be necessary to include a submodel for the flight behaviour of an insect; as long as such a submodel is not available, it is possible to use, for the time being, a very simple submodel which only generates an at-random flight distance.

4. COMPUTER LANGUAGES

There are now about 30 computer languages available, most of them being developed for simulation purposes. Some of these simulation languages are unsuitable for biological processes because they are tailored for discrete problems: others are outdated.

Table I shows the frequency of the use of languages as given at the Summer Computer Simulation Conference, Denver, 1970. The AICA Symposium on the Simulation of Complex Systems, Tokyo, 1971 showed a

TABLE I. SIMULATION LANGUAGE USAGE AT THE 1970 SCSC DENVER

FORTRAN (Compiler unspecified)	35
FORTRAN IV-H	4
CSMP	15
PL/1	3
MIMIC	4
EXTENDED ALGOL	2
GPSS	2
DSL	2
DARE	2
SIMSCRIPT	1
SCADS	1
MACRO 9	1
SIMULA	1
CSS/360	1
MOBSSL	1
MICROSYMBOL	1
SIMPL 1	1
DYNAMO	1
ASCENT	1
OPTRAN	1
MPS	1
ECAF	1
TOTAL	82

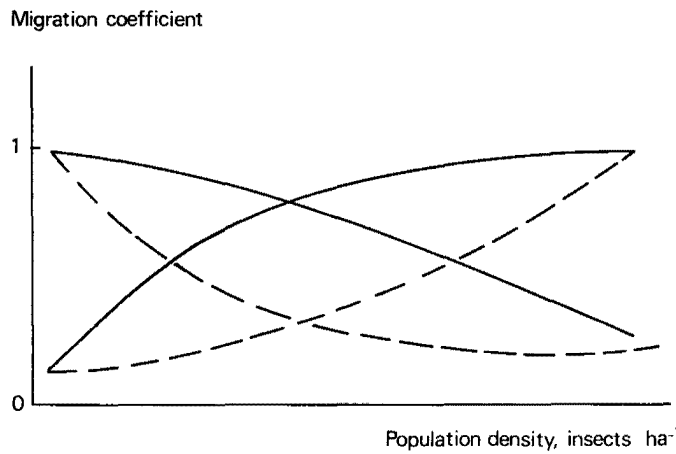


FIG. 3. Use of the simulation model as a tool. The figure shows four possible curves for the migration coefficient as a function of the population density. In four subsequent calculations the results of the use of each of the four curves can be compared. If, on the one hand, the results of the four calculations show hardly any difference, it is evidently not worthwhile in considering the migration coefficient as a function of the population density. If, on the other hand, the results of the four calculations differ considerably, it is clear that the migration coefficient is an important parameter. Field determinations of the coefficient therefore seem to be necessary. In this way a simulation model can be used as a guide for a research program.

similar picture. It appears that both FORTRAN and CSMP are very popular. (CSMP stands for Continuous Similation Modelling Program).

Amongst the other languages: PL1 is very suitable for complex calculations, but less suitable for simulation; CSSL (Continuous System Simulation Language) can be compared with CSMP; DYNAMO has become popular because Forrester of MIT has used this language for his well-known books "Industrial Dynamics" and "World Dynamics".

For an international program, where an exchange of ideas and thus exchange of program parts is intended, one should use the most common languages, these being FORTRAN and CSMP.

FORTRAN has the advantage that it can be used on most computers, CSMP is restricted to computers of the type IBM 360/40[1] and larger. The use of FORTRAN subroutines within CSMP is possible. CSMP has, together with CSSL, the advantage that the program structure is very clear. Even the inexperienced programmer, in this case the entomologist, should soon be able to use the program independently and to understand its structure. For those who want to use the computer as a tool which can be used to guide their further research, this is especially helpful (see Fig. 3). CSMP also contains many standard features, such as: interpolation, integration, instructions for plots and tables and debugging routines. So it is possible for the scientist to do the programming himself with minimum effort and to devote his main attention to the real problem: the development of a suitable model.

---

[1] The minimum machine configuration for CSMP III is a System/360 Model 40G CPU (2040) with Floating Point Arithmetic (No. 4427).

An example of the use of CSMP applied to an onion fly population has been shown by Wijnands-Stäb and Frissel [5]. The actual computer program has been added as an appendix to that paper.

REFERENCES

[1] CLYMER, A.B., BLADSOE, L.J., A Guide to the Mathematical Modelling of an Ecosystem, Ford Foundation sponsored Workshop on Ecological Effects of Weather Modification, Albuquerque, New Mexico, 1969.

[2] KARPLUS, W.J., Computational tools for the modelling of "large" distributed parameter systems, AICA Symp. Simulation of Complex Systems, Tokyo 1971.

[3] LINDQUIST, A.W., "Biological information needed in the sterile-male method of insect control", Sterile-male technique for eradication or control of harmful insects (Proc. Panel Vienna, 1968), IAEA, Vienna (1969) 33.

[4] BOGYO, T.P., BERRYMAN, A.A., SWEENEY, T.A., "Computer simulation of population reduction by release of sterile insects. I. A study of the relative importance of the parameters of a mathematical model", Application of Induced Sterility for Control of Lepidopterous Populations (Proc. Panel Vienna, 1970), IAEA, Vienna (1971) 19.

[5] WIJNANDS-STÄB, K.J.A., FRISSEL, M.J., "Computer Simulation for Genetic Control of Onion Fly Hylemia antiqua (Meigen), Computer Models and Application of the Sterile-Male Technique, this book.

COMPUTER SIMULATION OF POPULATION REDUCTION BY RELEASE OF STERILE INSECTS: II. The effects of dynamic survival and multiple mating

A.A. BERRYMAN, T.P. BOGYO, L.C. DICKMANN
Washington State University,
Pullman, Wash.,
United States of America

Abstract

COMPUTER SIMULATION OF POPULATION REDUCTION BY RELEASE OF STERILE INSECTS: II. THE EFFECTS OF DYNAMIC SURVIVAL AND MULTIPLE MATING.

A previous model described the effects of sterile male releases on wild populations as a function of several discrete parameters. In this model some of these parameters were assumed constant although it was acknowledged that they were in nature dynamic functions of population density. This paper describes simulations using a model which was extended by making the probability of survival as well as the probability of mating dependent on population density. The incorporation of these dynamic population components into the model has important effects on the outcome of sterile male release strategies.

1. INTRODUCTION

In 1967 a mathematical model was published which described the effects of sterile male releases on wild populations as a function of several discrete parameters [1]. This model was of the form

$$N_{g+1} = N_g F_p S_g \sum_{m=1}^{M} P_m \left\{ \sum_{i=1}^{m} E_i [1 - (P_s^i + C_s P_s - C_s P_s^i)] + \sum_{i=m+1}^{m} E_i [1 - (P_s^m + C_s P_s - C_s P_s^m)] \right\} \quad (1)$$

where N_g is the number of wild adults in the gth generation, F_p is the proportion of females in the population, S_g is the proportion of offspring that would normally survive to the next generation, M is the maximum possible number of matings per female, P_m is the probability of a female mating m times, E_i is the number of eggs laid per female after each successive mating, C_s is the competitiveness of sterile sperms (the ratio of the probability of a sterile sperm fertilizing the ovum to the probability of a fertile one fertilizing the same ovum).

P_s is the probability of mating with a sterile male and can be expressed as

$$P_s = \frac{N_s C_m}{N_g M_p + N_s C_m}$$

where C_m, the competitiveness of a sterile male, is the ratio of the probability of a sterile male mating with a female to the probability of a fertile male mating with the same female, M_p is the proportion of males in the population, and N_s is the number of sterile males released. At the time this model was constructed, the main concern was describing the probability of wild females mating with normal or sterilized males under different conditions of multiple matings, sterile male competitiveness, and sterile sperm competitiveness. For this reason certain population variables were assumed constant, i.e., survival, sex ratio, probability of mating, and oviposition, although it was acknowledged that they were in fact dynamic variables which were influenced by an array of factors, in particular population density.

In 1971, Bogyo and co-workers [2] discussed the effects of variations in some of the model parameters on the ratio of sterile to normal males needed to suppress a hypothetical population. Of the parameters tested, variations in survival had the greatest impact; e.g. release ratio 10 : 1 at a survival rate of 0.05, 220 : 1 at a survival rate of 0.95. For this reason we decided to attempt construction of a more realistic survival submodel which could respond to changes in population density.

It is also intuitively apparent that the probability of mating is also a function of population density. As the population density declines following sterile releases, the probability of mating and the incidence of multiple mating decrease due to difficulties in finding mates. We have therefore attempted to incorporate a submodel relating mating probability to population size.

2. THE SURVIVAL SUBMODEL

From a theoretical standpoint one can define the probability of an individual surviving from the egg stage to the adult as a function of population density by making the following assumptions:

(a) Survival decreases in a negatively exponential manner as population density increases.
(b) Population stabilizes as its density approaches the carrying capacity of the environment at which time the replacement rate is unity (i.e., one individual survives for each parent).

Under these assumptions the survival value approaches unity when the population gets very small, and survival approaches zero when the population approaches infinity. Furthermore at the carrying capacity the probability of survival (S_k) can be written as

$$S_k = \frac{1}{E\, F_p\, (1 - P_0)} \qquad (2)$$

where E is the number of eggs laid per female, F_p is the proportion of females in the population and P_0 is the proportion of females failing to mate with a fertile male. In other words, survival at the carrying capacity is equal to one female surviving for each parental female. The form of the survival function under these assumptions is shown in Fig. 1, with the following parametric values:

- K, the carrying capacity = 3 330 000
- E, mean number of eggs laid per female = 100
- F_p, the proportion of females = 0.5
- P_0, the probability of a female mating 0 times = 0 (when the mating submodel is incorporated into the simulation this parameter will be determined as a function of population density).

Thus survival at the carrying capacity

$$S_k = 1/(100 \times 0.5 \times 1) = 0.02$$

When survival is transformed to natural logarithms the relationship takes the form shown in Fig. 2.

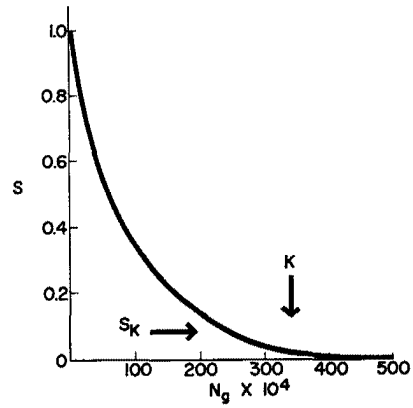


FIG. 1. Theoretical relationship between survival (S) and population density (N_g).

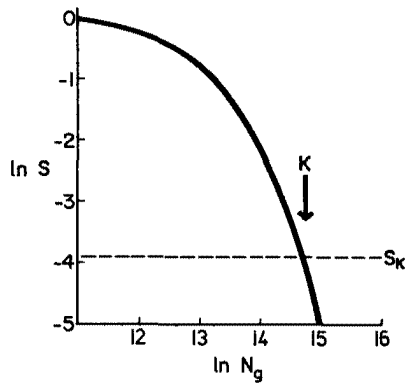


FIG. 2. Theoretical relationship between survival (S) and population density (N_g) on a logarithmic scale.

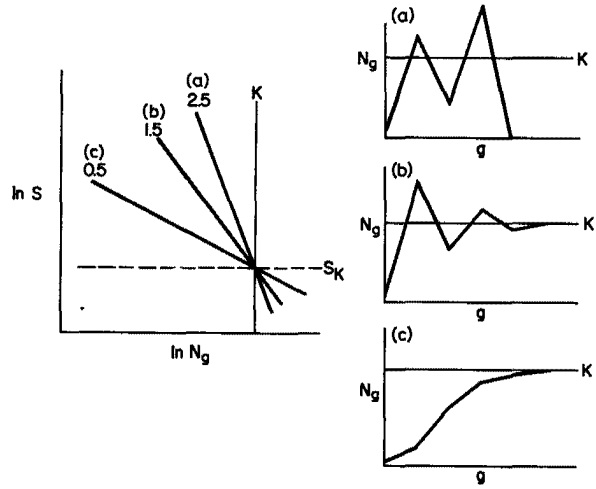


FIG. 3. Relationship between the slope of the survival curve as it intersects the point (K, S_k) and the stability of the population around K. (a) Slope = 2.5, gives undamped oscillations; (b) slope = 1.5, gives damped oscillations; and (c) slope = 0.5, no oscillations.

The important characteristic of the survival curve in defining population stability is its angle of intercept at the coordinates (K, S_k). Specifically, this means that if the rate of change in survival with change in population density is high as it approaches the carrying capacity (slope < -2) then population oscillations of increasing magnitude will occur before population extinction (Fig. 3a), i. e. an unstable equilibrium exists, brought about by overcompensating survival values for changes in population density. This type of system is presumably rather rare in nature but is a common characteristic of simple laboratory systems and population models [3, 4]. When the slope is between -1 and -2 the population stabilizes at the carrying capacity after an initial period of damped oscillations (Fig. 3b), and when greater than -1 the population stabilizes without fluctuation and the growth form resembles the logistic curve (Fig. 3c). These two growth forms are probably more characteristic of natural situations. This theory has been explained in detail by Ricker [5] and MacArthur and Connell [6]. These authors have a slightly different approach from the present paper, dealing with population chances from one point in a generation to the same point in the next (i. e., from egg to egg or adult to adult). The modification of this theory by the present authors was done so that survival could be calculated from egg to adult, a necessity before incorporation into the sterile male model.

The theoretical relationship between survival and population density was simplified for the purposes of the present simulation by assuming a linear relationship between ln S and ln N_g of the form

$$\ln S = \ln S_k + b\,(\ln K - \ln N_g) \qquad (3)$$

with the constraint that the maximum value ln S can take is zero. This constraint was necessary under the linear assumption to ensure that the probability values do not exceed unity.

3. THE MATING SUBMODEL

Our second objective was to construct a model describing the probability of multiple mating as a function of population density. We based this model on assumptions that the mean number of matings was an exponential function of population size, that matings occurred at random, and that the mean number of matings cannot exceed a certain fixed maximum which occurs at the carrying capacity.

Under these assumptions the mean number of matings in the gth generation, $\bar{M}_g$, can be expressed as (Fig. 4)

$$\bar{M}_g = \frac{\bar{M}_{max} \ln N_g}{\ln K} \tag{4}$$

where $\bar{M}_{max}$ is the maximum mean number of matings occurring at the carrying capacity. We had to impose the condition that when $N_g \geq K$, $\bar{M}_g = \bar{M}_{max}$.

Assuming that the number of times a female insect mates is a random variable with a Poisson distribution, the probability of a female mating m times is

$$P_m = \frac{\bar{M}_g^m}{m!\, e^{\bar{M}_g}} \tag{5}$$

and the probability of a female never mating during her lifetime is

$$P_0 = e^{-\bar{M}_g}$$

P_m will be very small when m is very large. In our simulations we truncate the series $\sum_{m=1}^{\infty} P_m = 1$ when P_m becomes negligibly small.

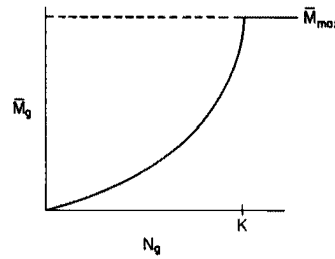


FIG. 4. Hypothetical relationship between the mean number of matings in a population ($\bar{M}_g$) and population density with a mean multiple mating threshold ($\bar{M}_{max}$).

4. INTEGRATING THE SUBMODELS

We have chosen to use an equation of moderate complexity to describe the sterile male principle, Eq. (7) from Berryman [1].

$$N_{g+1} = N_g F_p E S_g \sum_{m=1}^{M} P_m [1-(P_s^m + C_s P_s - C_s P_s^m)] \qquad (6)$$

In this model we assume that mating ceases after the female insect begins ovipositing. The symbols are the same as those used in Eq. (1).

A computer program was written to integrate the two submodels into this equation. The submodels were set up as subroutines which were called by the main program whenever survival or mating probabilities were required in solving Eq. (6). A variety of situations were then simulated to examine the influence of the new components of the model on the outcome of hypothetical sterile release programs.

In all simulation runs the following input parameters remained fixed:

(a) Carrying capacity = 3 333 000 per unit area
(b) Mean eggs laid per female = 100
(c) Sex ratio was 1 : 1
(d) Maximum mean number of multiple matings = 2.4
(e) Competitiveness of sterile males and sterile sperm equal to wild males and fertile sperm.

4.1. Simulation No. 1

Operating conditions:

(a) Survival model has the slope of the curve relating ln S to ln N_g set at 0.5.
(b) Multiple mating component included with $\bar{M}_{max} = 2.4$.
(c) No sterile males released.

Results: Figure 5a shows the behaviour of the population when survival compensation results in a damped "logistic" growth curve. This type of situation would probably occur in nature when rigid "territoriality" or "contest"-type competition occurred for limited resources; e.g. a set number of nesting sites, only one larva develops per unit of food, etc. In this system the functional, or breeding population never exceeds the carrying capacity and the utilization of environmental resources is highly efficient.

4.2. Simulation No. 2

Operating conditions:

(a) Survival model has the slope of the linear portion of the survival curve set at 1.5.
(b) Multiple mating model included
(c) No sterile male releases.

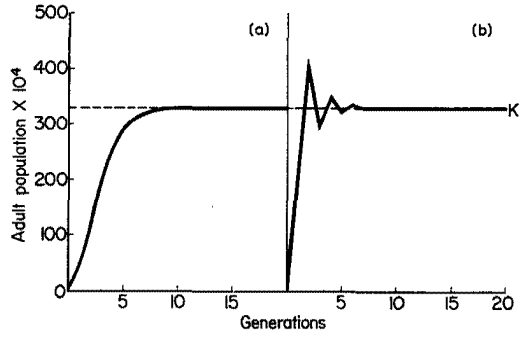


FIG. 5. Population growth when the survival curve has a slope of (a) 0.5 and (b) 1.5, showing effects on population stability at the carrying capacity.

Results: Figure 5b shows that the population undergoes a series of damped oscillations for six generations before stabilizing at the carrying capacity. In this system the population can exceed the carrying capacity but in so doing incurs overcompensating mortality which drives it below the carrying capacity. However, a survival value is eventually attained which stabilizes the population. Similar situations may occur in nature where a "scramble" type of competition for limiting resources is prevalent; i. e. when organisms utilize resources without concern for the future requirements for survival, thus denuding or denaturing their own environment.

4.3. Simulation No. 3

Operating conditions:

(a) Probability of survival is held constant at 0.1
(b) Mean number of multiple matings is held constant at 2.4 for all generations
(c) Prerelease population is held constant at the carrying capacity
(d) Sterile males are released at a constant rate per generation (4 : 1 ratio of sterile to wild males in the initial release or 6 666 000 sterile males per generation).

Results: This is essentially a control simulation based on the assumptions inherent in the original model [1]. As a result of continued sterile male releases the population declined to extinction in nine generations (Fig. 6a).

4.4. Simulation No. 4

Operating conditions:

(a) Dynamic survival model was used with the slope set at 0.5
(b) Multiple mating was held constant with the mean maximum number of matings at 2.4

(c) Sterile males were released at a constant rate of 4 : 1 (4 steriles: 1 normal) in the initial release (= 6 666 000 sterile males per generation).

Results: Continuous sterile male releases resulted in a population decline to extinction in 15 generations (Fig. 6b). The form of the decline curve, however, was considerably different from that when survival was fixed. Initially the decline rate was much higher due to a lower survival rate, but as the population density was reduced, compensation in survival caused a slower rate of decline.

4.5. Simulations No. 5-7

Operating conditions:

(a) Dynamic survival model was used with a slope of 0.5
(b) Probability of multiple mating was dependent on population size with a maximum mean number of matings at 2.4
(c) Sterile males were released at a constant rate dependent on the ratio of sterile to normal males in the initial release:

5: Ratio 4 : 1 = 6 666 000 sterile males per generation
6: Ratio 1 : 1 = 1 666 500 sterile males per generation
7: Ratio 0.5 : 1 = 833 250 sterile males per generation.

Results: Figure 7a shows the reduction curves for the three different simulations. At a release rate of 4 : 1 extinction was achieved in nine generations. At a release ratio of 1 : 1 the population was still in existence after 80 generations although it was still slowly decreasing. At a 0.5 : 1 ratio

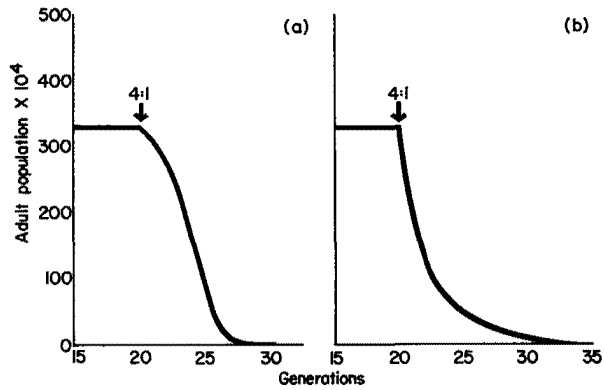


FIG. 6. Population decline to extinction with the continued release of a constant number of sterile males amounting in the initial release generation to 4 sterile males to 1 fertile male, (a) when the probability of survival is constant at 0.1, and (b) when dependent on population size with the slope of 0.5.

the population decreased but became stabilized at a new carrying capacity and extinction was never achieved. With this survival model the reduction curves for both adults (or surviving larvae) and larvae entering this stage (hatching larvae) were essentially similar, and both were reduced below their normal carrying capacity by sterile male releases. The sterile male release acted as a conditioning factor, in the sense that it set the level of population persistence and stability or the rate of decline to extinction. Compared with simulation No. 4 (Fig. 6b) where the same parameters were used, but with constant probabilities of mating, the rate of decline in this (No. 5) simulation was faster. This illustrates the effect of "underpopulation" on the probability of mating; i. e., as the population becomes sparse the individual adults have increased difficulty finding mates.

4. 6. Simulations No. 7-9

Operating conditions:

(a) Dynamic survival model was used with a slope of 1. 5
(b) Probability of multiple mating was dependent on population size with the maximum mean number of matings 2. 4
(c) Sterile males were released at constant rates of the initial population:

7: Ratio 4 : 1 = 6 666 000 sterile males per generation
8: Ratio 40 : 1 = 66 660 000 sterile males per generation
9: Ratio 50 : 1 = 83 325 000 sterile males per generation.

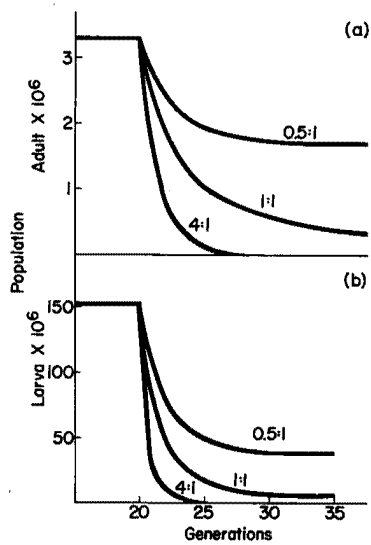


FIG. 7. Population reduction curves following release of different ratios of sterile to normal males into a population where the slope of the survival curve is 0. 5; (a) = adult population, (b) = larval population.

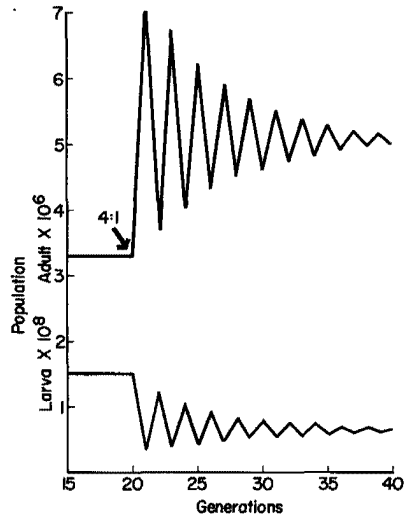


FIG. 8. Behaviour of a population in which the survival curve has a slope of 1.5 after continuous release of sterile males, initially at a 4 : 1 ratio.

Results: Release of a 4 : 1 ratio of sterile to normal males caused about a 57% decline in the young larval population but, owing to the increased probabilities of survival, the surviving adult population increased by 55% (Fig. 8). Introduction of sterile males also resulted in population oscillations of considerable magnitude although damping action eventually stabilized the population.

Increasing the ratio of sterile to wild males in the initial population to 40 : 1 resulted in an 83% decrease in the young larval population and a 67% increase in the adult population (Fig. 9). The initial effect was a drastic reduction in the larval population followed by a recovery phase, a period of population oscillations, and eventual stability. The adult population was not reduced at any time below the original carrying capacity.

Population extinction was only achieved after the ratio of sterile to normal males was increased to 50 : 1. Under this release strategy population decline to extinction occurred after seven generations (Fig. 10).

5. DISCUSSION

In this paper an attempt has been made to simulate, in a rather general way, the effects of releasing sterile males into insect populations which have built-in density-dependent survival probabilities. We have also included a general model of under-population effect resulting in decreased mating frequencies at low population densities.

These simulations should not be taken as representative of actual insect populations, but rather as illustrative of some possible outcomes of sterile male releases.

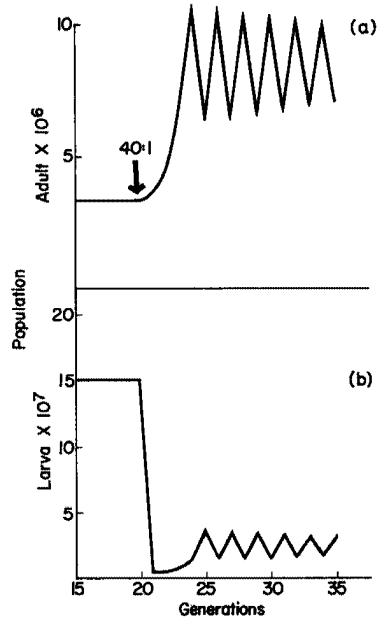


FIG. 9. Behaviour of a population in which the survival curve has a slope of 1.5 after continuous release of sterile males initially at a 40 : 1 ratio.

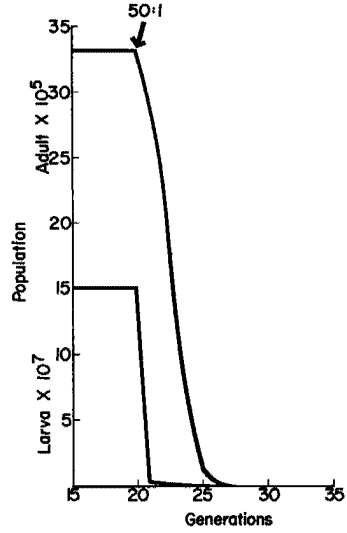


FIG. 10. Decline of a population (survival curve slope 1.5) to extinction following continuous release of sterile males initially at a 50 : 1 ratio.

Under the assumptions inherent in our generalized models, our simulations lead us to the conclusion that release of sterile males into a wild population will invariably result in the reduction of the hatching larval population, but may cause a decrease or an increase in the surviving larval population (= adults). The response behaviour of the population is qualified by the effects of population density on compensatory survival. When the rate of change in survival with change in population density is high, the recovery potential of the population following sterile release is correspondingly high and the release ratio must be significantly increased to ensure population extinction. When the compensatory survival rate is low a reduced release strategy may be employed.

It is apparent that our models are highly oversimplified and that the behaviour of natural insect populations will undoubtedly deviate in varying degrees from our simulations. Insect populations may compensate at different rates at different population densities; e. g. at high densities the compensation rate may be lower than at low densities. Furthermore, our model is based on an assumption of instantaneous compensation, more commonly called "perfect" density dependence; e. g. competitive struggle for food and space. In other words, compensation in survival for changes in population density is governed by the density of the current generation. Most insect populations are regulated by an array of mortality factors, some of which act in a "delayed" density-dependent manner; e. g. parasites, predators and disease, whose effect is at least partially dependent on the densities of preceding generations. The effects of these forces on the behaviour of populations following sterile releases should be the subject of further investigations.

Based on these simulations we have the following comments on some of the current sterile male programs:

(a) It is evident that sampling the adult population alone, a characteristic of most programs, may be misleading in evaluating the outcome of release strategies. In some instances the adult population may increase even though the release has been fairly successful in reducing larval populations. Ideally, sampling should include larval hatch as well as adult population density.

(b) Decisions on optimum release strategies will be difficult or impossible without an estimate of the recovery potential of the population. Such an estimate may be obtained by reducing a natural population and measuring survival rates as the population returns to its carrying capacity. Reduction may be achieved by a sterile male release, insecticide treatment, etc. The slope of a log log plot of survival on population density will provide an estimate of the required parameter.

(c) The commonly accepted premise that the sterile male principle of insect control is most effective at low populations may be at least partially in error. It may be true that smaller absolute numbers of sterile insects are required to deal with naturally sparse populations. However, the idea that the preliminary reduction of a naturally dense population with insecticides will increase the efficiency of the release program may be misleading. If instantaneous compensatory survival is inherent in the population, huge increases in the release ratio may be required to overcome the recovery potential of the population. The total number of insects needed for the initial release may be almost as high as that required to combat a population that had not been suppressed, although the number of releases to extinction may

be reduced. All the reduction curves resulting from our simulations show an initially rapid decrease in population following sterile releases, but the rate of decline gets slower and slower as the population nears extinction. This indicates that the method is less efficient at low population densities, although it may be comparatively superior to many other conventional methods such as insecticides.

If this study has achieved nothing else, we hope it has illustrated the necessity of detailed population studies in conjunction with sterile release programs. We believe that the blind, trial-and-error approach in deciding release strategies is wasteful both of time and money and may often lead to abandoning an otherwise productive program if the consequences of the release are not clearly understood. We think it is essential that some estimate is obtained of the recovery potential of the population, i.e. the rate of change in compensatory survival for changes in population density. Even a crude estimate would give the decision-maker some predictive ability, while an estimate based on sound quantitative data would allow rational decisions to be made on release strategies for given expectations of outcome.

The inclusion of a dynamic model relating the probability of multiple mating to population density had little effect on the outcome of sterile male release strategies. When this component was used, population reduction to extinction occurred more rapidly owing to increased frequency of mating zero times at low population densities. However, most insect species possess mechanisms for bringing the sexes together (sex pheromones, etc.) and thus the assumption of a Poisson distribution for the number of matings may not be quite realistic. This component of the model does not decisively influence the outcome of sterile releases and thus its precise description does not seem essential for decision-making on sterile insect release strategies.

REFERENCES

[1] BERRYMAN, A.A., Mathematical description of the sterile male principle, Can. Entomol. 99 (1967) 858.

[2] BOGYO, T.P., BERRYMAN, A.A., SWEENEY, T.A., "Computer simulation of population reduction by release of sterile insects. I. A study of the relative importance of the parameters of a mathematical model", Application of Induced Sterility for Control of Lepidopterous Populations (Proc. Panel Vienna, 1970), IAEA, Vienna (1971) 19.

[3] HUFFAKER, C.B., Experimental studies on predation: Dispersion factors and predator-prey oscillations, Hilgardia 27 (1958) 343.

[4] NICHOLSON, A.J., The balance of animal populations, J. Anim. Ecol. 2 (Suppl.) (1933) 132.

[5] RICKER, W.E., Effects of compensatory mortality upon population abundance, J. Wildl. Mgmt 18 (1954) 45.

[6] MacARTHUR, R.H., CONNELL, J.H., The Biology of Populations, John Wiley and Sons, Inc., New York (1966) 135.

AN APPROACH TO MODELLING SPATIALLY HETEROGENEOUS POPULATIONS AND THE SIMULATION OF POPULATIONS SUBJECT TO STERILE INSECT RELEASE PROGRAMS

C.F. WEHRHAHN
Institute of Animal Resource Ecology
and Department of Zoology,
University of British Columbia,
Vancouver, B.C.
Canada

Abstract

AN APPROACH TO MODELLING SPATIALLY HETEROGENEOUS POPULATIONS AND THE SIMULATION OF POPULATIONS SUBJECT TO STERILE INSECT RELEASE PROGRAMS.

Heterogeneity in density may be present at the start of an insect control program and is subsequently generated by sampling of successful parents and by variation in family size. This heterogeneity is markedly accentuated with time by a sterile insect release program. Of particular interest is the fact that models which do not take into account spatial heterogeneity in density provide very erroneous predictions of the total number of fertile insects present at any time. They also suggest "optimal" control strategies which are in error. Because variation in density is eroded by diffusion of insects, those species which have moderately high powers of dispersal are easiest to eradicate.

1. INTRODUCTION

Most ecologists who construct simulation models assume that ecological systems can be treated as spatially homogeneous units. Their implicit belief is that when a whole ecological system is of interest, averaging relationships over space enables them to construct models which accurately predict changes in state of the whole system. This may be true for linear systems and for systems with very little spatial variation in important parameters and variables. Otherwise, serious errors in prediction can occur.

In this paper I shall discuss, in detail, the considerations which must be taken into account in developing simulation models of spatially heterogeneous ecological systems. I shall then develop a reasonably general format for constructing such models and use it to simulate populations inundated by sterile insects. I shall then assess the magnitude of the errors which are made when the same systems are simulated by the more popular deterministic models. Finally, I hope to demonstrate that the insights and predictions which can be obtained are qualitatively different and far more useful than those obtained from deterministic models.

2. GENERAL CONSIDERATIONS

To an entomologist contemplating the eradication of a pest in a region, the "ecological system of interest" encompasses the entire region or, if pests in individual fields are monitored, one or more of the fields. In either case, population processes are likely to occur in much smaller spatial theatres – population events in one corner of a region are unlikely to have immediate effects on what happens elsewhere. If the region of interest to an entomologist is large, relative to neighbourhoods in which population processes occur, it is not practicable to simulate the entire system at the necessary level of resolution, nor is it desirable. One wants a concise and insightful way to characterize the state of the population at any time. In a spatially distributed population, there is variation in the number of animals from place to place, even in the absence of environmental heterogeneity. One is not really interested in the exact number of animals in each locale. The probability distribution of animal numbers for neighbourhoods of a given size serves to describe the population in a natural and convenient way. As shall be seen later, it is also sufficient to provide the information and insights that are needed.

In constructing a model, one chooses a sufficiently large spatial scale so that events far from the boundary of the area represented in the model have negligible effects on processes near the centre. Aside from this, one proceeds in much the same way as when modelling deterministic systems. One decides which variables are necessary to characterize the system adequately. Then a model is constructed in which changes in state variables for each local neighbourhood are functions of the state variables and of forcing variables which vary with time [1]. For ecological systems, the forcing variables are usually determined by temperature and other factors extrinsic to the system which can, in principle at least, be found empirically as time proceeds. One question a model builder must ask is whether a system is best formulated as a set of differential equations or as a set of difference equations. In engineering and the physical sciences, the former formulation is the natural one for the vast majority of problems. This is not the case in ecology. For example, in temperate areas some insects have one generation each year and a discrete generation model is appropriate. Other species have several reasonably well synchronized generations each year. Again, a difference equation model is appropriate.

Consider now the situation where components of a system are capable of diffusing spatially; and this is certainly the case for insects. One approach is to use an "individual oriented" Monte Carlo model. This kind of model has been used to investigate problems in ecology [2]. Each individual is assigned a name or identifying number and its position is recorded at all times. The position of a particular individual after dispersal is determined by obtaining a random value from a dispersal-displacement distribution and moving the individual to the indicated position. A slight variant of this procedure is to represent an area by a two-dimensional grid network with a finite number of cells. The individuals within a cell are not assigned identifying numbers. Dispersal is simulated by drawing for each individual a random value from a dispersal-displacement distribution and moving it to the indicated cell. Both of these procedures are practicable when population numbers are small, but require the calculation of an exorbitant number of pseudorandom numbers if populations are large.

The simulation model which I describe in this paper is based on a Monte Carlo procedure which does not involve the manipulation of individual insects. One first calculates grid cell to cell transition probabilities. Then, using an appropriate algorithm, one determines the proportion of individuals in a cell which stay in the cell or go to each of the neighbouring cells. In this procedure few more calculations are required when population numbers are high than when they are low. This constitutes a distinct advantage for modelling insect populations which change in numbers by several orders of magnitude over the course of an eradication program. The procedure provides results which are very nearly identical to those obtained when the previously mentioned Monte Carlo methods are used.

3. FORMULATION OF A FINITE DIFFERENCE EQUATION MODEL TO SIMULATE A POPULATION SUBJECT TO A STERILE MALE INSECT CONTROL PROCEDURE

For convenience, the following population processes are considered to occur sequentially.

3.1. Mating

The probability that a female mates with a fertile male is given by the equation

$$P_f = N_f/(N_f + wN_s)$$

where N_f and N_s are the number of fertile and sterile males in a grid cell, respectively, and w is the "relative mating success" of sterile males. Females are assumed to mate only once. If multiple mating occurs, modifications should be considered.

3.2. Production of juveniles and breeding adults

Ideally, one should have at one's disposal the distribution of family sizes for low-density populations of the kind amenable to control by male sterile programs. Instead, for the sake of simplicity, two extreme cases will be considered. (1) Species which lay eggs in many different sites: For such insects, the distribution of family sizes may, as a first approximation, be assumed to be Poisson. Variation in egg-laying capacity and mortality during the egg-laying period will, of source, tend to inflate the variance in family size. (2) At the other extreme are species which put all of their eggs in one basket. Their egg masses are often completely destroyed by predators, parasites, etc. In this case one lets G be the probability that an egg mass escapes destruction.

Mating, production of juveniles and survival to the adult breeding stage are all incorporated in the subroutine called RECRT listed in the Appendix. The input to the subroutine are the parameters K_1, K_2, K_3, W and G, and the numbers of individuals of various kinds in each grid cell. K_2 and K_3 are zero if survival is independent of density. K_1 is the intrinsic rate of increase for unsterilized members of the population.

The recruitment process incorporated in RECRT is very simplistic and would be realistic only for a few kinds of insect populations. It is my belief that this part of a simulation model is very dependent on the biology of the species under consideration. Consequently, RECRT should not be considered inviolable.

3.3. Dispersal

Let $g(x, y)$ be the probability density function that an individual will move from point $(0, 0)$ to point (x, y). The probability that an individual will move from somewhere in the cell centred at $(0, 0)$ to somewhere in the cell centred at (x, y) is

$$\int_{-\Delta x/2}^{\Delta x/2} \int_{x-\Delta x/2}^{x+\Delta x/2} \int_{-\Delta y/2}^{\Delta y/2} \int_{y-\Delta y/2}^{y+\Delta y/2} g(x+x', y+y')\, dy\, dy'\, dx\, dx' \tag{1}$$

In general, the grid which one has constructed will represent only a small part of the area of interest. Therefore, one needs to determine the number of animals dispersing into each grid cell from outside the boundary of the grid. If densities are equal, the expected number of individuals moving to a cell from any neighbourhood outside the grid is exactly the same as the expected movement in the reverse direction. Let N be the number of animals outside the grid for each unit of area equal in size to a grid cell. Furthermore, let (x, y), (x^*, y), (x, y^*) and (x^*, y^*) define the corners of the grid relative to a grid cell centred at $(0, 0)$. Then the expected number of animals moving to the cell from outside the grid is

$$N - N \int_{-\Delta y/2}^{\Delta y/2} \int_{y}^{y^*} \int_{-\Delta x/2}^{\Delta x/2} \int_{x}^{x^*} g(x+x', y+y')\, dx\, dx'\, dy\, dy' \tag{2}$$

The actual number moving to a cell should have a Poisson distribution with this mean.

If dispersal involves many random movements, then the dispersal distribution will be nearly normal [3] and equal to

$$g(x, y) = (\tfrac{1}{2}\pi S^2) \exp\{-(x^2+y^2)/2S^2\}$$

where S is the standard deviation of dispersal distance. The assumption of normal dispersal may not always be reasonable. I suspect, however, that simulation results are not highly sensitive to deviations from normality. If x and y are standardized and normal dispersal is assumed, expression (1) reduces to

$$\int_{-\Delta y/2}^{\Delta x/2} \left\{ F(x+\Delta x/2+x') - F(x-\Delta x/2+x') \right\} dx' \int_{-\Delta y/2}^{\Delta y/2} \left\{ F(y+\Delta y/2+y') - F(y-\Delta y/2+y') \right\} dy' \qquad (3)$$

where F denotes the cumulative normal distribution and Δx and Δy are the x and y grid interval lengths, respectively. Formula (2) reduces to

$$N - N \int_{-\Delta x/2}^{\Delta x/2} \left\{ F(x^*+x') - F(x+x') \right\} dx' \int_{-\Delta y/2}^{\Delta y/2} \left\{ F(y^*+y') - F(y+y') \right\} dy' \qquad (4)$$

Let N_j individuals be present initially in the j-th cell and P_{jk} be the probability that an individual will move to the k-th cell. Then the expected number of individuals moving to the k-th cell is $N_j P_{jk}$. The number of individuals actually moving to the k-th cell will be approximately normally distributed with variance $N_j P_{jk}(1-P_{jk})$. If N_j' of the original N_j animals remain after transfers have been made to cells $1, 2, \ldots, k-1$, one transfers to the k-th cell a random number of individuals from a normal distribution with mean $N_j' P_{jk}'$ and variance $N_j' P_{jk}'(1-P_{jk})$, where

$$P_{jk}' = P_{jk} \Big/ \sum_{i=1}^{k-1} P_{ji}$$

This procedure ensures that the expected mean and variance of numbers transferred to cells is independent of the order in which recipient cells are chosen.

Dispersal is simulated by the subroutine called DISPR which is listed in the Appendix. Prior to using DISPR, the subroutine SUBP must be called. It determines cell-to-cell transition probabilities as well as probabilities of transition to each cell from outside the grid.

4. IMPLEMENTATION OF THE MODEL

The subroutine RUN1, listed in the Appendix, simulates population change on a grid network over the course of a control program. Because of the Monte Carlo nature of the model, no two runs will provide identical output. The input to RUN1 consists of the parameters necessary to describe the dynamics of the population, including, of course, the standard deviation, S, of dispersal distance. The input also includes the mean density (number per thousand M^2) of the initial wild population and the number of sterile

males released per thousand M^2. The unit of length does not matter; M can stand for a metre, a mile, or even a 10-yd interval. The last array of input is the density of insects outside the boundary of the grid for each generation of the control program.

The basic function of RUN1 is to call the subroutines described previously for each generation of a control program and to provide information about the state of the population at any time. It performs one further function and that is to generate initial variability in the population on a grid. Even in homogeneous habitats, sampling effects will cause variability in the density of insects from local neighbourhood to neighbourhood. For simplicity, I assumed that populations were maintained at a uniform mean density for a number of generations by natural regulatory factors or by a biological or insecticide control program. If, in a particular situation, the course of population change is known, the necessary changes in RUN1 are easy to make.

The density of insects outside the grid boundary at any time is not known a priori. One can provide RUN1 with initial "guesstimates" based on deterministic calculations of the usual kind. One can then call RUN1 a large number of times and calculate the mean density in the central grid cells at all times. This will provide improved estimates of boundary densities. The procedure can be repeated until satisfactory mean population numbers are obtained.

5. RESULTS

To illustrate the nature of the results obtained from my simulation model, I considered a population with initial density of 10 individuals of each sex per 1000 M^2, potential rate of increase of five fold per generation and standard deviation of dispersal distance of S = 31.62 M. Each generation, one hundred sterile insects of each sex were assumed to have been released per 1000 M^2. The number of fertile females remaining in three locations, each 10 000 M^2 in area, are presented in Fig. 1. Deterministic mean numbers are indicated. Two things are apparent: no two simulation runs give identical results, and large deviations from deterministic means occur.

Figure 2 illustrates the effect of differences in the initial number of insects per unit area, for a fixed dispersal distribution. It is apparent that the error in deterministic predictions is much more severe for low-density than for high-density populations. In extreme cases, deterministic predictions underestimate the numbers of surviving insects by 10 orders of magnitude.

The area of a neighbourhood, for any useful definition of the word, should be related to the standard deviation of dispersal distance. This means that one can view the results in Fig. 2 in an alternative way. The results can be used to compare control programs involving species which differ in standard deviation of dispersal distance in the ratio $1 : \sqrt{10} : 10$ but have the same initial density.

An important implication follows. For those species which have naturally sparse populations, there has long been a premium on the ability to travel great distances and to find distant mates. This is not necessarily so, and I suspect is usually not so, for species which have dense populations. It

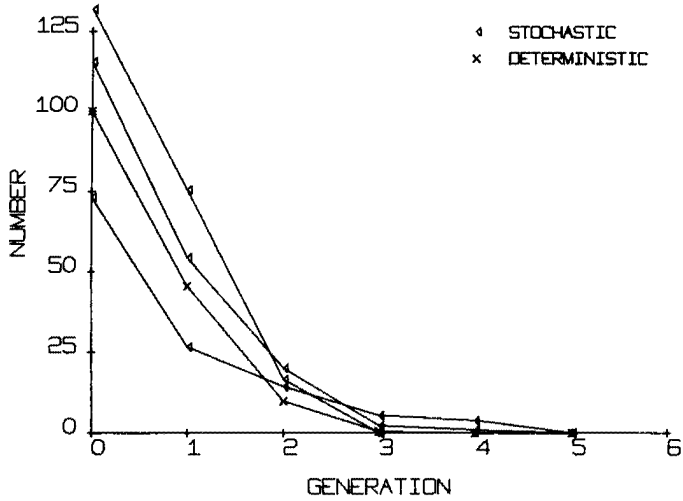


FIG. 1. Number of fertile females at three locations, each of which is 10 000 M^2 in area. Assumed parameters were: S = 31.62 M, G = 1, R = 5, initial density, per sex, of N = 10/1000 M^2, and 100 sterile males/1000 M^2.

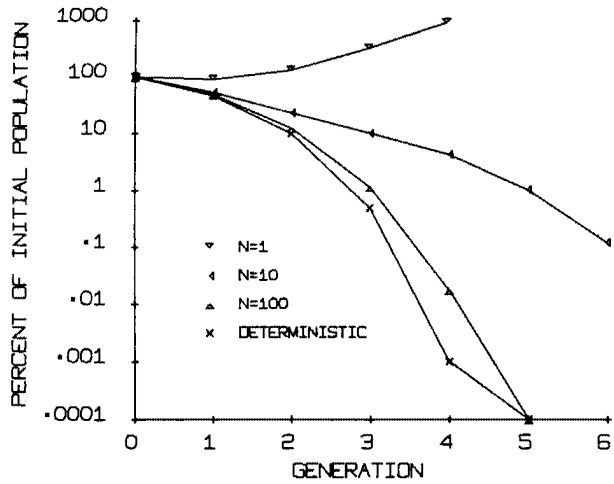


FIG. 2. Population remaining for initial densities of 1, 10 and 100 insects, of each sex, per 1000 M^2 inundated each generation by 10 times as many sterile insects. Assumed parameters are: S = 31.62 M, R = 5, and G = 0.1.

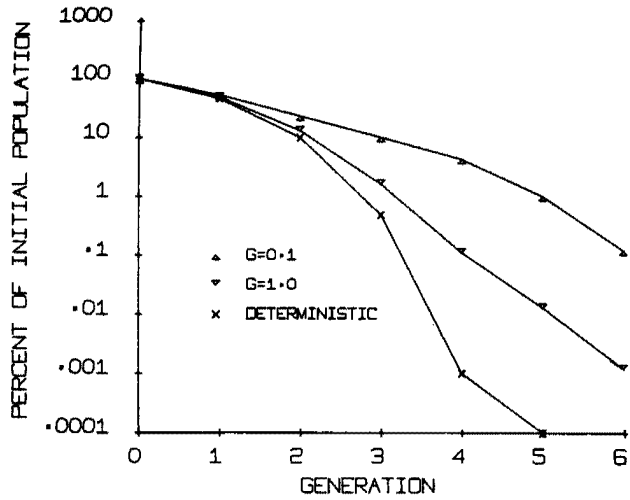


FIG. 3. Population remaining for G = 1.0 and 0.1. Assumed parameters are: S = 31.62 M, R = 5, initial density of N = 10/1000 M^2, and release of 100 sterile insects/1000 M^2.

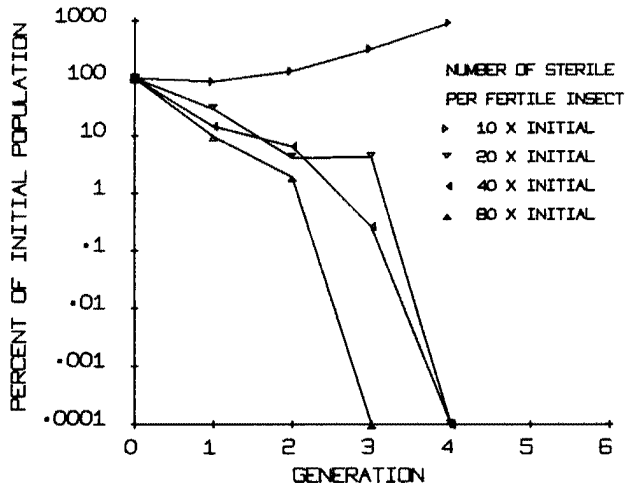


FIG. 4. Population remaining for release ratios of 10, 20, 40 and 80 times the initial population. Assumed parameters are: S = 31.62 M, R = 5, G = 0.1 and initial density, for each sex, of 1 per 1000 M^2.

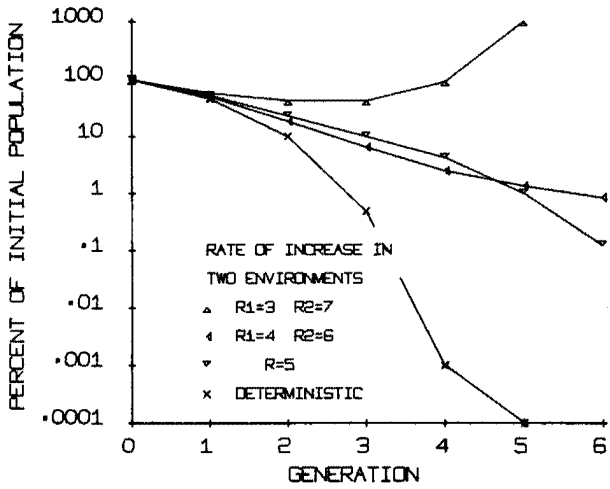


FIG. 5. Population size for levels of spatial heterogeneity in the potential rate of increase, R. Assumed parameters are: S = 31.62 M, R = 5, G = 0.1, initial density for each sex of 10 per 1000 M^2, and 10 times that many sterile insects released each generation.

follows, therefore, that a dense population which has been reduced to the same density as a naturally sparse one could be very much more difficult to eradicate.

The rate at which heterogeneity in density is produced is influenced to a large extent by the amount of variation in family size. Figure 3 presents simulation results for two extreme cases. The first, with G = 1.0, corresponds to a hypothetical insect which lays a large number of eggs, or many egg masses, in different sites. Family size will, therefore, have a Poisson distribution with a mean and variance equal to twice the potential rate of increase of the population. The second extreme, with G = 0.1, corresponds to insects which lay only one egg mass and the probability of its destruction is 0.9.

The percentage of fertile insects remaining for several different release ratios is presented in Fig. 4. The reduction in efficiency of a control program due to spatial heterogeneity in density can be compensated for by doubling the number of sterile insects released. This is not necessarily the case when there is "coarse-grained" spatial heterogeneity in initial density or in potential rate of increase. The effect of coarse-grained spatial heterogeneity in potential rate of increase is illustrated in Fig. 5. Two equally common habitats were assumed to occur.

6. DISCUSSION

Certain kinds of predictions about the course of population change can be obtained both from spatially stochastic and from deterministic models. In particular, it is possible to predict the mean number of fertile females at any time during the course of a sterile insect control program. A deterministic model may underestimate this number by up to 10 orders of

magnitude in the terminal generation of a control program. This result may appear to be counterintuitive to advocates of deterministic models. The explanation is really very simple. Consider the case where a population is divided into a large number of isolated subpopulations with initial number of females D_i in the i-th subpopulation. This case can be dealt with algebraically if one ignores the stochastic factors operative during the course of a control program. Using Knipling's model [4], one finds that the number in the generation after the release of N sterile males per subpopulation will be

$$F_{1i} = D_i \left(1 - \frac{N}{N+D_i}\right) R = \frac{D_i^2 R}{N+D_i} \approx D_i^2/(N/R)$$

for N much greater than D_i.

Next, suppose the mean and standard deviation in subpopulation numbers are $\bar{D} = 10^7$ and $S = 0.5 \times 10^7$, respectively, the rate of increase is $R = 5$, and 50×10^7 sterile males are released in each generation. Then, a deterministic model would predict the mean number of individuals in the second generation to be

$$\bar{F}_1 = \bar{D}^2/(N/R) = 10^{14}/(50 \times 10^7/5) = 10^6$$

However, the true mean is the average of the numbers in the m isolated subpopulations, i.e.

$$\sum_1^m (F_{1i})/m = \sum_1^m (D_i^2/(N/R))/m$$

Invoking a Taylor expansion, one finds

$$F_{1i} = F_1(\bar{D}) + F_1'(\bar{D})\,\Delta D_i + \tfrac{1}{2}F_1''(\bar{D})\,(\Delta D_i)^2 + F_1'''(\bar{D})\,(\Delta D_i)^3/(3 \cdot 2 \cdot 1) + \ldots$$

Thus, the expected F_1 mean is $F_1(\bar{D}) + \frac{1}{2} F_1''(\bar{D})\, S^2 + \ldots$ and, to the F_1 mean of 100 from a deterministic model, one must add the correction factor $\frac{1}{2} F_1''(\bar{D})\ S^2 = \frac{2}{2(N/R)} S^2 = 0.25 \times 10^6$. Hence, the true mean is 25% greater than predicted by a deterministic model, even after one generation of a control program. After three generations of a control program, the number in the i-th subpopulation is $F_{3i} = D_i^8/(N/R)^7$. The average number of survivors per population predicted by a deterministic model is $\bar{F}_3 = \bar{D}^8/(N/R)^7 = 10^7/(50 \times 10^7/5)^7 = 1$. Now, the third plus fifth terms in the appropriate series are $S^2 \cdot 28 \cdot \bar{D}^6/(N/R)^7 + S^4 \cdot 210 \cdot \bar{D}^4/(N/R)^7 = 20$.

Therefore, the true mean number of insects remaining after three generations is at least 20 times greater than the number predicted by a deterministic model. The same kind of argument can be used to show that spatial variation in the rate of increase, R, further magnifies the error inherent in deterministic prediction.

The mean number of insects per unit area at the cessation of an insect eradication program is not necessarily very relevant. It is, however, the only kind of information provided by a simulation model which treats the population as a homogeneous unit. It does not, for example, tell the number of pest outbreaks to be expected in an area after the cessation of a control program. To determine this one needs to know the distribution of insect numbers in a neighbourhood of any size. This information can be obtained from the model I have developed. It is then a simple matter to determine the probability that a male is sufficiently near a surviving female to respond to her sex-attractant pheromones or whatever it is that males respond to. This is the kind of information which is required to intelligently monitor a region for pests and to devise a strategy for dealing with outbreaks.

If the purpose of constructing a model is to investigate the feasibility of a control program, then one must face the fact that certain of the most critical parameters vary from generation to generation and from place to place. If the intrinsic rate of increase varies from generation to generation within a year and the same pattern persists from year to year, then very accurate predictions are possible. For most insect populations, I am sure, the critical parameters will vary from year to year. This means that temporal variation will then prevent precise prediction of even such simple population properties as the mean number of insects present. In this case one can base one's simulations on the worst conceivable set of circumstances, as suggested by W. Klassen. The simulations will provide one with an upper limit to the number of sterile insects needed for eradication of a population in a fixed number of generations. Alternatively, they will permit one to determine the number of generations of inundation with sterile insects necessary to ensure eradication of the population.

The model presented in this paper is designed for the simulation of populations with discrete generations. If generations overlap and individuals of one generation do not die as succeeding generations are produced, a modification of the life table approach discussed by J. Monro can be used. All that is necessary is to represent each age class by a new grid network. No changes need be made in the dispersal subroutine. This statement should be qualified since different age classes of insects most likely have different dispersal patterns. One can also extend the modelling procedure to deal with populations subjected to genetic [5] or to combined genetic and sterile insect control programs.

So far only variation in numbers of insects from place to place has been considered. In most real situations there is heterogeneity in a number of important variables. It may be essential to take this into account when constructing a simulation model. If the pattern of environmental variation is highly repetitive, then one can use the grid network to represent small parts of the total area of interest. For each grid cell one must keep track of the values of parameters which vary as well as the densities of different kinds of insects. With this difference, simulation can proceed as before.

A much more difficult problem to deal with occurs if dispersal patterns vary from place to place owing to heterogeneity in the spacing of desirable

host plants and other factors. In this case, the probability that an insect moves from one cell to any neighbouring cell is not a function of distance alone. One way of building a simulation model which takes this into account is to begin by first simulating the dispersal pattern to obtain cell-to-cell transition probabilities. This is feasible only if the dispersal process for the insect is extremely well understood. Mathematical models of the dispersal process can be formulated in several different ways. For example, as continuous time diffusion models [6, 7], in which case solutions should be obtained by means of an iterative implicit integration procedure.

I should like to make one final point which has undoubtedly occurred to all population geneticists concerned with insect control. After cessation of a control program, outbreak populations will result from one or at most two matings. The resulting populations are, therefore, highly inbred. If, in the early generations of a control program, insects are released which are only partially sterilized, then a considerable recessive lethal mutational load will be incorporated into the population. Because of the inbred nature of any new outbreak population, most individuals will be homozygous for one or more lethal genes and fail to survive.

ACKNOWLEDGEMENTS

I am grateful, for helpful discussions, to N. Gilbert, K. Reid, W. Wellington and W. Klassen, for information on the simulation of multi-dimensional diffusion processes, to D.G. Wehrhahn, and, for indispensible assistance, to Betty Anne Wang and Terry Miller.

APPENDIX

SUBROUTINE DOCUMENTATION

Description of parameters

DELX	– The length of each side of a grid cell
NGR	– The number of cells per dimension of a grid network
GRDF	– An NGR × NGR matrix representing the grid network for females
GRDM	– The same as GRDF, but for fertile males
GRDS	– The same as GRDF, but for sterile males
XS	– A three-dimensional array containing the number of fertile females after the dispersal phase, but before reproduction, for five generations preceeding and for all generations of a release program
XMAL	– The same as XS, but for fertile males
W	– Mating success of sterile males relative to wild ones
K1	– The rate of increase of a local population per generation
K2 and K3	– Parameters in Eq.(12) of RECRT, relevant only if the rate of increase is dependent on density; otherwise, they can be set equal to zero
G	– The probability that an egg mass escapes destruction
R	– K1/G

S – The standard deviation (in length units M, where M can be any unit of length) of dispersal distance

P – An NGR × NGR matrix containing probabilities of transition from outside a grid network into grid cells

TPR – An NGR × NGR matrix containing probabilities of transition from cell to cell

GX – A vector containing one-dimensional cell-to-cell transition probabilities; P, TPR and GX are obtained by calling SUBP

NGEN – Number of generations of sterile insect release

DENS – The initial density (number per 1000 M^2, where M can be any unit of length) of each sex

DST – A vector with the density of sterile males for each generation of a release program in elements 6 to 11

BRD – A vector containing the mean density of each sex outside a grid network, for each generation of a release program in elements 6 to 11

Standard library subroutines and functions required[1]

P = **GAUS**(Z) – The cumulative probability, P, of the standardized normal distribution at Z

X = **FRANCN**(O) – Generates a random value from a standardized normal distribution

X = **POISS**(XBR) – Generates a random value from a Poisson distribution with mean, XBR

QSF – A standard IBM numerical integration routine

Subroutine **RUN 1** :

RUN 1 simulates the course of population change in a small area before and during a sterile insect release program

Input parameters:

NGR, DELX, DENS, NGEN, DST, R, W, S, K1, K2, K3, G and BRD

Output:

XS – The number of *fertile females* on grid networks for five generations before and during a release program

XMAL – The same as XS, but for *fertile males*

Remarks:

SUBP – must be called before **RUN 1** is first used

Subroutines and functions needed:

RECRT, DISPR, POISS

[1] Words in bold-face type stand for subroutine names.

Listing:

```
C            *** RUN1    ***

      SUBROUTINE       RUN1(NGR,DELX,DENS,NGEN,DST,R,W,S,K1,K2,K3, GRDF
     1,GRDS,P,TPR,BRD ,XS,XMAL,G,GX)
      REAL N,K1,K2,K3
      DIMENSION DST(20), GRDF(20,20),GRDM(20,20),GRDS(20,20),P(20,20)
      DIMENSION TPR(20,20), BRD(35), XS(20,20,11)
      DIMENSION GX(20)
      DIMENSION XMAL(20,20,11)
C  **** INITIALIZE THE POPULATION ON THE GRID
      DSQ=DELX*DELX
      N=0.001 *DENS*DSQ
      R=K1/G
      DO 4 I=1,NGR
      DO 4 J=1,NGR
      GRDF(I,J)=N
4     GRDS(I,J)=0.0
C  ***FOR   5 GENERATIONS POPULATION REPRODUCES WITH NO INCREASE IN
C     DENSITY.
      GINV=1.0/G
      DO66NG=1,5
      DO 6 I=1,NGR
      DO 6 J=1,NGR
      Y=GRDF(I,J)*G
C  *****  Y IS =SUCCESSFUL FEMALES
      Z=POISS(Y)*GINV
C  *****  Z IS MEAN = ADULT SURVIVORS
      GRDF(I,J)  =POISS( Z)
      IF( NG- 5)  6,7,7
7     GRDM(I,J)=POISS( Z)
6     CONTINUE
      BRDEN=N
      CALL        DISPR (GRDF,NGR,DELX,P,BRDEN,TPR,GX)
      DO 88 I=1,NGR
      DO 88 J=1,NGR
88    XS(I,J,NG)=GRDF(I,J)
      IF( NG- 5) 66,67,67
67    DO 188 I=1,NGR
      DO 188 J=1,NGR
188   GRDM(I,J)=GRDF(I,J)
      CALL        DISPR (GRDM,NGR,DELX,P,BRDEN,TPR,GX)
66    CONTINUE
C  *** MALE STERILE RELEASE PROGRAM
      DO 99 NG=1,NGEN
      NN=NG+5
C   *** DISTRIBUTE STERILE MALES RANDOMLY
      DN=0.001*DSQ* DST(NG)
      DO  8 I=1,NGR
      DO 8 J=1,NGR
8     GRDS(I,J)=POISS(DN)
C  *****MATE AT RANDOM WITHIN GRID  CELLS AND DETERMINE SURVIVAL TO THE
C       BREEDING ADULT STAGE.
      CALL        RECRT(NGR, R, W, K1,K2,K3,GRDF,GRDM,GRDS,G)
C  ***SIMULATE DISPERSAL.
      BRDEN=BRD(NG+5)*0.001*DSQ
      CALL        DISPR (GRDF,NGR,DELX,P,BRDEN,TPR,GX)
      CALL        DISPR (GRDM,NGR,DELX,P,BRDEN,TPR,GX)
      DO 89 I=1,NGR
      DO 89 J=1,NGR

      XMAL(I,J,NN)=GRDM(I,J)
89    XS(I,J,NN)=GRDF(I,J)
99    CONTINUE
      RETURN
      END
```

Subroutine **SUBP** :

SUBP calculates grid cell to cell transition probabilities and puts them in matrix, TPR; it also calculates probabilities of transition into cells from outside the grid and puts them in matrix P

Input parameters:

NGR, DELX, and S

Output:

P, TPR and GX

Subroutines and functions required:

GAUS and **QSF**

Listing:

```
C             *** SUBP    ***

      SUBROUTINE SUBP(NGR,DELX,S,P,TPR,GX)
      DIMENSION P(20,20), TPR(20,20)
      DIMENSION GG(6),GX(20)
C  ****  CALCULATE TRANSITION PROBS TO CELL I,J  FROM OUTSIDE GRID
C***  PROB THAT AN INDIV MOVES FROM CELL K TO OUTSIDE  OF GRID
C      IS 1.0- SUM J (P K TO J ).
      XSTR=NGR*DELX
      SI=1.0/S
      ND=6
      H=DELX*0.2
      HDX=0.5*DELX
      DO 1 K=1,NGR
      X=( K -0.5) *DELX
      V= -0.7*DELX+X
      DO 2 L=1,6
      V=V+H
      GT= GAUS((  XSTR-V) *SI)  -GAUS(-V*SI)
2     GG(L)=GT
      CALL QSF(H,GG,GG,ND)
1     GX(K)=GG(6)/DELX
      DO 3 I=1,NGR
      DO 3 J=1,NGR
3     TPR(I,J)=1.0 - GX(I)*GX(J)
C   ***  PROBABILITY OF DISPERSING J CELLS  IN X AND K CELLS IN YDIRECT
      DO 8 K=1,NGR
      X= (K-1)*DELX
      V= -0.7*DELX
      DO 7 L=1,6
      V=V+H
7     GG(L)=GAUS(( X+HDX-V)*SI)  -GAUS(( X-HDX-V) *SI)
      CALL QSF(H,GG,GG,ND)
8     GX(K)=GG(6) /DELX
      DO 9 I=1,NGR
      DO 9 J=1,NGR
9     P(I,J) =GX(I)*GX(J)
      RETURN
      END
```

Subroutine **DISPR** :

DISPR simulates dispersal within and from outside a grid network

Input parameters:

NGR, DELX, P, TPR, GX, BRDEN and GRDF
BRDEN – *Mean* number of animals outside the grid network per neighbourhood equal in area to a grid cell

Output:

GRDF – The number of animals in each cell of an NGR × NGR grid network after dispersal

Remarks:

The area of grid cells, as determined by DELX, can be large, because transition probabilities derived from expressions (1) and (2) in this paper are precise.

Subroutine required:

KADR

Listing:

```
C            *** DISPR  ***

      SUBROUTINE DISPR (GRDF,NGR,DELX,P,BRDEN,TPR,GX)
C  ***SUBROUTINE  TO SIMULATE DISPERSAL WITHIN A GRID  AND FROM OUTSIDE
      REAL N
      DIMENSION GRD2(20,20), GRDF(20,20), P(20,20), TPR(20,20)
      DIMENSION GX(20)
      DO 1 I=1,NGR
      DO 1 J=1,NGR
1     GRD2(I,J)=0.0
      DO 60 I=1,NGR
      DO 60 J=1,NGR
      N=GRDF(I,J)
      NN=N
      IF(NN.GT.15)GO TO 17
C **** DETERMINE NUMBERS TO BE TRANSFERRED IF N IS SMALL.
      IF(NN.LE.0)GO TO 60
      DO 70 II=1,NN
      CALL KADR(NGR,I,K,GX)
      IF(K.EQ.999)GO TO 70
      CALL KADR(NGR,J,L,GX)
      IF( L.NE. 999)GRD2( K,L)= GRD2( K,L)+ 1.
70    CONTINUE
      GO TO 60
C **** DETERMINE NUMBERS TO BE TRANSFERRED IF N IS NOT SMALL.
17    DIV  =1.0
C  ******CALCULATE CELL ADDRESSES IN ORDER OF THEIR DISTANCE FROM
C     THE DONOR CELL.
C ***  FOR EFFICIENT EXECUTION, AN INITIALIZING ENTRY
C      SHOULD BE MADE AND THE RELATIVE CELL ADDRESSES STORED.
C     THEN INSTRUCTIONS FROM HERE TO STATEMENT 39 NEED
```

```
C     NOT BE REPEATED.
      DO 52 III=1,NGR
      II=III-1
      DO 52 JJJ=1,III
      JJ=JJJ-1
      K=II
      L=JJ
      LD=2
      IF(II-JJ) 30,31,30
31    LD=1
30    DO 52 IORD=1,LD
      GO TO (32,33),IORD
33    K=JJ
      L=II
32    LK=2
      IF(K)35,34,35
34    LK=1
35    DO 52 IK=1,LK
      GO TO(38,37),IK
37    K=-K
38    LF=2
      IF( L ) 51,50,51
50    LF=1
51    DO 52 IL=1,LF
      GO TO (39,40),IL
40    L=-L
39    CONTINUE
C  ****  ADD ADDRESS ADJUSTMENTS TO I AND J.
      KK=I+K
      LL=J+L
C *******  CALCULATE THE NUMBER OF INDIVIDUALS TO BE TRANSFERRED TO KL
      KI=KK-I
      IF(KI) 18,19,19
18    KI=-KI
19    KI=KI+1
      LJ=LL-J
      IF(LJ) 20,21,21
20    LJ=-LJ
21    LJ=LJ+1
      PR=P(KI,LJ)
      PPRIM=PR/DIV
      XBR=N*PPRIM
      SD=SQRT( XBR *(1.0-PR))
      NTR=XBR+SD*FRANDN(0)+0.5
      IF(NTR.LT.0)NTR=0
      N=N-NTR
      DIV=DIV-PR
      IF(KK)53,53,61
61    IF(LL)53,53,62
62    IF(NGR-KK)53,63,63
63    IF(NGR-LL)53,64,64
64    GRD2(KK,LL)=GRD2(  KK,LL)+NTR
53    IF(N.LE.0.0)GO TO 60
52    CONTINUE
60    CONTINUE
C  ***  FLOW FROM GRID EXTERIOR.
      DO 2 I=1,NGR
      DO 2 J=1,NGR
      XBR=BRDEN* TPR(I,J)
      TRAN=POISS(XBR)
2     GRDF(I,J) =GRD2(I,J)+TRAN
      RETURN
      END
```

Subroutine **RECRT** :

RECRT simulates mating, reproduction and survival in one generation for each neighbourhood of an area

Input parameters:

NGR, R, W, G, K1, K2, K3, GRDF, GRDM and GRDS

Output:

GRDF and GRDM

Remarks:

Large grid simulation can lead to errors if the quantities one calculates are non-linear functions of parameters and variables which vary within a grid cell; comments on the corrections needed can be found in the listing.

Function required:

POISS

Listing:

```
C            *** RECRT  ***

      SUBROUTINE RECRT(NGR, R, W, K1,K2,K3,GRDF,GRDM,GRDS,G)
      REAL NST,NFM,NFF,K1,K2,K3
      DIMENSION GRDS(20,20), GRDM(20,20),GRDF(20,20)
C  ***   MATE AT RANDOM WITHIN GRID CELLS AND PRODUCE JUVENILES.
      DO 9 I=1,NGR
      DO 9 J=1,NGR
      NST= GRDS(I,J)
      NFM=GRDM(I,J)
C ****THE PROB. OF A FEMALE BEING FERTILE IS PF=NFM/(NST*W+NFM)
C     NOTE A POSSIBLE PITFALL  IF BREEDING UNITS ARE SMALL
C     LARGE GRID SIMULATION WILL OVERESTIMATE PF BY AS MUCH
C     VAR(NFM)*NST/(NFM+NST)**3,IE. THE ERROR IN PF
C     IS PROPORTIONAL TO 1/N. WHERE N IS THE POTENTIAL NUMBER
C     OF MALES IN AN AVERAGE BREEDING UNIT.
C     THE ERROR DUE TO VARIATION IN NST IS SMALLER AND + IVE.
      DV=NST*W+NFM
      IF(DV.LE. 0.0)GO TO 20
      PF=NFM/DV
  21  AVFF=PF* GRDF(I,J)
C *****NFF IS NU FERTILE FEMALES
      NFF=POISS(AVFF)
C ****SFF IS MEAN NU OF SUCCESSFUL FERTILE FEMALES
      SFF=POISS(G*NFF)
      IF(K3) 12,11,12
12    GRDF(I,J) = ((K1*SFF-K2*SFF**2)/(1.0 +K3*SFF))/G
      GO TO 9
11    GRDF(I,J)=R*SFF
9     CONTINUE
```

```
C****  DETERMINE SURVIVORS TO ADULTHOOD.
       DO 13 I=1,NGR
       DO 13 J=1,NGR
       DJ=GRDF(I,J)
       IF (DJ) 14,14,15
15     X=DJ
       GRDM(I,J)=POISS(X)
       GRDF(I,J)=POISS(X)
       GO TO 13
14     GRDM(I,J)=0.0
       GRDF(I,J)=0.0
13     CONTINUE
       RETURN
20     PF=0.0
       GO TO 21
       END
```

Subroutine **KADR**:

KADR produces (on the basis of the transition probabilities in GX) random cell addresses for one-dimensional movement of individuals

Input parameters:

NGR, I and GX
I – address index for one dimension of a donor cell

Output:

K – Address index for one dimension of a recipient cell

Function required:

FRAND – Generates a random value from a uniform distribution

Listing:

```
C             *** KADR    ***

C ***** SUBROUTINE TO CALCULATE A RANDOM ADDRESS,K,
C       FOR TRANSITION PROBABILITIES  (FROM CELL I) GIVEN
C     IN THE VECTOR GX. IF K LIES OUTSIDE THE RANGE 1 TO NGR ,K IS
C     SET EQUAL TO 999.
       SUBROUTINE KADR(NGR,I,K,GX)
       DIMENSION GX(20)
       NU=NGR-I+1
       PR=FRAND(0.)
       IF(NU.LT.I)NU=I
       P=-GX(1)
       DO 1 M=1,NU
       P=P+2.*GX(M)
       IF(P.GE.PR)GO TO 2
1      CONTINUE
       K=999
       RETURN
2      P=P-GX(M)
       M=M-1
       IF(P.GE.PR)M=-M
       K=I+M
       IF(K.LT.1)K=999
       IF(K.GT.NGR)K=999
       RETURN
       END
```

REFERENCES

[1] PATTEN, B.C., Systems Analysis and Simulation in Ecology, 1, Academic Press, New York (1971).
[2] KITCHING, R., A simple simulation model of dispersal of animals among units of discrete habitats, Oecologia 7 (1971) 95.
[3] WRIGHT, S., Evolution and the Genetics of Populations, 2, University of Chicago Press, Chicago (1969) 303.
[4] KNIPLING, E.F., Possibilities of insect control or eradication through the use of sexually sterile males, J. Econ. Entomol. 48 (1955) 459.
[5] WEHRHAHN, C.F., KLASSEN, W., Genetic insect control methods involving the release of relatively few laboratory-reared insects, Can. Entomol. 103 (1971) 1387.
[6] WACHSPRESS, E.L., Iterative Solution of Elliptic Systems and Applications to the Neutron Diffusion Equations of Reactor Physics, Prentice-Hall, Englewood Cliffs, N.J. (1966).
[7] VARGA, R.S., Matrix Iterative Analysis, Prentice-Hall, Englewood Cliffs, N.J. (1962).

POPULATION SUPPRESSION WITH DOMINANT AND CONDITIONAL LETHAL MUTATIONS
Some important considerations and approaches

W. KLASSEN, J.F. CREECH*
Agricultural Research Service,
U.S. Department of Agriculture,
Washington, D.C.,
United States of America

Abstract

POPULATION SUPPRESSION WITH DOMINANT AND CONDITIONAL LETHAL MUTATIONS: SOME IMPORTANT CONSIDERATIONS AND APPROACHES.

The rate of increase of the population to be suppressed determines the effectiveness of combinations of levels of male sterility and release ratios. When the rate of increase is fivefold, 90% male sterility is effective at fairly low release ratios. By contrast, when the rate of increase is tenfold or greater, the level of sterility must be near 98% to induce a steep downward trend in the target population. The implication of these conclusions for the pilot boll weevil eradication experiment are discussed. Computations are presented to demonstrate the usefulness of the inability to diapause as a dominant conditional lethal trait. Such traits when combined with dominant lethals or with insecticide applications represent a potential powerful and practical tool for suppression of populations. The possible application of these methods is discussed for the pink bollworm in southwestern United States and adjacent areas of Mexico.

1. INTRODUCTION

The eradication of the screwworm from Curacao and from most of the United States continues to be the most outstanding success wrought by a genetic method of population suppression. We hope that this achievement will be matched by others of similar magnitude during the next 10 or 15 years. One decade ago it seemed that useful sterility could not be induced in key insects such as the boll weevil, the codling moth, and Heliothis. Today the prospects are so much brighter that large-scale field tests are in order to determine whether our technology is fully adequate to suppress or eradicate some of our most destructive pests including the corn earworm, the tobacco budworm, the pink bollworm, the codling moth, the cabbage looper, and the tobacco hornworm. Such a test, the pilot boll weevil eradication experiment, is currently underway on a test area of 25,000 acres of cotton centered at Prentiss, Mississippi. Even though the principles underlying the genetic technique are valid, and our technology, organizational structure, management skills, and resources may be adequate, such field tests could fail without an adequate quantitative understanding of the genetic method of population suppression.

2. RELATIONSHIPS BETWEEN RATE OF INCREASE, LEVEL OF STERILITY AND RELEASE RATIO

The theory of using fully sterile males to suppress pest populations has been explained primarily by Knipling (9, 10). In addition, preliminary appraisals of the use of partial sterility in Lepidoptera

* Model Cities Office, 1104 Second Avenue S., Fargo, N.D. 58102, USA.

have been made (5 in press, 11, 14). However, the genetic basis of sterility in this order differs from that in others. Indeed partial sterility appears to be advantageous in Lepidoptera because it is inherited and enhanced in descendants of treated males. We made a preliminary examination of the consequences of using partial sterility in insects in which sterility derives from dominant lethal mutations (6).

In some species, such as the boll weevil, there is difficulty in inducing full male sterility without attendant high mortality, reduction in longevity, or impairment of effectiveness. In such cases, a trade-off between the level of sterility and prolonged effectiveness might be desirable. Whether such a trade-off is feasible cannot be decided without an estimation of the minimum level of sterility in released males required to cause a downward trend in the target population. This problem can be illustrated in relation to the pilot boll weevil eradication experiment.

In order to examine quantitatively the relation between rate of increase, level of sterility, and release ratio, we established a model which assumed that the boll weevil population has been reduced to 1000 males and 1000 females on 200 acres (10 bollweevils of both sexes per acre) and that this population will have no more than five generations per year. We release a constant number of boll weevils per generation and the initial release ratios are 100:1, 50:1, 25:1, and 12.5:1 (treated males: native males); females if released are fully sterile. Level of sterility varies from 90 to 100 percent and rates of increase are 5-, 10-, 20-, and 40-fold.

The computations are shown in Table I. When the rate of increase is fivefold and the initial release ratio is 12.5:1, a downward trend in the population occurs with only 90 percent sterility. However, a sterility level of approximately 95 percent would be required to achieve total suppression within one season. If total suppression could not be achieved on 200 acres unless the population dropped below, say, 30 weevils by the F_4 generation, then with a fivefold rate of increase, 96 percent sterility would be required at a rate of 12.5:1, 95 percent sterility would be required at a ratio of 25:1, and 94 percent sterility at a ratio of 50:1 and of 100:1. Clearly, unless we have complete sterility, an adequate level of sterility is more critical to success than a high release ratio.

When the rate of increase is tenfold, the population is reduced to less than 30 by the F_4 generation when the release ratio is 12.5:1 and the level of sterility is virtually 100 percent. With a release ratio of 25:1, 99 percent sterility is required, with 50:1, 98 percent sterility is required, and with 100:1, 97 percent sterility is required. Thus, the requirement to achieve total suppression is considerably more stringent with a tenfold rate of increase than with a fivefold rate of increase.

When the rate of increase is twentyfold and with an initial release ratio of 100:1, 96 percent sterility nearly holds the population static and 99 percent sterility is required to reduce the population to less than 30 by the F_4 generation. With a release ratio of 25:1, complete sterility is required to substantially reduce the population.

When the rate of increase is fortyfold, 99 percent sterility is required to prevent the population from increasing when the release ratio is 100:1.

With reference to eradication of the boll weevil, we should assume that some populations will increase at a tenfold rate. Therefore, 97 or 98 percent sterility is required. Certainly 95 or 96 percent sterility would be inadequate. Methods for mass sterilization with chemosterilants have not yet been perfected. If 97 or 98 percent sterility cannot be achieved on a mass scale with chemosterilants, then gamma-

radiation must be used. Since radiation sterilized weevils under field conditions would be effective for only 3 or 4 days (3, 4, T. B. Davich, U.S.D.A., State College, Mississippi, personal communication), the numbers reared would have to be increased at least fivefold.

3. POPULATION SUPPRESSION WITH CONDITIONAL LETHALS

In recent years, we have considered the possibility of suppressing the boll weevil, the pink bollworm, and some other insects with dominant conditional lethal traits (7, 8). By definition, dominant conditional lethal genes express themselves in heterozygous insects only when permitted by environmental or certain other conditions. In some of our studies, we included temperature-sensitive lethals in computations (15). The use of temperature-sensitive lethals should not be restricted to those species for which a formal genetics has been erected; they should prove to be useful in major pest species. The inability to fly in boll weevils could be a conditional lethal trait (12). The lethality would be expressed when the weevils attempted to leave the cotton fields for hibernation or in leaving hiberation sites in search of cotton. A rich source of conditional lethals that may be useful for suppressing major agricultural insects is their adaptation to climate.

Insects require special adaptations for survival in regions of the world marked by climatic extremes during the annual cycle. These adaptations synchronize the insects' sensitive growing stages with seasons when food is present and freezing temperatures and droughts are absent. In addition, these adaptations permit survival during periods of extreme cold, lack of water or food. Characteristically, insects survive adverse periods by entering diapause prior to their onset and by terminating diapause only when favorable conditions again prevail. Since many of our pest species have rather wide ranges of distribution, the seasons may vary greatly between localities within the range of a given species. Therefore, the diapause characteristics of local populations must vary accordingly and these differences between local populations must be hereditary.

To date we have given most thought to utilizing the inability to diapause in the boll weevil and in the pink bollworm. However, other adaptations could also be exploited as conditional lethals such as inability to respond to the appropriate critical photo period, inadequate duration of diapause, and inability to develop sufficient cold hardiness.

In the case of the pink bollworm, Indian populations near the equator do not enter diapause (1). Moreover, nondiapausing strains can be obtained through selection (2, A. C. Bartlett, U.S.D.A., Phoenix, Arizona, and R. A. Bell, U.S.D.A., Fargo, N.D., personal communications). Barry and Adkisson (2) were able to show that this trait segregates as though determined mainly by a dominant gene.

The inheritance of the adult diapause in the boll weevil is obviously much more difficult to study than that of the larval diapause in the pink bollworm. Nevertheless, McCoy, Lloyd, and Bartlett (13) determined that the nondiapause trait is dominant and appears to be inherited rather simply in the boll weevil. In a field experiment, E. P. Lloyd (U.S.D.A., State College, Miss., personal communication) showed that the probability of a heterozygous weevil (obtained by crossing diapause and nondiapause strains) entering diapause and surviving the winter was reduced by 80 percent, and no homozygous nondiapause weevils were able to overwinter. In the pink bollworm, Barry and Adkisson (2) showed that the nondiapause allele in the heterozygous condition is about 90 percent

TABLE I. POPULATION TREND WHEN A NATIVE POPULATION OF 1000 MALES AND 1000 FEMALES IS OVERFLOODED IN EACH GENERATION BY 12,500, 25,000, 50,000 or 100,000 PARTIALLY OR COMPLETELY STERILE MALES. UNCONTROLLED NATIVE POPULATION INCREASES 5-, 10-, 20-, or 40-FOLD BETWEEN GENERATIONS

Case No.	Males Released	Percent Sterility	Rate of Increase	Progeny in Successive Generations 1	2	3	4	5
1	12,500	90	5-fold	1667	1302	941	624	381
2	"	91	"	1574	1133	733	425	223
3	"	92	"	1481	974	557	279	126
4	"	93	"	1389	826	412	175	67
5	"	94	"	1296	689	294	104	33
6	"	95	"	1204	564	200	58	15
7	"	96	"	1111	449	128	29	6
8	"	97	"	1019	346	75	12	2
9	"	98	"	926	255	38	4	0
10	"	99	"	833	174	15	1	0
11	"	100	"	741	107	2	0	0
12	25,000	90	"	1346	832	477	259	135
13	"	91	"	1250	701	360	174	81
14	"	92	"	1154	581	263	112	46
15	"	93	"	1058	472	186	62	24
16	"	94	"	962	374	125	39	12
17	"	95	"	865	286	79	20	5
18	"	96	"	769	210	46	9	2
19	"	97	"	673	144	24	4	1
20	"	98	"	577	90	10	1	0
21	"	99	"	481	47	3	0	0
22	"	100	"	385	15	0	0	0
23	50,000	90	"	1176	650	344	177	90
24	"	91	"	1078	538	255	118	54
25	"	92	"	980	436	183	75	30
26	"	93	"	882	345	126	45	16
27	"	94	"	784	264	82	25	8
28	"	95	"	686	194	50	13	3
29	"	96	"	588	134	28	6	1
30	"	97	"	490	85	13	2	0
31	"	98	"	392	47	5	0	0
32	"	99	"	294	19	1	0	0
33	"	100	"	196	2	0	0	0
34	100,000	90	"	1089	571	293	148	75
35	"	91	"	990	468	215	98	44
36	"	92	"	891	375	153	62	25
37	"	93	"	792	292	104	37	13
38	"	94	"	693	219	67	20	6
39	"	95	"	594	157	40	10	2
40	"	96	"	495	105	21	4	1
41	"	97	"	396	63	10	1	0
42	"	98	"	392	47	5	0	0
43	"	99	"	294	19	1	0	0
44	"	100	"	99	0	0	0	0
45	12,500	97	10-fold	2037	2100	2208	2401	2761
46	"	98	"	1852	1622	1293	882	471

TABLE I. (Continued)

Case No.	Males Released	Percent Sterility	Rate of Increase	Progeny in Successive Generations 1	2	3	4	5
47	12,500	99	10-fold	1667	1198	662	235	45
48	"	100	"	1481	829	266	28	0
49	25,000	93	"	2115	2279	2520	2888	3488
50	"	94	"	1923	1823	1697	1542	1359
51	"	95	"	1731	1415	1078	755	484
52	"	96	"	1538	1056	632	329	152
53	"	97	"	1346	746	330	120	39
54	"	98	"	1154	486	143	33	7
55	"	99	"	962	276	43	5	0
56	"	100	"	769	117	3	0	0
57	50,000	91	"	2157	2356	2613	2958	3435
58	"	92	"	1961	1916	1864	1805	1738
59	"	93	"	1765	1520	1275	1042	830
60	"	94	"	1569	1169	828	561	366
61	"	95	"	1373	863	502	275	144
62	"	96	"	1176	602	275	117	48
63	"	97	"	980	386	130	41	12
64	"	98	"	784	217	48	10	2
65	"	99	"	588	93	10	1	0
66	"	100	"	392	15	0	0	0
67	100,000	90	"	2178	2389	2643	2954	3340
68	"	91	"	1980	1959	1936	1911	1885
69	"	92	"	1782	1571	1369	1181	1008
70	"	93	"	1584	1225	927	688	504
71	"	94	"	1386	921	593	372	230
72	"	95	"	1188	661	351	181	92
73	"	96	"	990	443	187	76	31
74	"	97	"	792	268	84	25	8
75	"	98	"	594	136	28	6	1
76	"	99	"	396	47	5	0	0
77	"	100	"	198	2	0	0	0
78	12,500	100	20-fold	2963	6279	25,210	253,155	4.6 M
79	25,000	98	"	2308	2919	4,322	8,470	27,435
80	"	99	"	1923	1795	1,591	1,289	899
81	"	100	"	1538	918	331	44	1
82	50,000	96	"	2353	2921	3,928	5,993	11,302
83	"	97	"	1961	1908	1,838	1,746	1,629
84	"	98	"	1569	1102	676	360	169
85	"	99	"	1176	506	152	35	7
86	"	100	"	784	122	3	0	0
87	100,000	95	"	2376	2906	3,697	4,972	7,264
88	"	96	"	1980	1957	1,930	1,898	1,861
89	"	97	"	1584	1192	852	581	382
90	"	98	"	1188	613	282	120	50
91	"	99	"	792	220	49	10	2
92	"	100	"	396	16	0	0	0
93	25,000	100	40-fold	3077	7135	35,640	593,270	21.8 M
94	50,000	99	"	2353	3083	4,885	10,964	47,283
95	"	100	"	1569	969	372	55	1
96	100,000	98	"	2376	2995	4128	6574	13,460
97	"	99	"	1584	1127	701	377	179
98	"	100	"	792	125	3	0	0

penetrant. Therefore, there is good reason to consider the use of a nondiapause strain as an important component in attempts to suppress or eradicate the bollweevil and the pink bollworm populations.

Let us consider the consequences of releasing insects homozygous for the inability to diapause. Suppose that the inability to diapause is controlled by a single dominant allele, D, and that the ability to diapause is controlled by a recessive allele, d. Releases are made once every spring for i years, mates are chosen randomly and all matings yield the same number of offspring. S is the proportion of heterozygotes that enter diapause ($0 \leq S \leq 1$). The frequency of genotypes is given by:

$$\frac{(X^2)_{DD}}{T^2} + \frac{2\,(XY)_{Dd}}{T^2} + \frac{(Y^2)_{dd}}{T^2} = 1$$

where X and Y are the number of D and d alleles respectively and X+Y=T. We assume that in the absence of control measures the population will increase k-fold per generation, for each of the four generations in a year. If insecticides are required to prevent the population from causing economic damage, the probability of surviving these applications in each generation will be p_1, p_2, p_3, and p_4. The impact of the series of insecticidal applications for the entire season may be accounted for by the factor

$$K_i + p_{i_1}\, p_{i_2}\, p_{i_3}\, p_{i_4}\, k^4$$

Thus, at the end of the season, the total population Pi_4 and the numbers of each genotype are given by:

$$P_{i_4} = \tfrac{1}{2}\, K_i T_i \left\{ \frac{(X_i^2)_{DD}}{T_i^2} + \frac{2\,(X_i Y_i)_{Dd}}{T_i^2} + \frac{(Y_i^2)_{dd}}{T_i^2} \right\}$$

If W is the overwintering survival rate of diapause individuals, then the number overwintering is:

$$\frac{W S K_{i-1}\,(X_{i-1}\, Y_{i-1})_{Dd}}{T_{i-1}} \text{ individuals}$$

and

$$\frac{W K_{i-1}\,(Y_{i-1}^2)_{dd}}{2\, T_{i-1}} \text{ individuals}$$

These expressions can be used iteratively to compute the number of each genotype in a series of years (see (7)).

In order to visualize the application of the above theory, consider a population which each spring numbers about 1000 overwintered insects on 10 acres (Table II). Conventional control measures are applied so that the fall generation has only 10,000 insects or an increase rate over all generations of tenfold (1000 per acre). Further, we assume that winter survival of diapausing insects is normally ten percent. If this representative normal population were further suppressed by intensive cultural measures to 100 insects (10 per acre), then it could be overflooded with nondiapause insects in a 10:1 ratio without any greater hazard to the crop than would normally occur in the absence of the special control efforts. If 1000 nondiapause insects were added in three consecutive seasons, and if survival of heterozygous (Dd) insects was 20 percent of diapause insects (dd), then the population would be virtually eliminated in the third winter. Moreover, if control measures during the regular season were intensified so that mortality doubled, the population would be virtually eliminated in the second winter.

If the insects could be reared for approximately $2.00 per thousand, the cost per acre per year for this insect would be about 20 cents. If releasing the insects cost 80 cents per acre, then the cost would be $1.00 per acre per year. The cost for 3 years would total $3.00 per acre. The regular costs for control with insecticides would not diminish the first year, but would be somewhat less in the second year due to some reduction in the initial overwintered population. These costs should be substantially less in the third year because of the substantial reduction in the overwintered population.

A program of the nature projected would require some special effort to reduce the overwintered population in the first year. Such special effort should not be required in the following years. The total cost of rearing and releasing the moths should be more than offset by reductions in insecticide applications, especially in the third year. However, the need to continue insecticide applications for 3 years could aggregate total costs of the order of $100 per acre.

An alternate program of greater effectiveness and lower cost would entail the release of 7800 partially sterile nondiapause males per acre. No losses in yield and no control costs other than the rearing and releasing of insects would be incurred. Therefore, the immediate savings to the growers would be substantial. If we assume a cost of $2.00 per acre for rearing and releasing 1000 moths, then the total cost per year would be of the order of $15.00 per acre. As shown in Table III, the overwintered generation (100 insects/acre, 50 males and 50 females) and each subsequent generation would be overflooded with 1950 nondiapause males that are 90 percent sterile. No insecticides would be applied; yet by the F_4, there would be only 307 insects/acre. Moreover, 214 of these would be homozygous nondiapause insects, totally incapable of overwintering. Of the remainder, a b o u t two insects with the diapause allele would overwinter. With completely sterile and fully competitive males, this same degree of suppression could be obtained with just two releases. Therefore, a single conditional lethal trait would be advantageous only if full sterility cannot be induced without adverse effects.

In contrast to the above results, partial sterility in Lepidoptera may have a greater impact than complete sterility (11). Recently, Graham et al. (5) developed a model for control of the pink bollworm in which a single release of partially sterile males is made to the overwintered generation. We have developed a model based insofar as possible on the experimental data of Graham et al. (5). We assume that individuals treated with 5 kr. or 10 kr. of gamma radiation[1] show full

[1] kr. = krad

TABLE II. DEVELOPMENT OF A NORMAL DIAPAUSING (dd) POPULATION SUBJECTED TO CONVENTIONAL CONTROL MEASURES VS. THE DEVELOPMENT OF POPULATIONS FIRST REDUCED BY 90 PERCENT AND OVERFLOODED IN PARENT (OVERWINTERED) GENERATIONS WITH A NONDIAPAUSING (DD) STRAIN. THE MORTALITY FROM INTENSIFIED CONVENTIONAL CONTROLS IS DOUBLED IN ONE CASE. THE MODEL INVOLVES INSECTS ON 10 ACRES.

Generation	Normal diapausing population (dd) on 10 acres	Introduced nondiapause strain (DD) each year in parent generation	Mortality from control measures is doubled Introduced nondiapause strain (DD) each year in parent generation
		First year	
Overwintered	1,000 (dd)	1,100 - (100 dd, Add 1,000 DD) a/	1100 -100 dd, Add 1000 DD)
Fall	10,000 (dd)	11,000 - (9091 DD, 1818 Dd, 91 dd)	5500 - (4546 DD, 909 Dd, 45 dd)
		Second year	
Overwintered	1,000 (dd)	1,045 - (36 Dd, 9 dd, Add 1000 DD)	1023-(18 Dd, 5 dd, Add 1000 DD)
Fall	10,000 (dd)	10,450 - (9917 DD, 526 Dd, 7 dd)	5115-(4976 DD, 138 Dd, 1 dd)
		Third year	
Overwintered	1,000 (dd)	1,012 - (11 Dd, 1 dd, Add 1000 DD)	3 - (3 Dd, 0 dd)
Fall	10,000 (dd)	10,120 - (9990 DD, 129 Dd)	
		Fourth year	
Overwintered	1,000 (dd)	3 - (3 Dd)	

a/ Normal population reduced to 100 by conventional control measures.

TABLE III. DEVELOPMENT OF A NORMAL DIAPAUSING (dd) POPULATION SUBJECTED TO REGULAR CONTROL WITH INSECTICIDES VS. THE DEVELOPMENT OF A POPULATION OVERFLOODED WITH NONDIAPAUSE MALES (DD) STERILIZED AT THE 90 PERCENT LEVEL. PARTIAL STERILITY IS NOT INHERITED.

Generation	Normal diapausing population (dd) on 1 acre	Field population	Released nondiapause population
		First Year	
Overwintered	100 (dd)	100 (dd)	1950 (DD)
F_1	1000 (dd)[a]	25 (dd) 97.5 (Dd)	1950 (DD)
F_2	1000 (dd)[a]	13.5 (dd) 89.4 (Dd) 53.2 (DD)	1950 (DD)
F_3	1000 (dd)[a]	8.4 (dd) 84.1 (Dd) 117.8 (DD)	1950 (DD)
F_4	1000 (dd)[a]	6.2 (dd) 87.0 (Dd) 213.8 (DD)	
		307.0 Total in F_4	
		Second Year	
Overwintered	100 (dd)	.62 (dd) 1.74 (Dd)	
		2.36 Total	

a/ Regular insecticide treatments would hold population static.

mating competitiveness. The progeny per female and sex ratio pertaining to various crosses are shown in Table IV. We also assumed that field populations can be reduced to 100 per acre by cultural and other means. In addition, we assume that populations will increase at a tenfold rate.

Although growers may spend in the neighborhood of $50 per acre to control the pink bollworm, our goal is to totally suppress the population for no more than one-half of this cost. Currently, pink bollworms can be reared for $1.40 per thousand. If we assume, as before, that the costs for production and release of moths will be $2.00 per thousand, the production cost for release of 10,000 to 15,000 pink bollworms per acre should be economically feasible and less costly than the application of insecticides.

In an actual program, releases would be made to every generation. However, we cannot calculate the impact of such a program because the expectations from many of the crosses which would occur have not been

TABLE IV. PARAMETERS AND ASSUMPTIONS UNDERLYING MODELS ON SUPPRESSION OF PINK BOLLWORM POPULATIONS WITH INHERITED STERILITY AND NONDIAPAUSE GENE. INSOFAR AS POSSIBLE, RESULTS OF CROSSES ARE BASED ON DATA OF GRAHAM et al.

Males treated with 5 kr., 10-fold increase[a]

Cross	Progeny per female	Percent males
U x U	20	50.0
U x T	11.4	61.5
U x (UxT)	.36	65.5
(UxT) x U	.36	65.5
(UxT) x (UxT)	.014	50.0
Ux((UxT) x U)	8.4	65.5
U x (Ux(UxT))	8.4	65.5
(Ux(UxT)) x U	8.4	65.5
((UxT)xU) x U	8.4	65.5

[a] Assumption:
All other second generation matings involving descendants of a treated male yield no progeny. Sterility is not transmitted to the third generation.

Both sexes treated with 10 kr., 10-fold increase[b]

Cross	Progeny per female	Percent males
U x T	7.4	68.8
T x U	2.34	50.0
T x T	.68	68.8
(TxU) x U	20.00	50.0
U x (TxU)	11.8	50.0
(TxU) x (TxU)	11.8	50.0

[b] Assumptions:
All other first generation matings yield no progeny. Sterility is not transmitted to the second generation.
The release strain (DD) is homozygous for the inability to diapause.
The probability of a heterozygote entering diapause is 20%.
The probability that homozygous diapause insects (dd) overwinter is 0.10.

determined experimentally. Therefore, in our models, releases are made only in those generations which do not transmit the sterility induced in an ancestral generation. When males treated with 5 kr. are released to the parent generation, no further releases are made until after two generations. On the other hand, when moths treated with 10 kr. are released to the parent generation, only one generation is skipped before another release is made.

If methods were available to either separate sexes or to completely sterilize females without fully sterilizing males, then results could be obtained as shown in Table V. In the first example, releases of 950 males are made to the overwintered and third generation. This program would provide good control at a cost of the order of $8.00 per acre. The second example entails two releases of 1950 males. This program would provide total suppression at about $16.00 per acre.

TABLE V. MODEL OF DEVELOPMENT OF TWO PINK BOLLWORM POPULATIONS SUPPRESSED BY RELEASES OF PARTIALLY STERILE MALES TO THE OVERWINTERED AND THIRD GENERATIONS. AN UNCONTROLLED POPULATION UNDER SIMILAR CIRCUMSTANCES WOULD INCREASE 10-FOLD BETWEEN GENERATIONS. THE NUMBERS REPRESENT THE PROGENY FROM THE RESPECTIVE CROSS. THE OVERWINTERED POPULATION CONSISTS OF 50 MALES AND 50 FEMALES PER ACRE. THE RATIOS OF RELEASED TO OVERWINTERED MALES ARE 19:1 AND 39:1. MALES WERE TREATED WITH 5 KR. OF GAMMA RADIATION[a]

Cross	950 males per release		1950 males per release	
	Females	Males	Females	Males
Overwintered Generation (Release partially sterile males)				
U x U	25.0	25.0	12.5	12.5
U x T	208.0	333.0	214.0	341.8
Total	233.0	358.0	226.5	354.3
First Generation				
U x U	17.5	17.5	4.1	4.1
U x (UxT)	2.9	5.5	1.5	2.8
(UxT) x U	1.8	3.4	0.9	1.8
(UxT) x (UxT)	1.4	1.4	1.4	1.4
Total	23.6	27.8	7.9	10.1
Second Generation				
U x U	110.0	110.0	16.6	16.6
U x (Ux(UxT))	10.1	19.0	3.3	6.3
U x ((UxT) x U)	6.2	11.8	2.1	4.0
(U x (UxT)) x U	5.3	10.0	1.7	3.4
((U x T) x U) x U	3.3	6.2	1.0	2.0
Total	134.9	157.0	24.7	32.3
Third Generation (Release partially sterile males)				
U x U	191.3	191.3	3.1	3.1
U x T	508.2	811.6	107.1	171.0
Total	699.5	1002.9	110.2	174.1
Fourth Generation				
U x U	364.9	364.9	0.6	0.6
U x (UxT)	19.2	36.5	0.4	0.7
(UxT) x U	12.0	22.9	0.3	0.4
(UxT) x (UxT)	2.9	2.9	0.7	0.7
Total	399.0	427.2	2.0	2.4
Overwintered Generation				
	39.9	42.7	0.2	0.2

[a] KR. = krad.

TABLE VI. DEVELOPMENT OF TWO PINK BOLLWORM POPULATIONS SUPPRESSED BY RELEASES OF PARTIALLY STERILE NONDIAPAUSE (DD) INSECTS OF EACH SEX TO ALTERNATE GENERATIONS. AN UNCONTROLLED POPULATION UNDER SIMILAR CIRCUMSTANCES WOULD INCREASE 10-FOLD BETWEEN GENERATIONS. THE NUMBERS REPRESENT THE PROGENY FROM THE RESPECTIVE CROSS. THE OVERWINTERED POPULATION CONSISTS OF 50 MALES (dd) AND 50 FEMALES (dd) PER ACRE AND THE INITIAL RELEASE RATIOS INTO THE TWO POPULATIONS ARE 24:1 AND 29:1 RESPECTIVELY. BOTH SEXES WERE TREATED WITH 10 KR. GAMMA RADIATION.

	Case No. 1		Case No. 2	
	Overwintered Generation			
	(Release 2400 Insects)		(Release 2900 Insects)	
Cross	Females	Males	Females	Males
U x U	20.0	20.0	16.7	16.7
U x T	110.8	244.4	111.5	246.1
T x U	56.2	56.2	56.6	56.6
T x T	244.4	539.0	297.3	655.8
Total	431.4	859.6	482.1	975.2
	First Generation			
U x U	4.7	4.7	2.9	2.9
U x (TxU)	7.7	7.7	5.7	5.7
(TxU x U	13.1	13.1	9.7	9.7
(TxU) x (TxU)	21.7	21.7	19.4	19.4
Total	47.2	47.2	37.7	37.7
	Second Generation			
	(Release 2400 Insects)		(Release 2900 Insects)	
U x U	17.9	17.9	9.6	9.6
U x T	104.8	231.2	84.8	187.1
T x U	53.1	53.1	43.0	43.0
T x T	244.9	540.2	299.8	661.2
Total	420.7	842.4	437.2	900.9
	Third Generation			
U x U	3.8	3.8	1.0	1.0
U x (TxU)	6.7	6.7	0.3	0.3
(TxU) x U	11.3	11.3	4.6	4.6
(TxU) x (TxU)	19.7	19.7	12.1	12.1
Total	41.5	41.5	18.0	18.0
	Fourth Generation			
	(Release 2400 Insects)		(Release 2900 Insects)	
U x U	13.9	13.9	0.1	0.1
U x T	94.6	204.2	41.1	90.5
T x U	46.9	46.9	20.8	20.8
T x T	246.1	542.6	303.8	670.1
Total	401.5	807.6	365.8	781.5

TABLE VI (Continued)

Cross	Fifth Generation			
	Females	Males	Females	Males
U x U	2.4	2.4	0.0	0.0
U x (TxU)	4.8	4.8	0.0	0.0
(TxU) x U	8.1	8.1	0.0	0.0
(TxU) x (TxU)	16.1	16.1	3.3	3.3
Total	31.4	31.4	3.3	3.3
	Overwintered Generation			
	.24 dd	.24 dd		
	.25 Dd	.25 Dd		
Total	.49	.49	<0.33	<0.33

A model which does not require the separation of sexes was used to calculate the population trends shown in Table VI. Nondiapause males and females irradiated with 10 kr. are released to every other generation. In case No. 1, each release would require 1200 males and 1200 females or 7,200 irradiated insects throughout the season. The relative frequencies of genotypes in the final generation would be 0.075 dd, 0.398 Dd, and 0.526 DD. Although the population would have been held static throughout the season, the number which could overwinter would average less than one insect per acre. This program of total suppression would cost of the order of $15.00 per acre. In case No. 2, each release would require 1450 males and 1450 females or 8700 irradiated insects throughout the season. This rate of overflooding would be sufficient to decimate the target population by means of sterility alone. The genes for the inability to diapause would serve as a backstop to insure success in the event that the rate of increase exceeded tenfold or in the event the released insects were not appropriately distributed. This program of total suppression would cost of the order of $18.00 per acre.

4. DISCUSSION

In a previous publication (8), we showed that if two or more conditional lethal traits were combined into one release strain, the number of insects that would have to be released could be reduced considerably. Also, we showed that a conditional lethal trait could be equally effective when under polyfactorial control as when under the control of a single gene. However, from the standpoint of eliminating or reducing the cost of control even while a program of total suppression is underway, our first choice would be the use of totally sterile males and not the use of conditional lethals. However, if complete sterility cannot be induced without drastic adverse effects, then partial sterility should be considered. If the rate of increase is modest, then partial sterility alone would be effective. However, at high rates of increase (tenfold, which we might expect in a favorable environment), partial sterility could hold the population static and simultaneously permit the introduction of conditional lethals. In Lepidoptera, partial sterility alone would be as effective as partial sterility plus conditional lethals provided that partially sterile females would not be

released. However, if sexes cannot be separated or if females cannot be totally sterilized with a treatment that induces only partial male sterility, then partial sterility could be used to hold the population static while a conditional lethal at a sufficient frequency is introduced to eliminate the population.

This analysis of the potential role of sterile or genetically altered pink bollworm moths strongly suggests that the genetic approach to pink bollworm population suppression or elimination would be entirely feasible and practical if the suppression effects projected are reasonably realistic. Several alternative approaches for the use of this method could be employed. The technology for mass production, handling, and release of the moths has already been developed as the result of the current program jointly sponsored by the U.S.D.A. and the California Department of Agriculture to prevent the establishment of the pest in the San Joaquin Valley in California. A basic requirement would be for regulatory agencies and growers to develop a program of prior suppression of the insects to a level of the order of 100 native insects per acre in Arizona, Southern California, and Northwestern Mexico. It should then be possible to achieve the overflooding ratios required for complete suppression of the populations in a single season. However, for reasonable assurance of success under practical conditions, a suppression program should be continued for at least two years. If, in addition, allowances are made for costs somewhat greater than those projected here for a technically feasible program, the prospects seem excellent that the pink bollworm could be eliminated from the southwestern cotton growing area at a per acre cost that should not exceed the annual cost for insecticidal treatments alone. Moreover, if this pest could be eliminated by a completely selective means such as the genetic method, the serious environmental effects of the intensive use of insecticides for its control would be obviated. Then the cotton-growing ecosystems would be restored so that other cotton insect pests could be controlled with an integrated system.

REFERENCES

(1) Atwal, A. S. 1967. Diapause among insect pests of crops. Tropical Entomol. 8:1-16.

(2) Barry, B. D. and P. L. Adkisson 1966. Certain aspects of the genetic factors involved in the control of the larval diapause of the pink bollworm. Ann. Entomol. Soc. Amer. 59(1): 122-125.

(3) Bartlett, A. C., P. A. Hooker and D. D. Hardee 1968. Behavior of irradiated boll weevils. I. Feeding, attraction, mating, and mortality. Jour. Econ. Entomol. 61(6): 1677-1680.

(4) Bartlett, A. C., 1968. Behavior of irradiated boll weevils. II. Reproduction and mortality in cages with untreated boll weevils. Jour. Econ. Entomol. 61(6): 1680-1684.

(5) Graham, H. M., M. T. Ouye, R. D. Garcia and H. H. De La Rosa. Dosages of gamma irradiation for full and inherited sterility in adult pink bollworms. Jour. Econ. Entomol. 68 4 (1972) 645.

(6) Klassen, W. and J. F. Creech 1970. Suppression of pest population with sterile male insects. USDA, ARS, Misc. Publication No. 1182, 8 pp.

(7) Klassen, W., E. F. Knipling and J. U. McGuire 1970. The potential for insect population suppression by dominant conditional lethal traits. Ann. Entomol. Soc. Amer. 63: 238-255

(8) Klassen, W., J. F. Creech and R. A. Bell 1970. The potential for genetic suppression of insect populations by their adaptations to climate. USDA, ARS, Misc. Publication No. 1178, 77 pp.

(9) Knipling, E. F. 1964. The potential role of the sterility method for insect population control with special reference to combining this method with conventional methods. USDA, ARS-33-98, 54 pp.

(10) Knipling, E. F. 1966. Some basic principles in insect population suppression. Ann. Entomol. Soc. Amer. 12(1): 7-15.

(11) Knipling, E. F. 1970. Suppression of pest Lepidoptera by releasing partially sterile males. Bioscience 20: 465-70.

(12) LaChance, L. E. and E. F. Knipling 1962. Control of insect populations through genetic manipulation. Ann. Entomol. Soc. Amer. 55: 515-520.

(13) McCoy, J. R., E. P. Lloyd, and A. C. Bartlett 1968. Diapause in crosses of a laboratory and wild strain of boll weevils. Jour. Econ. Entomol. 61(1): 163-166.

(14) North, D. T. and G. G. Holt, 1969. Population suppression by transmission on inherited sterility to progeny of irradiated cabbage loopers, Trichoplusia ni. Canad. Entomol. 101: 513-520.

(15) Wehrhahn, C. F. and W. Klassen 1971. Genetic insect control methods based upon the release of relatively few laboratory-reared insects. Canad. Entomol. 103: 1387-1396.

SOME APPLICATIONS OF COMPUTER MODELLING IN POPULATION SUPPRESSION BY STERILE MALES

J. MONRO
Seibersdorf Laboratory,
International Atomic Energy Agency,
Vienna

Abstract

SOME APPLICATIONS OF COMPUTER MODELLING IN POPULATION SUPPRESSION BY STERILE MALES.
The size of a population is dependent only on the initial population size and age distribution and the age-specific survival and fecundity over any later time interval. Thus the basis of modelling a population is simple though the models themselves may be complex. Computer simulation has value in suggesting general strategies of control and in predicting the outcome of specific treatments of specific pest populations. Several examples are given. Application of this technique is to some extent blocked by a shortage of relevant data. Simulation will make its full contribution to the sterile-male technique when ecological, programming and administrative skills are brought together from the beginning to plan, operate and assess a complete campaign.

1. INTRODUCTION

Although the techniques which are used to model pest populations originated in human demography, in the efforts of eighteenth century actuaries to calculate insurance premiums and annuity rates, it was only in the middle of this century that entomologists and others interested in pest control began to consider the population dynamics of pest species in any detail. It is ironic that one should come to use techniques which were originally developed for the study of human populations just as one begins to realize that man himself has many of the characteristics of a pest species and that his unrestrained increase is the biggest threat to human and other terrestrial life. One is still hampered by imprecise data and considerable ignorance of the functions which relate environment to population growth. Perhaps one can take cold comfort from the plight of one's colleagues in human demography whose data are often much more precise than those of the entomologist but whose predictions are easily upset by the uncertainties of future patterns of survival and reproduction.

Modelling for actual field operations in entomology is not at a very advanced stage and it is worth looking at the reasons for this. One difficulty is that many practising entomologists do not appreciate the aid which demographic principles and computer models could give to them. Also, the computer specialist who is only competent in his own field does not necessarily have the entomological background which would enable him to appreciate all the difficulties of data collection and all the subtleties of insect ecology. The most fruitful approach is probably a two-man team in which both parties can learn. It is also important for the entomologist to learn at least the elements of programming so that he can understand

what is going on in the model and what is required of him. Perhaps even more valuable to him than the actual models which are developed, at least in the early stages, is the salutary exercise of refining what may be only woolly concepts and reducing them to sets of precise parameters. Imprecise concepts can lead to the collection of useless data, whereas a precise model with precise numerical requirements forces us to collect data which are relevant to the model. This does not mean, of course, that one is always able to collect the relevant data in the field or that the collected data are always accurate. But at least the model tells the form of the questions one should ask of the natural population. And of course one should continually be bringing the models closer to reality; closer to the mechanisms which determine population dynamics.

2. METHODS OF MODELLING POPULATION DYNAMICS

I would like briefly to show how populations may be modelled. For entomologists the most useful and easiest models to work with are deterministic; in such models it is assumed that the populations dealt with are very large and all the parameters specified are accurately known. Stochastic models are more realistic, require more data and may be built up later from deterministic models. But for comparing methods of control and for large populations with predictable rates of growth, deterministic models are easier to construct and understand.

The dynamics of any population may be calculated in a deterministic model from three sets of data:

(a) The age structure of the initial population (n_x) (i.e. the number of individuals in each age class).
(b) The age-specific survival of members of the population (l_x).
(c) The age-specific fecundity of females in the population (m_x).

Typical l_x and m_x values are shown in Table I.

TABLE I. MEAN SURVIVAL (l_x) OF LABORATORY-REARED FEMALE MEDFLY, Ceratitis capitata (Wied.) IN FIELD CAGES AT SEIBERSDORF AND MEAN FECUNDITY (m_x) FROM THE SAME STOCK REARED IN LABORATORY CAGES AT 25°C

Week	l_x	m_x
1	-	0 } Immature stages[a]
2	-	0
3	-	0
4	0.305	97.61
5	0.087	106.9
6	0.033	60.7

[a] Survival from oviposition to adult emergence is assumed to be 0.5.

TABLE II. SCHEME FOR COMPUTING AGE STRUCTURE, TOTAL POPULATION AND TOTAL BIRTHS OVER SUCCESSIVE TIME INTERVALS. NOTE THAT THIS SCHEME REFERS ONLY TO FEMALE BIRTHS, AGE STRUCTURE AND TOTAL POPULATION

A. COMPUTATION OF TOTAL POPULATION IN TIME INTERVAL 1

Age class	Number in age class	Operation	
		Summation	
1	n_{11}		
2	n_{21}		
3	n_{31}		
4	n_{41}		
	= 0		Total population

B. COMPUTATION OF TOTAL BIRTHS IN TIME INTERVAL 1

Age class	Number in age class	Operation 1	Fecundity	Operation 2	
		Multiplication		Summation	
1	n_{11}	×	m_1		
2	n_{21}	×	m_2		
3	n_{31}	×	m_3		
4	n_{41}	-	-		
	= 0				Total births

C. COMPUTATION OF AGE STRUCTURE IN TIME INTERVAL 2

Age structure in time interval 1	Operation	Survival from one age class to the next	New age structure
	Multiplication		
Total births	×	l_1	n_{12}
n_{11}	×	l_2/l_1	n_{22}
n_{21}	×	l_3/l_2	n_{32}
n_{31}	×	$l_4/l_3 = 0$	

D. COMPUTATION OF TOTAL POPULATION AND TOTAL BIRTHS FOR TIME INTERVAL 2 AS IN STEPS A AND B

The operation of models which follow the history of a population through time may be understood by following the transfer of surviving individuals from one age class to the next and by estimating their contribution to the number of births occurring during a particular time interval. These relationships are indicated in Table II by the arrowed lines which show how survivors from the youngest age class during time interval 1 are transferred to the next age class during time interval 2 and so on down the table of age distribution until the last survivors in the oldest age category die. In a similar way the contributions of any age class in the population to total births may be calculated by multiplying the number of individuals in that age class by the mean fecundity m_x and transferring this to the box labelled "Total births". By repeating this process down the table one sums the total births in the first time interval and the two boxes labelled "Total population" and "Total births" give the population with which one begins to calculate the births and population in the next time interval. These processes are easy to follow and to program in FORTRAN, the language which I have used.

Such a simple basic model is very flexible because any environmental change, natural or artificial, has only two possible influences; it can change either the survival rate (the l_x value in Table I) or the fecundity rate (the m_x value in Table I). By specifying the quantitative effect of any treatment in Table I, one can use the model to predict the population after the treatment has been applied. This is true whether one uses sterile males, insecticides, male annihilation or any other treatment. The model is also more powerful than models based on discrete generations because it can handle any type of generation distribution, discrete or overlapping.

3. SOME PRACTICAL APPLICATIONS

3.1. Harvesting

In predicting the size of a factory which will give a particular output of sterile males it is usually fairly easy to predict the size of the larval rearing unit (larval rearing rooms and equipment) because this is a linear function of output. It is not so easy to predict the size and management of the adult population which must be kept. Models have been developed for this purpose by Curtis and Jordan [1] and by Monro and Osborn [2]. For a given rate of production the relevant independent variables are the stocking rate per cage of young adult females (F) and young adult males (M), the total number of cages held (C), the age at which old adults are discarded (d), the egg to adult survival of males (K_m) and of females (K_f) and the age-specific survival (λ_x) of females from adult-emergence onward.

The relevant equations are:

Number of eggs (or other immature stages) harvested per time interval

$$= \frac{2CF}{d} \sum_{x=0}^{d} \lambda_x m_x$$

Number of young adult males stocked per time interval

$$= \frac{CM}{d}$$

Number of young adult females stocked per time interval

$$= \frac{CF}{d}$$

Number of young adult males harvested per time interval

$$= \frac{C}{d}\left[\left(FK_m \sum_{x=0}^{d} \lambda_x m_x\right) - M\right]$$

Number of young adult females harvested per time interval

$$= \frac{CF}{d}\left[\left(K_f \sum_{x=0}^{d} \lambda_x m_x\right) - 1\right]$$

The most interesting use of these equations is to calculate maximum production for a given adult rearing space (Fig. 1). This is done by an iterative program which varies the age at which adults are discarded. This is a useful and probably fairly realistic model which at least gives some help with planning insect factories for the sterile male method. However, as pointed out by Monro and Osborn [2] it says nothing about the quality of the harvested insects in stocks subjected to laboratory selection and conditioning.

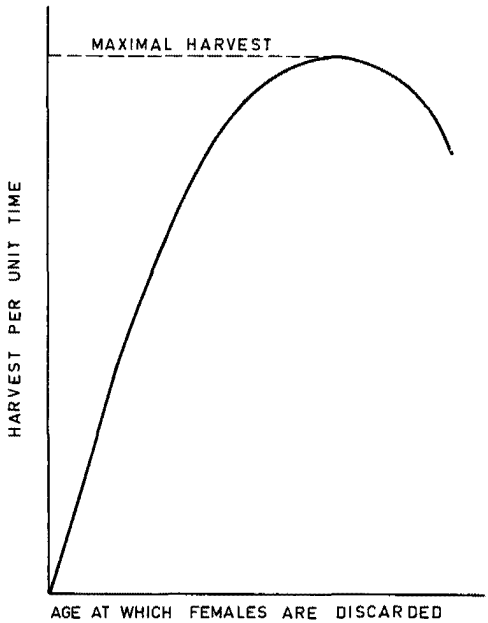


FIG. 1. General form of the harvesting curve (harvest per unit time against age at which adult females are discarded). Stocking rate is constant.

3.2. Residual fertility

One of the difficulties of producing sterile males is to strike a balance between the conflicting demands of sterility and mating efficiency in the field. As the sterilizing dose of radiation increases, damage to the whole physiology also increases and there is some evidence that in some species field longevity and mating performance fall off with increasing dose. The question is: what is the minimum dose which will allow population suppression?

The rate at which sterile males will suppress a population given a fixed rate of release rises from zero as radiation dose increases and fertility falls, but after reaching a maximum it declines again to zero as physiological damage decreases the competitiveness of the irradiated males. The lowest acceptable dose of radiation will be that at which an overwhelming ratio of irradiated to normal males just fails to suppress a population under the most favourable environmental conditions (i.e. those conditions which would give the maximum rate of increase). One assumes an almost infinite sterile to fertile ratio for males and from appropriate l_x and m_x values in Table I calculates the level at which the residual fertility will just allow population replacement. Theoretically, at levels above this the population should increase indefinitely and at levels below it the population should decrease to extinction. By repeated variation of values for the residual fertility of males in a program (RESFER) which simulates unlimited increase, one can obtain critical values of the order of 1% residual fertility for Ceratitis capitata (Wied.), (Mediterranean fruit fly). A word of caution: Under adverse environmental conditions, the pest population may be eradicated by released males with residual fertilities higher than the critical value.

3.3. Laboratory and field predictions of population dynamics in sterile release campaigns

The foremost aim in modelling population suppression on a computer is to predict the rate at which sterile males will achieve suppression. Because the computer can carry out iterative processes very rapidly it can also be used to devise strategies which will optimize the use of sterile males either alone or in combination with other methods. For example, it could predict the optimal number of spray treatments before sterile release and determine the optimal time pattern and rate of release. Ultimately a program could be developed for a particular species in a particular region which would use current spraying, release, weather, crop and field population data to revise the suppression campaign week by week.

Examples of simple computer models of population suppression follow. Details of these models and their FORTRAN programs will be published elsewhere.

(a) Suppression of Cadra cautella Walker (Lepidoptera; Phycitidae): Cadra cautella is a cosmopolitan moth whose larvae attack stored products. Its suppression by sterile males has been simulated on a program of the STER series using the IBM 360 at the IAEA in Vienna.

The life tables on which this is based were experimentally derived by M. T. Ouye and his co-workers at the IAEA Laboratory at Seibersdorf. They also derived a survival table for males which had been sterilized by 40 krad of gamma radiation from ^{60}Co and found a mating competitiveness value of 0.5 compared with unirradiated males.

In the model the population was regarded as starting from a unit population of zygotes consisting of equal numbers of males and females. Population growth was then simulated for a number of different rates of release, these rates of release being multiples of the original number of zygotes; that is, for each original male zygote 10, 20, etc. irradiated male adult moths were released per day. Such constant rates of release lead, in time, to constant standing populations of sterile males. However, because of the origin of the wild population from one batch of eggs, the wild population fluctuates tremendously with long intervals in which there are no adults present. Obviously the best strategy of release would be to release sterile moths only before periods of adult emergence. However if one assumes a constant population of sterile male moths at the time of adult emergence, one can determine release rates of sterile males at which the wild population will stop increasing. From Fig. 2 it is seen that this level is achieved with a daily release rate somewhere between 12.2 and 16.2 times the original population of the male zygotes.

To recapitulate: The assumptions made in constructing this deterministic model are that the population was founded by a single infestation and that this infestation was made up of unit male and female populations as fertilized eggs. The release rates which are shown in Fig. 2 are factors

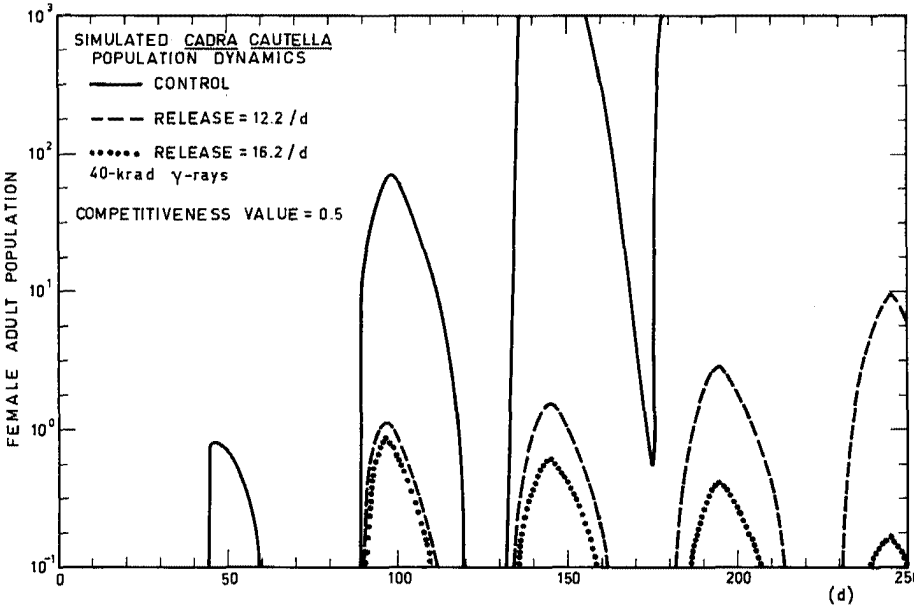


FIG. 2. Simulated population growth of Cadra cautella from a single infestation with no sterile releases and with sterile releases at two rates.

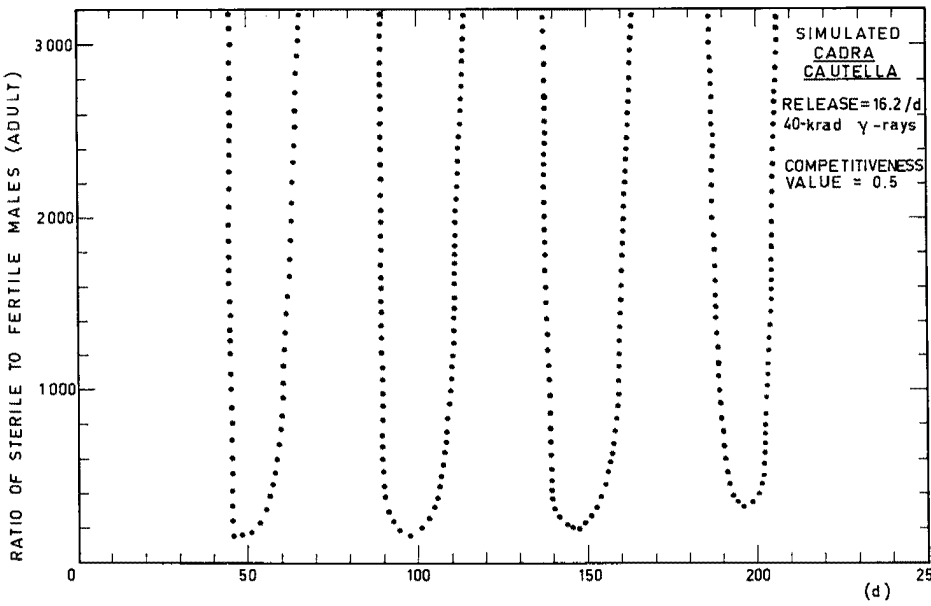


FIG. 3. Changing sterile:fertile male ratios for a constant release rate into the simulated Cadra cautella population.

of this initial founding population; that is, if one had 1000 female eggs and 1000 male eggs in the original infestation, then the release rates represent 12 200 and 16 200 adult sterile moths per day. These curves strikingly demonstrate the effect of population age-structure on the growth of the population. It is not by any means the smooth curve which many of the more mathematical models have predicted in the past.

The model also brings out another point which is worth stressing. One does not achieve some particular sterile to fertile male ratio but rather observes a process in which the ratios fluctuate according to the number of sterile insects present and the age structure of the population. In this example the fluctuations are most extreme because the initial age structure was reduced to a single cohort of eggs. One sees in Fig. 3 that, because most of the life history of Cadra is spent in the egg, larval and pupal stages, the sterile-to-fertile ratio fluctuates tremendously. For this species it is little use to look for any constant or monotonically changing ratio. One should look at the ratios between successive troughs in the ratio of sterile to fertile males. These successive trough-ratios should be increasing if one is suppressing the population. Steadily increasing trough-ratios could be a useful index of success for those many insect pests whose adult population is recruited in bursts. For Cadra this model not only predicts the consequences of various experiments but narrows the range of release rates which should be tested. It also suggests that release rates for this species might be prohibitively high.

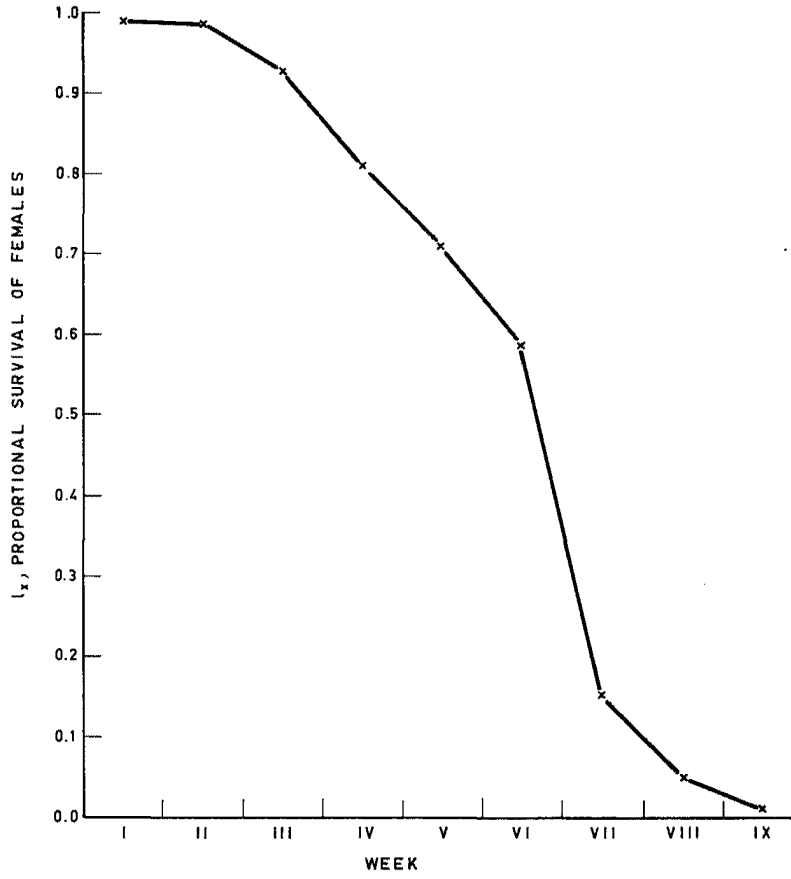


FIG. 4. Survival of female Ceratitis capitata from Seibersdorf Laboratory strain in the laboratory at 25°C.

(b) Population growth and suppression in Ceratitis capitata: One of the most difficult parts of computer simulation is not the modelling, at least not in principle. The real block lies in supplying reliable data to the programmer. For example, much time and care have been spent in collecting laboratory data which are suitable for modelling. The validity of such data in the field is extremely doubtful. Figures 4 and 5 show the age-specific survival and the fecundity curves of the Mediterranean fruit fly (Ceratitis capitata) in the laboratory at 25°C. What happens if one estimates these in the field? Unfortunately, nobody has done this. One can go some of the way towards field conditions by confining adults in field cages and supplying them with food and water. In summer 1971 at Seibersdorf the female survival curve shown in Fig. 6 was obtained and this is quite different from the laboratory curve in Fig. 4, though similar to the survival of

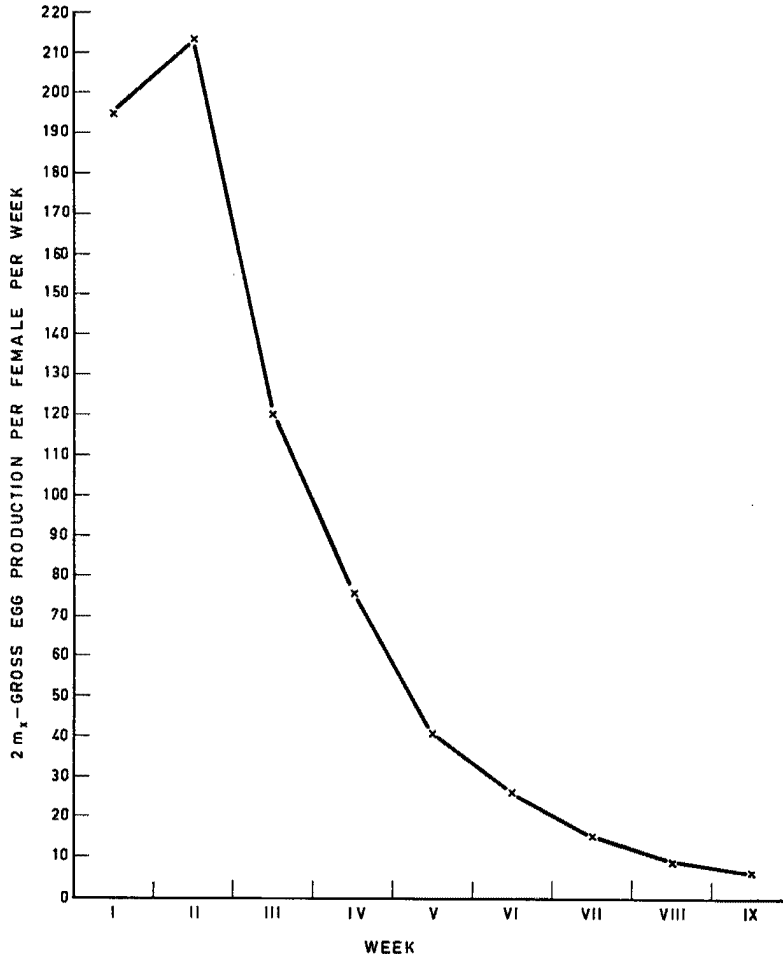


FIG. 5. Gross egg production per female per week for laboratory strain of Ceratitis capitata at 25°C. m_x values are half the values shown.

laboratory stock females in the same field cages. Similar but lower survival rates were found for male Ceratitis both normal and irradiated with 9 krad in the late pupal stage. Survival of both types of male was much lower than survival in laboratory cages.

Finally, I would like to show you a simulation of population growth and suppression in Ceratitis capitata. I have assumed that both male and female survivals are the same as in the field cages at Seibersdorf and that the fecundity is the same as for laboratory flies of the same age. This is a very dangerous assumption but I had no data on field fecundity. It seems that wild flies in nature are seldom short of food and they probably die so rapidly under conditions of food shortage that the effect on mortality is

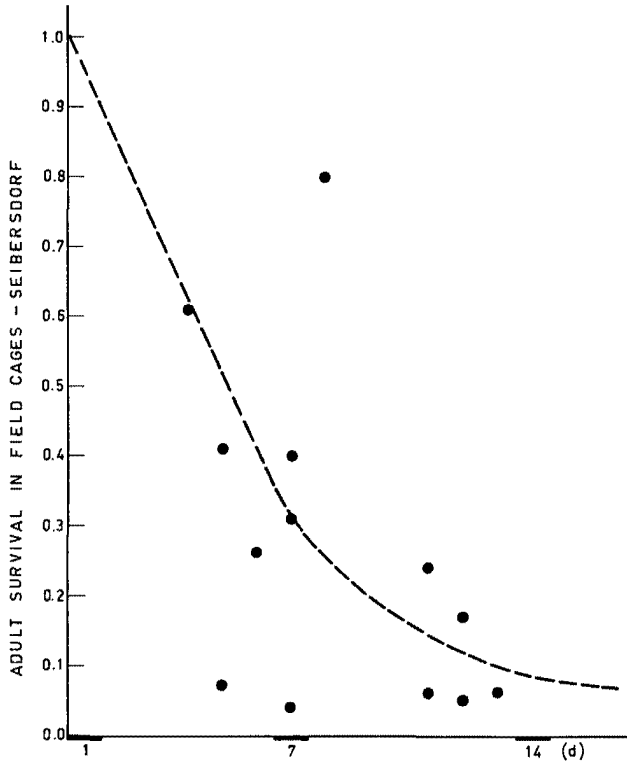


FIG. 6. Survival of wild female Ceratitis capitata in field-cages at Seibersdorf (summer 1971).

likely to be greater than the effect on fecundity. Support for the assumption that the field cage data on survival are reasonably accurate is provided by field observations in the Central American program [3] in which irradiated flies were recovered at about the rate predicted from the survival curves in field cages at Seibersdorf. For modelling Ceratitis I have assumed a competitiveness of 1.0. This figure is at variance with that of many laboratory workers, but based on our field cage experiments in summer 1971 at Seibersdorf.

At first glance it seems surprising that such a short-lived species can survive and increase. Indeed on comparing laboratory and field-cage survivals, I thought that the field cages might be providing an even more severe environment than the natural one. But when modelled, the population increased quite rapidly (Fig. 7). Indeed the simulated population did rather better than the field population which Rhode followed in Central America, suggesting that in the field the rates of survival and fecundity are even lower than assumed.

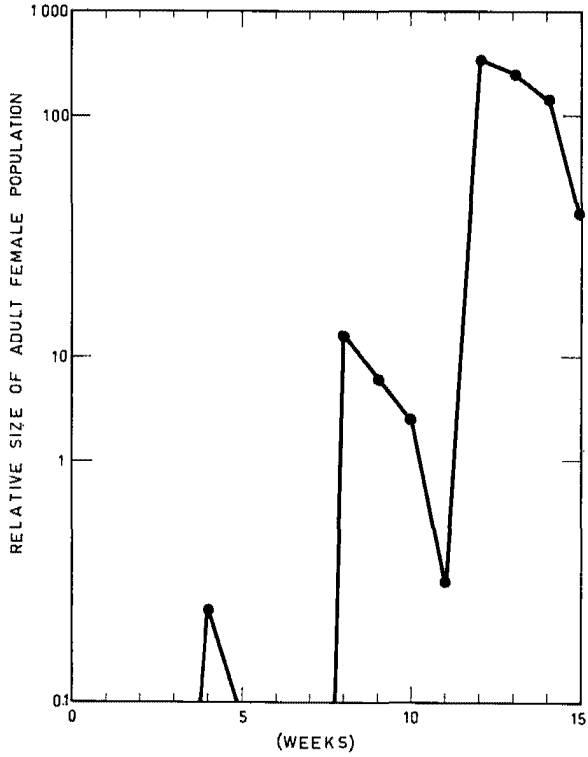


FIG. 7. Simulated Ceratitis capitata population dynamics – unrestricted increase.

Figure 8 presents the results of simulated suppressions of Ceratitis capitata assuming an initial single cohort of eggs, the rate of adult sterile male release being expressed as a ratio to the assumed initial population of either male or female zygotes. A release rate of 20 adult sterile males per week per original male zygote is sufficient to suppress the population. This is quite a cheering result and one may continue to refine this model as more data become available. In particular, one will be able to take account of real age distributions in the field when these data have finally been given by field workers. The time required to achieve a given level of suppression decreases as one would expect with increasing release rate but with declining efficiency as measured by the total number of sterile males released. At approximately 20 : 1 one is achieving suppression in 28 weeks with release of about 600, and at 100 : 1 in about 14 weeks with a total release of about 1400. Of course one should not be simple-minded and imagine that the best strategy here is to reduce one's release rate to the minimum. The major cost is often not that of the insects themselves but of the means of delivering them. One may then have to compromise between number of releases and total number of insects released. For such reasons one's computer models must become more complicated

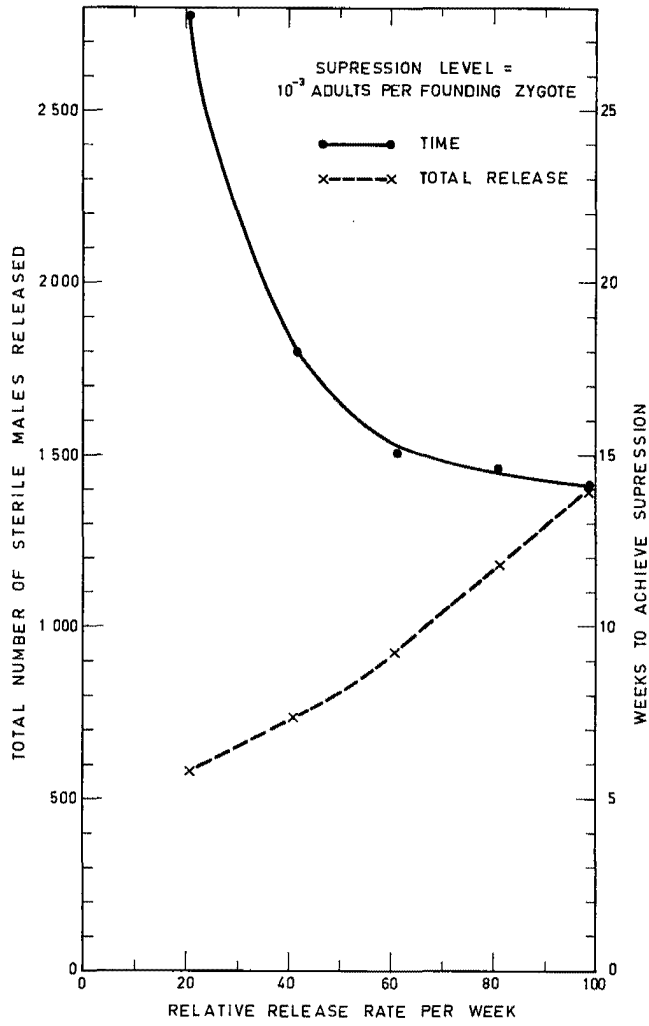


FIG. 8. Simulated suppression of Ceratitis capitata (release rates as a ratio with founding population of fertile zygotes of either sex).

because they must combine all the information which is relevant to the campaign, and this information can only be provided by field workers who are familiar with the principles and the operation of the campaign.

I have not talked about the environmental effects on the treated populations. There are several reasons for this and one of them is that most sterile male programs are aimed at populations which start from a low point in the population cycle and therefore may be assumed to be increasing in an unrestricted way. One does not really know very much about the effects which massive releases have in altering the normal

pattern of population increase except through the effect on fecundity, but adults may also disperse as a result of crowding by the released insects and this would increase the efficiency of the sterile male method. On the other hand, one would expect that, if the treated population is already small, the effects of larval crowding would also be small. In other populations, such as tsetse fly, one might assume that the populations are roughly in equilibrium and these would present other problems.

To incorporate environmental and density dependent influences on the l_x and m_x values in Table I one has no alternative but to measure these in the field. In the long run, assumptions are not going to provide the answers needed. In the future, soundly based sterile male campaigns and indeed almost any campaign of population control are going to depend more and more on good collaboration between ecologists, field operators and computer programmers.

REFERENCES

[1] CURTIS, C.F., JORDAN, A.M., Calculations of the productivity of Glossina austeni Newst. maintained on goats and rabbits, Bull. Entomol. Res. 59 4 (1970) 651.

[2] MONRO, J., OSBORN, A.W., The use of sterile males to control populations of Queensland fruit-fly, Dacus tryoni (Frogg) (Diptera: Tephritidae). I. Methods of mass-rearing, transporting, irradiating, and releasing sterile flies, Aust. J. Zool. 15 (1967) 461.

[3] RHODE, R.H., SIMON, J., PERDOMO, A., GUTIERREZ, J., DOWLING, C.F., Jr., LINDQUIST, D.A., Application of the sterile-insect-release technique in Mediterranean fruit fly suppression, J. Econ. Entomol. 64 3 (1971) 708.

COMPUTER SIMULATION FOR GENETIC CONTROL OF THE ONION FLY Hylemya Antiqua (Meigen)

K.J.A. WIJNANDS-STÄB, M.J. FRISSEL
Association Euratom-Ital,
Institute for Atomic Sciences in Agriculture,
Wageningen,
The Netherlands

Abstract

COMPUTER SIMULATION FOR GENETIC CONTROL OF THE ONION FLY Hylemya Antiqua (Meigen).

A computer model for simulation of onion fly populations in the field is described. The model works with a density-related growth rate and the possibility to randomize the values of growth rate by a Gauss distribution. Equations for the reproductive process are given which allow calculations with steriles as well as with aberrant genotypes. Computer simulations for releases of steriles, translocations and incompatible strains are discussed. The release of translocations can be useful to prevent recovery of a population at the end of a sterile-release program. Suppression of an onion fly population by release of one single translocation seems impossible. Statistical fluctuation of the growth rate may simulate environmental influences, like weather conditions. The influence of statistical fluctuations on the application of sterilized flies is discussed. Schedule and data of a sterile-release field experiment with the onion fly are mentioned, with emphasis on the consequences for computer simulations.

1. INTRODUCTION

The onion fly, Hylemya antiqua (Meigen), has been chosen as one of the models for the genetic control of an agricultural pest in the Netherlands. A team of specialists, experienced in economic entomology, ecology, rearing methods, radiobiology, histopathology and genetics, concentrated in Wageningen[1], are investigating the application of the sterile male technique and the use of translocations for the control of this fly. The computer simulations reported here are part of this research.

2. ONION FLY POPULATION

The adults of the onion fly (F_0) emerge in spring from fields which were infested during the preceding year. The females deposit their eggs (G_1), the first generation of the year, on young onion plantlets, which can be severely affected by the feeding larvae. After two months the adults of the second flight (F_1) emerge, their offspring (G_2) attack the onion bulbs once more. Diapause is induced in some of the pupae of both generations (D_1 and D_2). The first flight of the following spring will emerge

[1] Members of the onion fly team: Inst. of Phytopathological Res.: W. Kelderman, M. Loosjes, J.P.W. Noordink, J. Noorlander, J. Theunissen, J. Ticheler; Agric. Univ., Dept. of Genetics: C. van Heemert; Inst. for Atomic Sci. in Agr.: K.J.A. Wijnands-Stäb.

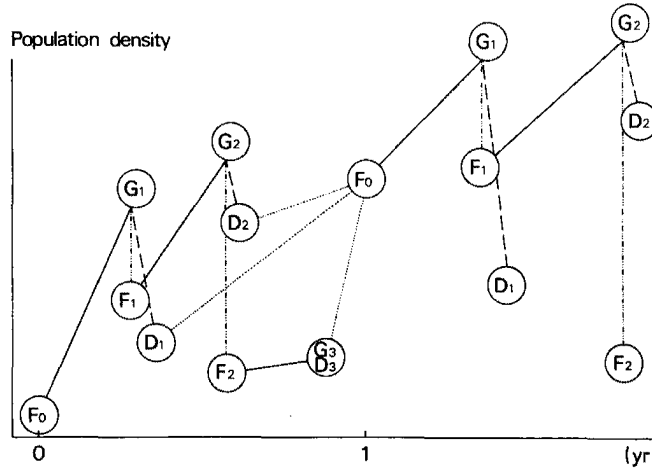


FIG. 1. Population of onion fly. F: adults; G: larval production; D: diapause. Subscripts denote the generations in the course of a year.

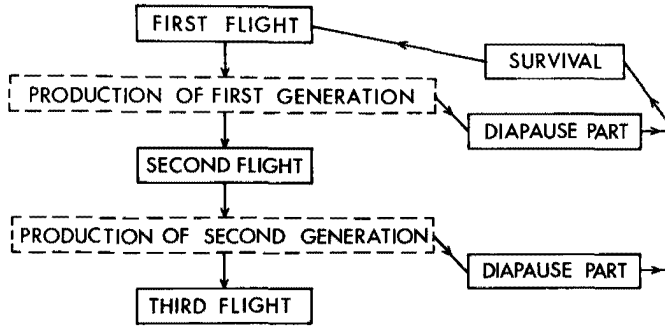


FIG. 2. Simplified flow chart for the model of an onion fly population.

from these pupae. The adults (F_2) of the second generation (G_2) may produce a third generation under favourable circumstances (G_3), which yields only diapause pupae (D_3) and no immediate adults. The scheme of such a population is shown in Fig. 1. The flow chart (Fig. 2), which forms the basis of the computer model, has an analogous construction. The third flight is neglected in the model. The generations are treated as discrete units.

3. SIMULATION MODEL

We assumed that the growth rate of the population was density dependent. Figure 3 represents the curves for growth rate for the first and second generation, as used in the model. The following values were assumed for

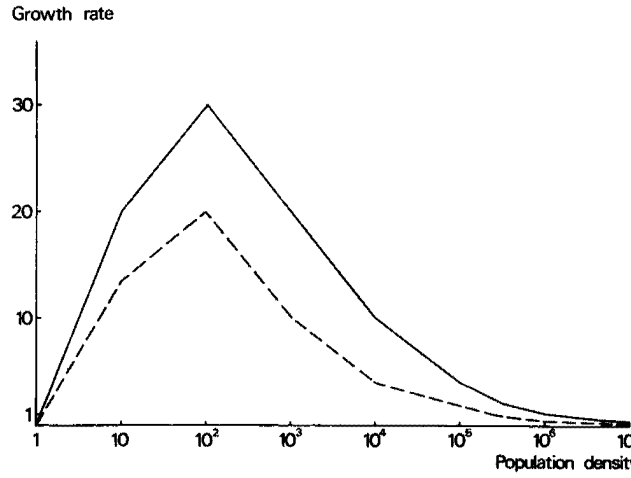


FIG. 3. Growth rate for the first generation (———) and second generation (------) of onion flies.

an undisturbed growth: at very low densities (because mating may be reduced) there is almost no reproduction; the growth rate increases rapidly to 30 for the first generation and 20 for the second generation at densities of 100 flies ha^{-1}. At higher densities it diminishes gradually to 1 and 0.5 respectively at a density of 10^6 flies ha^{-1}, which is supposed to be the maximum density. The real growth of the population is strongly related to the weather. Both temperature and rainfall determine the activity and longevity of the flies and the survival of the larvae, as well as the food supply of the larvae by the growing crop. This variation is simulated by randomizing the values of growth capacity by a Gauss distribution.

For the description of the reproductive process the equations mentioned below were used, which allow calculations of the release of sterilized flies, flies with a chromosomal translocation or with incompatible strains, and combinations of them in the same program. As the sex ratio of the onion fly is 1:1 and both sexes were released, no distinction was made between males and females.

The quantity TT symbolizes translocation homozygotes as an incompatible strain. TN stands for the quantity of hybrids, S for the sterilized flies. Both TT and TN are corrected for the occurrence of inviability of the genotype (correction factors γ_{TT} and γ_{TN}) and sterility of the hybrids (correction factor γ_S). All TT, TN and S are corrected for fitness (factors F_{TT}, F_{TN} and F_S). The corrected values are defined as TT_{eff}, TN_{eff} and S_{eff}. The quantity of normal flies, NN, is of course not corrected.

$$TT_{eff} = TT \times F_{TT} \times \gamma_{TT}$$

$$TN_{eff} = TN \times F_{TN} \times \gamma_{TN}$$

$$S_{eff} = S \times F_S + TN \times F_{TN} \times \gamma_S$$

The effect of sterile flies on reproduction is expressed by the factor DILUTION:

$$SUM = TT_{eff} + TN_{eff} + NN$$

$$TOTAL = SUM + S_{eff}$$

$$DILUTION = SUM/TOTAL$$

The quantities of filial genotypes, $\underline{NN}^*$, $\underline{TT}^*$ and $\underline{TN}^*$ are then calculated by:

$$NN^* = V \times SUM \times \left(\frac{NN + Alt \times TN_{eff}}{SUM}\right)^2 \times DILUTION$$

$$TT^* = V \times SUM \times \left(\frac{TT_{eff} + Alt \times TN_{eff}}{SUM}\right)^2 \times DILUTION$$

$$TN^* = V \times SUM \times \left\{2 \times \frac{TT_{eff} + Alt \times TN_{eff}}{SUM} \times \frac{NN + Alt \times TN_{eff}}{SUM} + \left(\frac{Adj1 \times TN_{eff}}{SUM}\right)^2 + \left(\frac{Adj2 \times TN_{eff}}{SUM}\right)^2\right\} \times DILUTION$$

V is the growth rate, and is a function of the density of the parents (see Fig. 3). Alt, Adj1 and Adj2 are ratios for alternate and adjacent segregation in translocation heterozygotes (Alt + Adj1 + Adj2 = 0.5). Alternate segregation results in the production of normal gametes (N) and gametes with the complete translocation (T) in equal quantities. Adjacent segregation produces unbalanced gametes with part of the translocation. These unbalanced gametes are lethal in combination with N or T, but may survive in combination with a gamete that is their complement. Genetic death, the frequency of lethal zygotes, in the reproductive process equals:

$$1 - \text{filial generation}/(\text{parental generation} \times V)$$

Its complement, the "viability", was used as a correction factor for increased growth capacity if the number of larvae is reduced by genetic death.

The equations for the reproductive process (MACRO-MATING), the Gauss distribution of the growth capacity (MACRO-GAUSS) and the correction of larval survival for viability (MACRO-PRODUCTION) were combined in a subprogram (Fig. 4). This subprogram is called for each time a calculation of growth, viability, etc. is necessary (see Fig. 5).

4. RESULTS OF THE COMPUTER SIMULATION

The model has been used to simulate 10-yr periods in which various releases are applied.

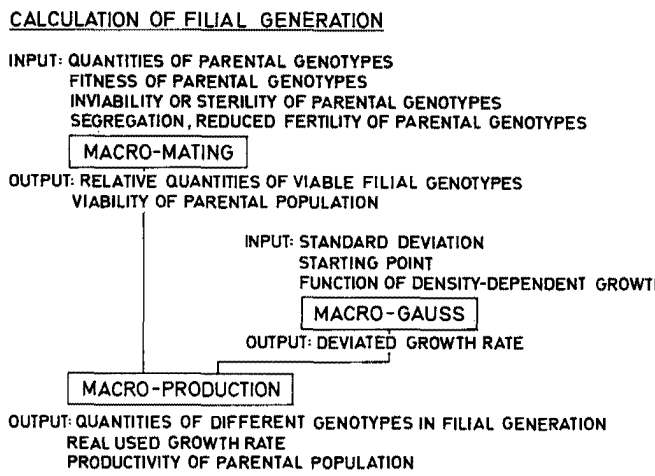


FIG. 4. Construction of the subprogram which is used to calculate growth, viability, etc.

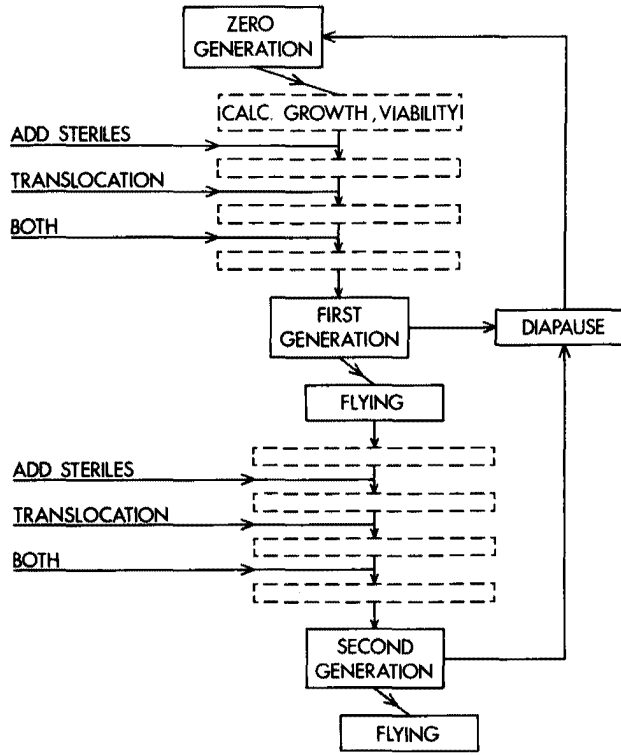


FIG. 5. Flow chart which explains the use of the subprogram for the calculation of growth, viability, etc.

4.1. Translocations

The influence of translocations was investigated first. Calculations were made with only three genotypes, TT, TN and NN, but with various assumptions of their fitness and reduced fertility of the heterozygote.

Figure 6 represents the influence of one release of translocation homozygotes at a ratio 1 : 1 for TT:NN into a population of 10^4 flies ha^{-1}, in fact an idealized case. In curve 1 the growth of the untreated population is represented. Curve 2 shows the growth of the population after release of a translocation with predominantly alternate segregation, which means with only a slight effect on fertility. After release of a translocation with alternate and adjacent segregation in equal proportions, which means a translocation with more impact of fertility, growth occurs following curve 3.

Thus we can conclude that the release of one translocation, although it causes severely reduced fertility in the heterozygous condition, cannot compete with a growth rate as is assumed to occur in the onion fly. Evidently not all possibilities of applying translocations for genetic control have been simulated. Furthermore we have simulated the release of an incompatible strain, producing no viable offspring (curve 4), and a case of hybrid sterility (curve 5), which is the best. Unfortunately, these phenomena have not yet been found in the onion fly, whereas we have indeed induced autosomal translocations. We selected six different strains with semi-sterile heterozygotes. C. van Heemert is investigating their cytogenetics and is trying to obtain them in a homozygous condition.

Figure 7 shows the result of the release of sterilized flies compared with the results after release of a combination of translocated genotypes and steriles.

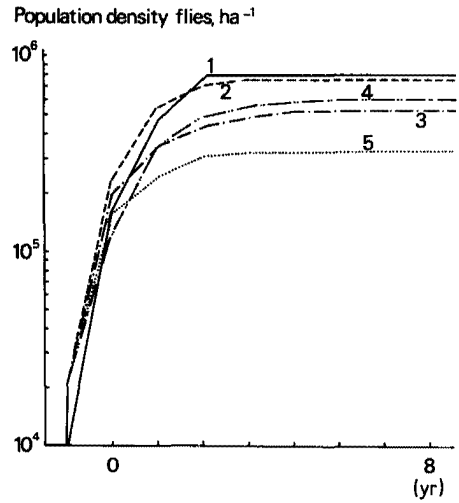


FIG. 6. Release of homozygotes of aberrant genotypes at a ratio TT : NN = 1:1. (1) Population growth without release, initial population $F_0 = 10^4$ flies ha^{-1}; (2) growth after release of translocation with predominantly alternate segretation; (3) growth after release of translocation with alternate and adjacent segregation in equal proportions; (4) growth after release of incompatible strain, producing inviable offspring; (5) growth after release of strain producing sterile hybrids.

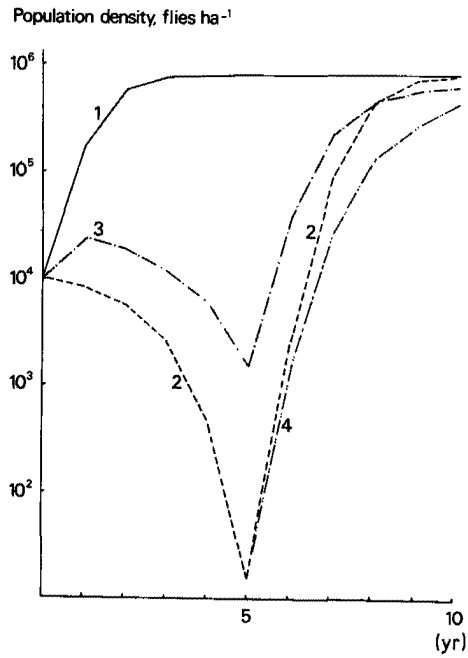


FIG. 7. Population growth after release of steriles compared to the growth after release of translocated genotypes in combination with steriles. (1) Growth of untreated population, initial density 10^4 flies ha^{-1}; (2) release of 2×10^5 steriles to the first flight and of 2×10^5 steriles to the second flight, for 5 yr; (3) same release of steriles as (2), plus initial release of 10^4 translocation homozygotes; (4) same release of steriles as (2), plus release of translocations (ratio 1:1) at the end of the treatment with steriles.

The release of 2×10^5 sterilized flies to the first and the second flight for 5 yr nearly eradicates an initial population of 10^4 flies ha^{-1}. At the end of the release, the population recovers rapidly (Fig. 7(2)). Curve 3 represents the release of the same number of steriles plus an initial release of 10^4 homozygotes of a translocation with semi-sterility in a heterozygous condition. Here the release of the same number of steriles is less effective, because the population is doubled at the start. Finally its recovery is delayed. For curve 4 the same sterile release is applied and translocation homozygotes have been added at the end of the treatment with steriles. With much less translocated flies than in curve 3, the growth rate of the population could be reduced, in the same way as for curve 3.

4.2. Statistical fluctuations

The effect of statistical fluctuations of the growth capacity, as a simulation of environmental factors, is demonstrated in Fig. 8. A Gauss distribution was used with a standard deviation which equals 0.2×the expected growth. Curves 1 and 2 give the growth of an untreated population with an initial density of 10^4 flies ha^{-1} in different runs. Curves 3, 4 and 5 represent populations controlled by an annual release of 228 000 steriles to the first flight and 80 000 to the second flight. For curve 6 no statistical fluctuations

were applied while the population was stabilized by the same release of steriles. In run 3 the allowed fluctuation lead to expansion of the controlled population, in run 4 and 5 the same amount of variation caused extinction of the population. From these curves we may conclude that statistical variation of the growth can be used to simulate the fluctuations in a pest population dependent on variable weather conditions, as long as no better relationship between growth and weather is available.

5. CONFRONTATION OF THE SIMULATION MODEL WITH FIELD EXPERIMENTS

The onion fly team has given priority to the development of a sterile release method [1-4]. In the 1971 season the first field experiment of a series was carried out in an isolated onion field of 1 ha. Pupae consisting of both sexes were sterilized by γ-irradiation. The release was aimed at a ratio of S : N = 20 : 1.

Data were collected on different items during the field experiment. They will be published elsewhere by the members of the team.

Data on the onion fly population as such contain:

(a) Estimation of the number of flies for first and second flight (F_0 , F_1)
(b) The emergence of flies as a function of time
(c) The percentage of mated females
(d) The diapause in the first, second and third generation (D_1, D_2 and D_3).

Data on the performance of sterilized flies consist of:

(a) The emergence of released pupae as a function of time
(b) The percentage of mated females
(c) Estimations of longevity
(d) Estimations of dispersal.

Measurements after release were:

(a) The ratio S/N in females which were trapped and brought back into the laboratory
(b) The ratio S/N for mating, by measuring the number of eggs hatched
(c) The number of pupae produced.

The density of the onion fly during this growing season was very low all over the country. The damage to the crop was scanty.

Measurements on population density in small fields, used as check areas, have failed to be accurate. No reliable estimation for the growth capacity of both generations has been obtained. The second generation produced only diapause pupae, a third flight did not occur.

5.1. Consequences of the simulation model

It is of course impossible to verify from the scarce data which have been obtained till now the correctness of the assumptions used in the model. However, no experimental evidence emerged to indicate that the model was

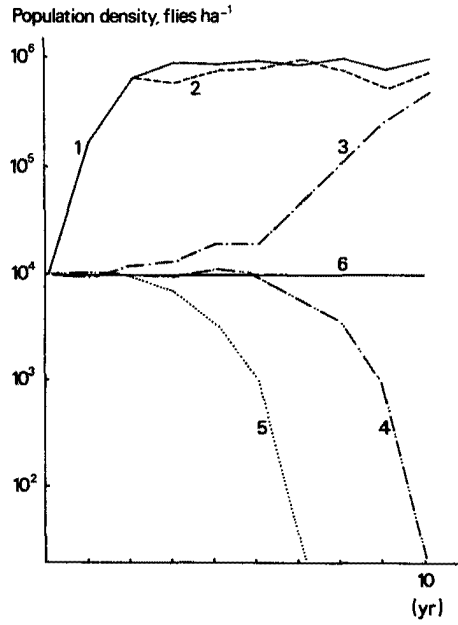


FIG. 8. Effect of statistical fluctuations of the growth capacity. The Gauss distribution is used with a standard deviation which equals 0.2 times the expected growth. (1) and (2) Growth of untreated populations, initial population is 10^4 flies ha^{-1}; (3), (4) and (5) growth of populations controlled by annual release of 228 000 steriles to the first flight and 80 000 steriles to the second flight; (6) growth of the population without statistical fluctuations, stabilized by the same release of steriles.

incorrect. The curve for the growth capacity seems to overestimate the expected growth, the statistical variation of 0.2× the expected growth seems to be too low. As shown in Fig. 8 curve 3, even a statistical variation of 0.2×the expected growth can lead to serious errors in the estimation of the quantities of sterilized flies which are needed. Thus the determination of both the growth rate and its standard deviation deserves much more attention.

A few phenomena, which until now were not included in the model, could be measured in the field rather easily, e.g. the emergence of flies as a function of time, the longevity of sterile flies and the dispersal of the flies. Because these data are of importance for the characterization of the population and the release, they will be included in the next version of the computer program.

ACKNOWLEDGEMENTS

The authors are indebted to all members of the onion fly team for their information and critical advice.

APPENDIX

The program which has been used for computer simulation for the genetic control of the onion fly is represented on pages 105-110. Some points may need comment.

The release of steriles is defined in two different ways:

(a) Following release tables in which the number of sterile flies to be added into the first or second reproductive period is stated beforehand for each year (Function S0TB and S1TB) or
(b) By a fixed ratio between the steriles to be added and the number of fertile flies already present (Parameter EXC0 and EXC1).

In the output data are tabulated for each year

(a) The number of emerging flies in spring of a population controlled by release of sterile flies at a fixed ratio (WNTR).
(b) The viability as a result of the release of steriles into the first reproductive period (VIA0S), and the second reproductive period (VIA1S).
(c) The total number of sterile flies released in the preceeding years (ACCSTE).
(d) The number of emerging flies in spring of an untreated population in the same conditions (R0CC).

In addition, WNTR is represented graphically on a logarithmic scale.

The simulated case should be considered as an illustration for the program, not as a proposal for a campaign.

```
TITLE POPULATION REDUCTION BY RELEASE OF STERILE OR TRANSLOCATED FLIES
*                                  WIJNANDS AND FRISSEL, ASS EURATOM-ITAL

*                                6 JAN.1972, VERSION 2

*   SEQUENCE FOR TRANSLOCATIONS IS ALWAYS TT NN TN

*  DESCRIPTION SUBPROGRAMS (CALLED MACRO'S)

*   DESCRIPTION OF GENEPOOL AND FORMATION OF NEW VIABLE COMBINATIONS

MACRO   RP, RQ, RH,   VIABF = MATING (PP, Q, HH, SS, V)
PROCEDURAL

*   PP=QUANTITY OF TT, Q=QUANTITY OF NN, HH=QUANTITY OF TN,...
*   SS=QUANTITY OF STERILISED FLIES, V=GROWTH RATE.

      P=PP*FITTT
      H=HH*FITTN
      P=P*FLAGTT
      H=H*FLAGTN
      S=SS*FITS+H*INSW(FLOG,1., 0.)
      H=H*INSW(FLOG,0., 1.)

*   P,H,S ARE EFFECTIVE QUANTITIES CORRECTED FOR FITNESS AND COMPETITIVENESS
*   FLAG= 0, IN CASE OF INVIABILITY OF A GENOTYPE  , NORMALLY FLAG= 1.
*   NORMALLY FLOG=+1, FLOG=-1, IN CASE OF HYBRID STERILITY
*   FLAGTN AND FLOG ARE NEVER AT THE SAME TIME UNEQUAL TO +1.

       T = P+Q+H

*          BA STANDS FOR THE FRACTION OF BALANCED GAMETES, N OR T.
*          U1 AND U2 STAND FOR FRACTIONS OF UNBALANCED GAMETES
*          OF ADJACENT1 AND ADJACENT2 SEGREGATION.

      DIL=T/(T+S)
*   DILUTION = FACTOR FOR THE INFLUENCE OF STERILISED FLIES

*   RP, RQ AND RH ARE QUANTITIES OF FILIAL GENOTYPES
      RP = V*T*((P+BA*H)/T)**2 *DIL
      RQ = V*T*((Q+BA*H)/T)**2 *DIL
      RH=V*T*((P+BA*H)/T*(Q+BA*H)/T*2.+((U1*H)/T)**2+((U2*H)/T)**2)*DIL
      RP=RP*FLAGTT
      RH=RH*FLAGTN

      VIABF =(RP+RQ+RH)/((PP+Q+HH*INSW(FLOG,0.,1.))*V)
*   1-VIABF = GENETIC DEATH
*     VIABF = VIABILITY FACTOR DUE TO BOTH TRANSLOCATIONS AND STERILES
ENDMAC

**************************************************************************

*   GENERATION OF RANDOM VALUES FOR GROWTH RATE

MACRO VUIT = GAUS(VIN, P1, A)

                              A  = STANDARD DEVIATION OF GROWTH RATE
                              P1 = ARBITRARY ENTRY POINT

      VD = A*VIN
      VUIT1 = GAUSS(P1, VIN, VD)

*                             GENERATED IS A GAUSS DISTRIBUTION
*                             WITH A MINIMUM OF 5 PERCENT AND
*                             WITH A MAXIMUM OF 195 PERCENT

      VUIT2 = FCNSW(YEAR, VUIT1, VIN, VUIT1)
      VUIT3 = INSW((VUIT2 - 1.95*VIN), VUIT2, (1.95*VIN))
      VUIT  = INSW((VUIT3 -0.05*VIN), (0.05*VIN), VUIT3)

ENDMAC

**************************************************************************
```

```
*   CALCULATION OF REAL NUMBER OF ADULTS IN NEXT GENERATION
*   ROUTINE MATING IS COMBINED WITH GROWTH RATE CORRECTIONS

MACRO XW,YW,ZW,VIAB,VVUIT,PR = PROD(TT,NN,TN,S,SEULT,VTB, PP1, AA)
*  CALCULATION VIABILITY
*   W = DUMMY VALUE FOR V
      W=1.
      XX,YY,ZY, VIAB = MATING(TT,NN,TN,S,W)

      HOEVLH=(TT+NN+TN*INSW(FLOG, 0.,1.))* VIAB
      ALL=TT+NN+TN+S
      SEUL=AFGEN(SEULT,ALL)
      VV=SEUL*AFGEN(VTB,HOEVLH)

*   HOEVLH = TOTAL OF PARENTS, STERILES EXCLUDED
*   SEUL = FACTOR FOR EFFECT OF NO MATING AT VERY LOW DENSITIES
*   VV = GROWTH RATE AS FUNCTION OF DENSITY AND CORRECTED FOR ...
*   INCREASED SURVIVAL AT RELATIVE REDUCED NUMBERS.

      VVUIT=GAUS(VV,PP1,AA)
*   VVUIT = GROWTH RATE MODEFIED FOR AT RANDOM VARIATIONS
*   DEFINITE CALCULATION OF NEXT GENERATION.
      XW,YW,ZW,VIB = MATING(TT,NN,TN,S,VVUIT)

      PR=VVUIT*VIAB
*   PR = PRODUCTIVITY (GROWTH RATE * VIABILITY )
ENDMAC

**********************************************************************


*        INITIAL DATA MAIN PROGRAM
INITIAL

PARAMETER CASENR=10.
PARAMETER  RONNI = 10000.
*         INITIAL QUANTITY OF FLIES PER HA

PARAMETER BA=0.25, U1=0.25,  U2=0.

PARAMETER FLAGTT=1., FLAGTN=1.
PARAMETER FITTT=1.,  FITTN=1.
PARAMETER FITS=1.
PARAMETER FLOG= 1.

FUNCTION VNT  = 0., 30.              ,100., 30.   ,  1000., 20.  ,  ...
10000., 10., 1.E+05,4.,  2.25E+05, 3., 4.E+05, 2., 7.E+05, 1.35,   ...
9.E+05, 1.1, 1.E+06, 1., 1.5E+06, 0.9, 6.E+06, 0.6, 1.E+07, 0.4

FUNCTION VET  = 0.,  20.              ,  100., 20.  ,  1000.,  10., ...
1.E+04, 4., 1.E+05, 2., 2.6E+05, 1.4, 4.5E+05, 1., 7.E+05, 0.7,     ...
1.E+06, 0.5,  1.5E+06, 0.3

*   VN AND VE ARE GROWTH RATES SPECIFIED FOR FIRST AND SECOND REPROD. PERIOD

FUNCTION SEULTB = 0., 0.   ,   10., 0.67    ,    100., 1.,   1.E+07,  1.

FUNCTION S0TB = 0., 0.  ,10., 0.
FUNCTION S1TB = 0., 0.  ,  10., 0.
*                            TABLES FOR RELEASE OF STERILISED FLIES

PARAMETER EXC0 = 24., EXC1 = 8.
*    EXC = RATIO STERILISED/OTHERS AT RELEASE TIME

      FUNCTION LTT0TB =  0., 0., 10., 0.
      FUNCTION LTT1TB =  0., 0., 10., 0.
      FUNCTION LTN0TB = 0., 0., 10., 0.
      FUNCTION LTN1TB =  0., 0., 10., 0.
*                            TABLES FOR RELEASE OF TT AND TN
```

```
PARAMETER  D1 = 0.5,    D2 = 0.9,        SV = 0.9
*         FRACTION DIAPAUSE IN PUPAE , SURVIVAL FRACTION.
*                                    M = MORTALITY = 1-SV

      FIXED P1, P2
PARAMETER A = 0.0, B = 0.0, P1 = 1
*   PARAMETERS FOR STANDARD DEVIATION IN MACRO GAUSS

**********************************************************************


*        DYNAMIC PART MAIN PROGRAM
DYNAMIC
NOSORT
*   TREATED POPULATION

*      OVERWINTERING
*      =============
       ROTT=DIAPTT
       RONN=DIAPNN
       ROTN=DIAPTN

       IF(YEAR.EQ.0.) ROTT = 0.
       IF(YEAR.EQ.0.) RONN = RONNI
       IF(YEAR.EQ.0.) ROTN = 0.

       WNTR=ROTT+RONN+ROTN

*                              ( CALCULATION OF VIABILITY )
*                              (NO TRANSLOCATIONS, NO STERILES)
       S0 = 0.
SORT
       X,Y,Z,VIA0 ,V0 ,PR0  = PROD(ROTT,RONN,ROTN,S0,SEULTB,VNT,P1,A)
NOSORT


*                              ( CALCULATION OF VIABILITY )
*                              (NO TRANSLOCATIONS,BUT STERILES)
       S0 = EXC0* WNTR
*   ADDITION OF STERILES ACCORDING RATIO STERILES/NORMALS
SORT
       X,Y,Z,VIA0S,V0S,PR0S = PROD(ROTT,RONN,ROTN,S0,SEULTB,VNT,P1,A)
NOSORT


*                              ( CALCULATION OF VIABILITY )
*                              (   TRANSLOCATIONS, NO STERILES)
       S0=0.
*                 ADDITION OF TRANSLOCATIONS ACCORDING RELEASE TABLES
       LTT0 = AFGEN(LTT0TB, YEAR)
       LTN0 = AFGEN(LTN0TB, YEAR)
       ROTN = ROTN + LTN0
       ROTT = ROTT+LTT0
SORT
       X,Y,Z,VIA0T,V0T,PR0T = PROD(ROTT,RONN,ROTN,S0,SEULTB,VNT,P1,A)
NOSORT

       WNTRTR = ROTT+RONN+ROTN
       NEGTR0 = WNTRTR/WNTR
*      NEGTR0 = CORR FACTOR OF PRODUCTIVITY (PROT AND PROST) DUE TO EXTRA PARENTS
       PR0T   = PR0T*NEGTR0

*                              ( CALCULATION OF VIABILITY AND RESULT OF MATING)
*                              (   TRANSLOCATIONS AND STERILES)
       S0 = EXC0* WNTR

*         PRODUCTION  OF FIRST GENERATION
*          ============================
SORT
R1TT,R1NN,R1TN,VIA0ST,V0ST,PR0ST=PROD(ROTT,RONN,ROTN,S0,SEULTB,VNT,P1,A)
NOSORT
       PR0ST = PR0ST*NEGTR0
```

```
      MAT1 = R1TT+R1NN+R1TN
      F1TT = (1-D1)*R1TT
      F1NN = (1-D1)*R1NN
      F1TN = (1-D1)*R1TN

*   MAT1 = TOTAL SURVIVING OFFSPRING, PRODUCED IN FIRST MATING PERIOD
*   F1TT, F1NN, F1TN ARE QUANTITIES OF ADULTS IN SECOND FLIGHT

      P2 = P1+2

*                              ( CALCULATION OF VIABILITY )
*                              (NO TRANSLOCATIONS, NO STERILES)
      S1 = 0.
SORT
      X,Y,Z, VIA1 ,V1 ,PR1  = PROD(F1TT,F1NN,F1TN,S1,SEULTB,VET,P2,B)
NOSORT


*                              ( CALCULATION OF VIABILITY )
*                              (NO TRANSLOCATIONS,BUT STERILES)
      S1 = EXC1 * F1T
*    EXC= RATIO STERILISED/OTHERS AT RELEASE TIME
SORT
      X,Y,Z, VIA1S,V1S,PR1S = PROD(F1TT,F1NN,F1TN,S1,SEULTB,VET,P2,B)
NOSORT

*                              ( CALCULATION OF VIABILITY )
*                              (   TRANSLOCATIONS, NO STERILES)
      S1 = 0.
      F1T = F1TT+F1NN+F1TN
*                   ADDITION OF TRANSLOCATIONS ACCORDING RELEASE TABLES
      LTT1 = AFGEN(LTT1TB, YEAR)
      LTN1 = AFGEN(LTN1TB, YEAR)
      F1TT = F1TT + LTT1
      F1TN = F1TN + LTN1
SORT
      X,Y,Z, VIA1T,V1T,PR1T = PROD(F1TT,F1NN,F1TN,S1,SEULTB,VET,P2,B)
NOSORT

      F1TTR = F1TT+F1NN+F1TN
      NEGTR1 = F1TTR/F1T
*   NEGTR1 = CORR. FACTOR OF PRODUCTIVITY (PR1T AND PR1ST) DUE TO EXTRA PARENTS
      PR1T = PR1T*NEGTR1

*                              ( CALCULATION OF VIABILITY AND RESULT OF MATING)
*                              (   TRANSLOCATIONS AND STERILES)
      S1 = EXC1 * F1T


*        PRODUCTION OF SECOND GENERATION
*        ===============================
SORT
R2TT,R2NN,R2TN,VIA1ST,V1ST,PR1ST=PROD(F1TT,F1NN,F1TN,S1,SEULTB,VET,P2,B)
NOSORT
      PR1ST = PR1ST*NEGTR1


      MAT2 = R2TT+R2NN+R2TN

*   MAT2 = TOTAL SURVIVING OFFSPRING, PRODUCED IN SECOND MATING PERIOD


*         DIAP = NUMBERS OF PUPAE SURVIVING WINTER

      DIAPTT = (D1*R1TT+D2*R2TT)*SV
```

```
      DIAPNN = (D1*R1NN+D2*R2NN)*SV
      DIAPTN = (D1*R1TN+D2*R2TN)*SV
      DIAP = DIAPTT+DIAPNN+DIAPTN

      VREAL = DIAP/WNTR
*                   VREAL = GROWTH RATIO FOR ONE YEAR

      ACCSTE = INTGRL (0.,(S0 + S1))
*                   ACCSTE = ACCUMULATOR FOR RELEASED STERILES ...
*                   ACCUMULATES OVER TOTAL TIME INTERVAL

    LWNTR = ALOG10(WNTR+1.E-50)
*   LWNTR = LOGARITME OF WNTR

************************************************************************

* CALCULATION FOR UNTREATED POPULATION AS REFERENCE

*                       A1CC = FLYING PART OF FIRST GENERATION
*                       A2CC = FLYING PART OFSECOND GENERATION
*                       DIAPCC = PUPAE SURVIVING WINTER

*   SAME CALCULATION SCHEME, NOT SPECIFIED

      R0CC = DIAPCC
      IF (YEAR.EQ.0.) R0CC = R0NNI
      CV0  = AFGEN(VNT , R0CC)
      VCV0 = GAUS(CV0, P1, A)
      R1CC = VCV0*R0CC
      A1CC = (1-D1)*R1CC
      CV1  = AFGEN(VET , A1CC)
      VCV1 = GAUS(CV1, P2, B)
      R2CC = VCV1*A1CC
      A2CC = (1-D2)*R2CC
      DIAPCC = (D1*R1CC + D2*R2CC)*SV

************************************************************************

*    FINTIM = SIMULATED TIME, OTHER INSTRUCTIONS ARE MACHINE CONTROL STATEMENTS
TIMER    FINTIM = 10., DELT = 1., OUTDEL = 1., PRDEL = 1.
RENAME  TIME = YEAR
METHOD  RECT
/     CALL ERRSET (209, 256, -5, 1)
/     CALL ERRSET (208, 256, -5, 1)

*   OUTPUT INSTRUCTIONS
PRINT WNTR, VIA0S, VIA1S, ACCSTE, R0CC
PRTPLT  LWNTR(3., 6., VIA0ST, VREAL)
END
```

YEAR	=	0.0	WNTR	=	1.0000E 04	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	5.0000E 04	VIAOST=		1.0000E 00	VOST =	1.0000E 01	VIAIST= 1.0000E 00
			DIAP	=	1.7100E 05	ACCSTE=		0.0	ROCC =	1.0000E 04	
YEAR	=	1.0000E 00	WNTR	=	1.7100E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	2.9344E 05	VIAOST=		1.0000E 00	VOST =	3.4320E 00	VIAIST= 1.0000E 00
			DIAP	=	5.8012E 05	ACCSTE=		0.0	ROCC =	1.7100E 05	
YEAR	=	2.0000E 00	WNTR	=	5.8012E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.6692E 05	VIAOST=		1.0000E 00	VOST =	1.6097E 00	VIAIST= 1.0000E 00
			DIAP	=	7.9075E 05	ACCSTE=		0.0	ROCC =	5.8012E 05	
YEAR	=	3.0000E 00	WNTR	=	7.9075E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.8891E 05	VIAOST=		1.0000E 00	VOST =	1.2366E 00	VIAIST= 1.0000E 00
			DIAP	=	8.1754E 05	ACCSTE=		0.0	ROCC =	7.9075E 05	
YEAR	=	4.0000E 00	WNTR	=	8.1754E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.9178E 05	VIAOST=		1.0000E 00	VOST =	1.2031E 00	VIAIST= 1.0000E 00
			DIAP	=	8.2097E 05	ACCSTE=		0.0	ROCC =	8.1754E 05	
YEAR	=	5.0000E 00	WNTR	=	8.2097E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.9208E 05	VIAOST=		1.0000E 00	VOST =	1.1988E 00	VIAIST= 1.0000E 00
			DIAP	=	8.2133E 05	ACCSTE=		0.0	ROCC =	8.2097E 05	
YEAR	=	6.0000E 00	WNTR	=	8.2133E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.9211E 05	VIAOST=		1.0000E 00	VOST =	1.1983E 00	VIAIST= 1.0000E 00
			DIAP	=	8.2137E 05	ACCSTE=		0.0	ROCC =	8.2133E 05	
YEAR	=	7.0000E 00	WNTR	=	8.2137E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.9212E 05	VIAOST=		1.0000E 00	VOST =	1.1983E 00	VIAIST= 1.0000E 00
			DIAP	=	8.2137E 05	ACCSTE=		0.0	ROCC =	8.2137E 05	
YEAR	=	8.0000E 00	WNTR	=	8.2137E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.9212E 05	VIAOST=		1.0000E 00	VOST =	1.1983E 00	VIAIST= 1.0000E 00
			DIAP	=	8.2137E 05	ACCSTE=		0.0	ROCC =	8.2137E 05	
YEAR	=	9.0000E 00	WNTR	=	8.2137E 05	VIAO	=	1.0000E 00	VIAOS =	1.1983E 00	VIAOT = 1.0000E 00
			FIT	=	4.9212E 05	VIAOST=		1.0000E 00	VOST =	1.1983E 00	VIAIST= 1.0000E 00
			DIAP	=	8.2137E 05	ACCSTE=		0.0	ROCC =	8.2137E 05	
YEAR	=	1.0000E 01	WNTR	=	8.2137E 05	VIAO	=	1.0000E 00	VIAOS =	1.0000E 00	VIAOT = 1.0000E 00
			FIT	=	4.9212E 05	VIAOST=		1.0000E 00	VOST =	1.1983E 00	VIAIST= 1.0000E 00
			DIAP	=	8.2137E 05	ACCSTE=		0.0	ROCC =	8.2137E 05	

LWNTR VERSUS YEAR

MINIMUM 3.0000E 00 — MAXIMUM 6.0000E 00

YEAR	LWNTR	I	VIAOST	VREAL
0.0	4.0000E 00	----------+	1.0000E 00	1.7100E 01
1.0000E 00	5.2330E 00	----------+	1.0000E 00	3.3925E 00
2.0000E 00	5.7635E 00	----------+	1.0000E 00	1.3631E 00
3.0000E 00	5.8980E 00	----------+	1.0000E 00	1.0339E 00
4.0000E 00	5.9125E 00	----------+	1.0000E 00	1.0042E 00
5.0000E 00	5.9143E 00	----------+	1.0000E 00	1.0004E 00
6.0000E 00	5.9145E 00	----------+	1.0000E 00	1.0000E 00
7.0000E 00	5.9145E 00	----------+	1.0000E 00	1.0000E 00
8.0000E 00	5.9145E 00	----------+	1.0000E 00	1.0000E 00
9.0000E 00	5.9145E 00	----------+	1.0000E 00	1.0000E 00
1.0000E 01	5.9145E 00	----------+	1.0000E 00	1.0000E 00

REFERENCES

[1] FRISSEL, M.J., WIJNANDS-STÄB, K.J.A., "Computer modelling of the dynamics of insect populations", these Proceedings, Paper IAEA-PL-466/2.

[2] NOORDINK, J.Ph.W., "Irradiation, competitiveness and the use of radioisotopes in sterile-male studies with the onion fly, Hylemya antiqua (Meigen)", Sterility Principle for Insect Control or Eradication (Proc. Symp. Athens, 1970), IAEA, Vienna (1971) 323.

[3] THEUNISSEN, J., "Radiation pathology in Hylemya antiqua (Meigen): outlines of research", Ibid., p.329.

[4] TICHELER, J., "Rearing of the onion fly, Hylemya antiqua (Meigen), with a view to release of sterilized insects", Ibid., p.341.

DYNAMIC ASPECTS OF THE PALA STERILE HYBRID FIELD EXPERIMENT

C. B. CUELLAR
Ross Institute of Tropical Hygiene,
London School of Hygiene and Tropical Medicine,
University of London,
London
United Kingdom

Abstract

DYNAMIC ASPECTS OF THE PALA STERILE HYBRID FIELD EXPERIMENT.
In Pala, near Bobo Dioulasso, Upper Volta, West Africa, about 240 000 sterile male hybrids of the cross Anopheles gambiae species B/Anopheles melas were released over nine weeks into a declining population of Anopheles gambiae species A. On prima facie evidence it was concluded that the sterile males were not mating on any significant scale with the target females. However, a reassessment of the available data has suggested the strong possibility that many of the captured females could have been survivors from the massive emergencies which took place before the beginning of the trial and from the period where the releases were insufficient, and also that the emerging target females suffered extra mortality in the field during the period of releases. For the scientist, field experiments are not success-failure gambles, but an opportunity for practical feedback and the generation of ideas for further field and laboratory work.

In Pala, near Bobo Dioulasso, Upper Volta, West Africa, some 240 000 sterile male hybrids were released into a declining wild population of Anopheles gambiae species A mosquitoes from October 1968 through January 1969 [1]. These hybrids were produced from a cross of Anopheles gambiae species B (Kano) males and Anopheles melas females. Laboratory experiments had been very encouraging, showing in many cases that the observed proportion of fertilized females was less than that expected on the basis of the proportion of sterile males [2]. It was concluded that the sterile hybrids showed increased mating ability.

The cross used in the field experiment produced a distorted sex ratio in favour of the males, thus simplifying logistics and predictions. In the event of the few hybrid females mating with the wild males of the target population their offspring would be triple hybrid, exhibiting male sterility as well, since the target species was not a parent of the selected cross. Anopheles gambiae-transmitted malaria has proved to be very resilient to orthodox residual insecticide spraying in tropical Africa, and this fact alone justifies the exploration of new methods and techniques, even when, in the event of their being successful, their application on a mass scale would involve almost insuperable difficulties.

The high spirits at the beginning of the trial turned into gloom when the great majority of the females captured in the houses of the village where the releases were made oviposited fully fertile clutches. Only 3.36% of those females laid eggs presumably attributed to a mating with a sterile hybrid. At the same time a very high proportion of the male mosquitoes captured inside houses were sterile hybrids (from 38% to 91% in the last seven weeks of the releases). G. Davidson, discoverer of the method and

scientist in charge of the field experiment wrote [1]: "It was concluded from this field trial that the sterile males were not mating on any significant scale with the natural species A females. This could have been due to a number of factors but the most important is considered to be an ethological one – a mating barrier preventing mating between introduced sterile males and natural females. This is strongly expressed under natural conditions but not operative in the limited confines of a cage."

These conclusions stimulated a search for mating barriers between the members of the complex, especially between the two better-known freshwater forms provisionally designed as species A and B which have been found coexisting in some localities. Cubbin [3] recorded male and female activity of four species of the Anopheles gambiae complex and hybrids between them in individual soundproof chambers after lights off and also in complete darkness. Little difference between all studied species in amount and pattern of activity was evident. However there is still at least one hypothesis in need of testing: it has been thought possible that mating may occur in different spatial locations at the same time or at different times in the same places, in the latter case triggered by responses to different light intensities. Thus two populations could remain reproductively isolated when sharing the same area and breeding places.

In terms of the field experiment proper another approach would also be the explorations of the theoretical dynamics of the target population. This was done through modifying the original computer simulation model [4, 5] to consider a target population during a seasonal decline. Anopheles gambiae species A in Pala reaches high densities during the rainy season. When the dry weather comes the high-yield temporary pools dry up and breeding is restricted to a few low-yield places in which it is difficult to find larvae and pupae. These permanent breeding places have an abundance of predators (frogs and fish). This situation was easily simulated in the form of a diminishing daily yield using for guidance the female-per-room index (fpr). This index was 6.8 during the first week of releases, dropping steadily week by week until the value of 0 was recorded during the 9th week. There was a recovery to 0.02 during the 10th and last week of the experiment, in which no releases were made.

Taking all these figures as input data for the simulation model would have meant that the target population had no daily yield during the 9th week. For this reason the seasonal drop was "stabilized" (for the model) slightly above 0.4 fpr, i.e. a daily yield of 200 mosquitoes of both sexes, using the same conversion factors as Davidson's [1].

Even though the maximum length of life of individual females was taken as 32 d it was possible to approximate the low proportion of sterile layings, as Table I shows. The ratio of sterile to total males was approximated by introducing a partial mating barrier. For the purposes of the sterile layings only, the model suggested that 500 sterile hybrids, introduced daily into a declining population that in the 6th week stabilized at a ratio of 5 : 1 (5 introduced males to 1 wild), could produce only a low proportion of sterile layings. The reason for this was the high number of female survivors from the period before and at the beginning of the releases where the probability of a fertile mating was either 1.0 or not much lower (a properly fertilized female continues to lay fertile eggs until the end of her life). The next step was to run a series of "mock trials" to explore the possibility of eradication utilizing the same input as that shown in Table I, with the

TABLE I. WEEKLY DATA OBTAINED IN THE VILLAGE OF PALA AFTER INITIATION OF STERILE MALE RELEASES

Week	1	2	3	4	5	6	7	8	9	10
Females per room	6.8	5.0	1.9	1.3	0.9	0.4	0.3	0.1	0	0.02
Observed sterile layings	1/96	—	3/57	3/87	2/34	3/58	0/10	0/4	0/0	0/2
Females per room (input data)	6.8	5.0	1.9	1.3	0.9	0.4	0.4	0.4	0.4	0.4
Expected sterile layings	—	—	0.7/57	2.7/87	1.7/34	6.2/58	1.8/10	1/4	—	—

Input data: Daily survival of females: 0.9.
Oviposition: the first oviposition on the 4th day after emergence and all the others every 2 d thereafter.
Maximum life of a female: 32 d.
Aquatic cycle: 7 d.
Maximum probability of aquatic survival (egg to adult emergence): 0.9.
Size of egg clutch: 150 eggs.
Daily releases: 4000 sterile males.
Partial mating barrier: 0.125 (8 sterile males as competitive as 1 wild fertile male).

exception of the maximum probability of aquatic survival which was deemed to be very low in the permanent breeding places on account of their different ecological conditions. When that probability was reduced to a figure whose meaning in biological terms was a potential rate of increase of less than 5x, eradication would have been accomplished, but only after a further 14 weeks of releases as a minimum. However tempting, these considerations should remain in the realm of speculation for the time being.

With respect to a potential rate of increase of 5x or less, it can be said that accurate quantitative data on anopheline populations under pressure in the field do not appear to exist, though the very high biotic potential of laboratory colonies under "ideal" conditions of density and food and in the absence of obvious pathogens and predators is well known. Thus it would appear somewhat risky to assume that in the dry season the potential rate of increase of a population of Anopheles gambiae s.l., even in low-yield permanent breeding places, would not surpass 5x. This led to further analyses of the Pala Field Experiment.

Interestingly, the computer simulations done under different "yield trend" situations showed that it is easier to detect an impact on a target population (e.g. the proportion of sterile layings) if sterile males are released when the daily yield is increasing. However, if the aim is to

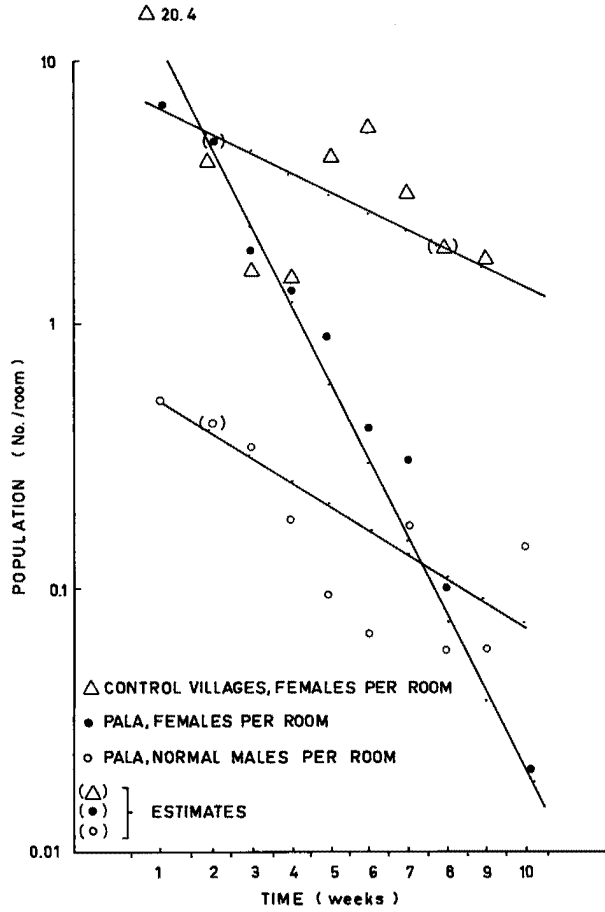


FIG. 1. Weekly changes in density of normal males and females in the village of Pala while sterile males were being released, and of females in the control villages during the same period (straight-line fitting by least squares method).

eradicate a population it is best to do the releases when the daily yield is declining or is oscillating around its lowest possible level. A critical factor seems to be the length of time during which the population is under "seasonal pressure" and some time is gained if the releases start before the low level is reached. Of course, unlimited logistic capabilities of a sterile male factory may change these considerations accordingly.

Taking a second look at the fpr figures for both the control and the target population, the differences between the two populations had a different meaning altogether when the wild males per room index was computed for every week of the experiment. The slope of the control females and that of the males of the target population were practically identical while the target females declined more abruptly. The fitted lines appear in Fig. 1

TABLE II. FEMALE SURVIVAL IN LABORATORY TESTS TO EVALUATE EFFECT OF VARIOUS RATIOS OF STERILE MALE HYBRIDS TO NORMAL PAIRS[a]

Normal		Sterile male hybrids	Replicates	Female survival (all replicates pooled) (%)
Males	Females			
20	20	0	53	81
20	20	5	7[b]	67[b]
20	20	10	19	72
20	20	20	40	76
20	20	40	36	69
20	20	60	19	67
20	20	80	15	63

[a] From Table I in Ref. [2].

[b] A group of nine replicates was not considered in the pooling for this row because the relevant figure in the original table is very much at variance with the general pattern and it might well be a misprint.

and are self-evident. Unfortunately, data on the males of the control population were not available. Nevertheless, the evidence is suggestive enough of a possible excess mortality falling on the target females.

Excess female mortality has been used by Baumhover [6] to measure the sexual aggressiveness of screw-worm (Cochlomyia hominivorax) flies. It has also been found that placing in the same container one female with more than six males of Cimex lectularius may kill the female [7] because of too frequent insemination and its traumatic nature as normally seen in the Cimicidae. In the mating of Hesperocimex cochimiensis males to Hesperocimex sonorensis females the female dies on account of the inflicted trauma [8]. In tsetse flies, males of Glossina palpalis martinii invariably kill females of Glossina palpalis fuscipes because the large claspers of the male "pierce her abdomen and gut, occasionally protruding in the dorsal side" [9].

Coming back to the Anopheles gambiae sterile hybrids, pooling of part of the information available in some of the original experiments [2] appears in Table II. The overall female survival can be considered reasonably good for the purposes of experimenting, and there is no indication of lethal copulation as dramatic as in the cases described above, but the general pattern of Table II seems to indicate that fewer females survive if the proportion of sterile male hybrids increase. A further series of experiments with this particular problem in mind is now in progress and it is hoped that the effects of a distorted sex ratio alone can be separated from hybrid vigour.

With this the sterile hybrid simulation model for Anopheles gambiae will have to be revised again. There probably never will be a perfect or definitive model. The constant feedback between laboratory, field and computer is undoubtedly stimulating and fruitful, and in the specific instance of the Pala Field Experiment even suggests a complete revision of the disappointing immediate conclusions. Certainly a heavy extra mortality of newly emerged virgin females would obscure the mating ability of the sterile hybrids and would underestimate the daily yield of the area, i.e. the real size of the target population when under pressure.

These novel approaches, in the case of anopheline vectors of malaria, do require a degree of ecological knowledge and precision formerly thought unnecessary in the golden days of residual insecticide spraying. Field experiments are now an integral part of research and development in this subject and justifiably so. Science is coming out of its secluded cloisters (for the better, hopefully).

ACKNOWLEDGEMENTS

I wish to thank Dr. G. Davidson (Ross Institute, University of London), Dr. R.C. Wallis, Prof. W. Downs and Dr. L. Whitman (Yale University, Dept. of Epidemiology and Public Health) for their valuable advice and comments. This work was supported by the United Kingdom Medical Research Council and a Bliss Scholarship of the Yale University School of Medicine, Department of Epidemiology and Public Health.

REFERENCES

[1] DAVIDSON, G., ODETOYINBO, J.A., COLUSSA, B., COS, J., A field attempt to assess the mating competitiveness of sterile males produced by crossing 2 member species of the Anopheles gambiae complex, Bull. World Health Organ. 42 (1970) 55.

[2] DAVIDSON, G., The potential use of sterile hybrid males for the eradication of member species of the Anopheles gambiae complex, Bull. World Health Organ. 40 (1969) 221.

[3] CUBBIN, C., Personal communication. Address: Hilgard 335, Insect Pathology, Univ. of California, Berkeley, Cal., 94720.

[4] CUELLAR, C.B., A theoretical model of the dynamics of an Anopheles gambiae population under challenge with eggs giving rise to sterile males, Bull. World Health Organ. 40 (1969) 205.

[5] CUELLAR, C.B., The critical level of interference in species eradication of mosquitoes, Bull. World Health Organ. 40 (1969) 213.

[6] BAUMHOVER, A.H., Sexual aggressiveness of male screw-worm flies measured by effect on the female mortality, J. Econ. Entomol. 58 (1965) 544.

[7] MELLANBY, K., Fertilisation and egg production in the bed bug Cimex lectularius, Parasitology 31 (1939) 193; as quoted in USINGER, R.L., Monograph of Cimicidae, Thomas Say Foundation Vol. VII, Entomol. Soc. Amer., College Park, Md. (1966).

[8] RYCKMAN, R.E., UESHIMA, N., Biosystematics of the Hesperocimex complex (Hemiptera: Cimicidae) and avian hosts (Piciformes: Picidae; Passeriformes: Mirundinidae), Ann. Entomol. Soc. Amer. 57 (1964) 624 as quoted in USINGER, R.L. Op. cit.

[9] VANDERPLANK, F.L., Experiments in cross-breeding tsetse flies (Glossina species), Ann. Trop. Med. Parasitol. 42 (1948) 131; as quoted in BUXTON, P.A., The Natural History of Tsetse Flies, London School of Hygiene and Tropical Medicine Memoir No. 10, Lewis, London (1955).

DEVELOPMENT OF A POPULATION MODEL OF COTTON RED BOLLWORM AS A BASIS FOR TESTING PEST CONTROL STRATEGIES

G. MURDIE
Department of Zoology and Applied Entomology,
Imperial College, London,
United Kingdom

Abstract

DEVELOPMENT OF A POPULATION MODEL OF COTTON RED BOLLWORM AS A BASIS FOR TESTING PEST CONTROL STRATEGIES.

This paper discusses the approach adopted in developing a population model as a basis for computer simulation of control methods against the red bollworm, Diparopsis castanea Hmps., a pest of cotton in Central and Southeast Africa. The ecological model described simulates field populations of the bollworm and is based on published information of its biology and ecology. The model is being developed for use as an experimental tool to compare control strategies in preparation for field trials. A comparison is made between computer experimental results obtained using the ecological model and those from a simple Berryman model. The importance of integrating field and computer experiments for development of computer and field control programs is discussed.

1. INTRODUCTION

Theoretically, nullifying the reproductive potential of the female of a species by sterile insect release is an attractive, and perhaps the most powerful, tool available for the eradication of a pest population. From the point of view of environment conservation it provides a method less disruptive than pesticides, which are well documented as having serious effects on local non-pest fauna of often desirable species and in some cases on fauna further from the site of application than was ever anticipated. In addition, most pesticides advocated today only have short-term effects and provide incomplete protection. The target specificity of sterile-male-release control programs guarantees some freedom from such harmful and mostly unpredictable side effects but obviously some problems might be anticipated, for example, assuming that the target pest is to be eradicated, a potential pest might be released from competition pressure, usually provided by the controlled pest, and in turn become a major problem.

The advantages of sterile male release have been well documented (see, for example, Refs [1-4].) One of these includes the elimination of species which are pests at natural low population levels or which have been reduced to low levels by the use of pesticides for example. In fact Knipling [5] considers pests at low densities as the only real candidates for eradication by sterile male release. However, many species are pests only at high population densities, but nevertheless the possibility of using sterile males can still be envisaged provided that the release program can be timed and located so as to coincide with periods and areas of low

densities; well-timed intervention could pre-empt a population increase to levels of pest proportions. Most insects have periods of low density, for example following overwintering periods, after which there is a buildup of numbers such as in aphids and mosquitoes, while others, locusts for example, are normally at low density but sporadically exhibit spectacular outbreaks.

The method of timing and sealing releases must be varied according to population characteristics of the species concerned, since it is obviously unrealistic that a single stratagem could be applied equally successfully to the world-wide range of pest species. The successful eradication of the screw-worm [6] obviously had an enourmous influence on the protocols for subsequent eradication attempts. However, to gear a release program to a specific pest requires considerable knowledge of its biology and ecology. For certain species this would involve a complete ecological study with greater attention to details such as mating frequency and success, dispersal, fecundity, levels of survival and the environmental factors which govern the real values of these parameters.

Mating is axiomatically central to the study while dispersal has important implications for adequate mixing of the sterile releases with the wild population and possible re-colonization of a cleared area. However, a factor such as density has an equally important role in the population dynamics of pest species many of which are known to have density-dependent control mechanisms operating on mating, fecundity [7, 8], survival and dispersal. The successful depression of a population to low densities could release these constraints with a subsequent increase in mating success, average fecundity of fertile-mated females, survival and decrease in emigration leading to an upward response in the population level. These factors are obviously important but have often been ignored in attempts to model progressive eradication through successive generations (called "generation" models here for convenience) [5, 9], where assumptions have been made of a constant capacity for increase regardless of the prevailing density conditions. In the short term an unexpected upsurge of the pest population might be beyond the control capabilities of the current release program, or at the least delay eradication.

The omission of these well-known dynamic population processes is the basic weakness of the simple generation model. A safety margin for releases could be imposed by assuming the maximum rate of increase between generation and numbers released would then be adjusted accordingly, but for most species practical and economic considerations would make gross overflooding unacceptable. In addition, these models assume a constant rate of intervention over a whole generation which would be difficult to achieve in practice. As indicated above, populations infrequently maintain steady densities, and then for only short periods, and while the estimated rate of release would be adequate before and after the population peak it would almost certainly be inadequate at the time of peak numbers and produce less than the estimated number of sterile matings.

In an attempt to anticipate and overcome the problems outlined above, a red bollworm population model is being developed [10]. This model uses submodels of all the basic biological processes making up the insect's life cycle including interactions with the host plant. It is accepted that population models can never be made completely realistic nor can they precisely mimic events in the real world. Nevertheless the increase in

realism compared with the generation type of model is considered an essential improvement providing a more adequate background for the testing of release strategies.

The choice of the red bollworm was stimulated by studies of the effects of chemosterilants on its reproductive behaviour [11] and a need to study the feasibility of field releases and the scale of intervention which would be required to achieve eradication. The bollworm has several advantages for the development of a sterile male technique. The insect is almost completely dependent on one host [12]; and estimates of the numbers of overwintering pupae from soil samples [13] could be used to indicate the potential attack rate in the following cotton season, while females are considered to require only one mating [14].

The model, however good conceptually, cannot be better than the available biological information. Most of the data for the driving parameters have been extracted from sources in the literature (Refs [12, 13, 15]) and from colleagues working in the field. The development of the model has indicated deficiencies in the essential information of the population dynamics of the bollworm, for example, factors affecting dispersal and the scale of dispersal and mating behaviour in the field, and is being used to stimulate field research into specific aspects of the pest's biology. It is anticipated that further data will be required as updating of information proceeds and that the feedback between field and model and vice versa will be an essential feature of the program and field evaluation. The procedures adopted will be time-consuming but should provide invaluable preparations for sterile male field trials if the experimental outcomes are favourable.

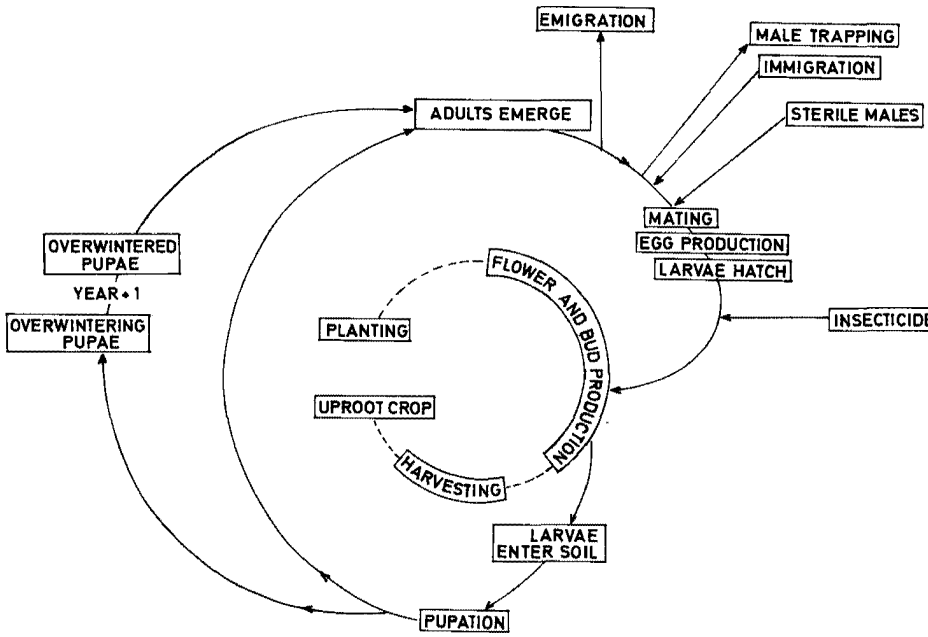
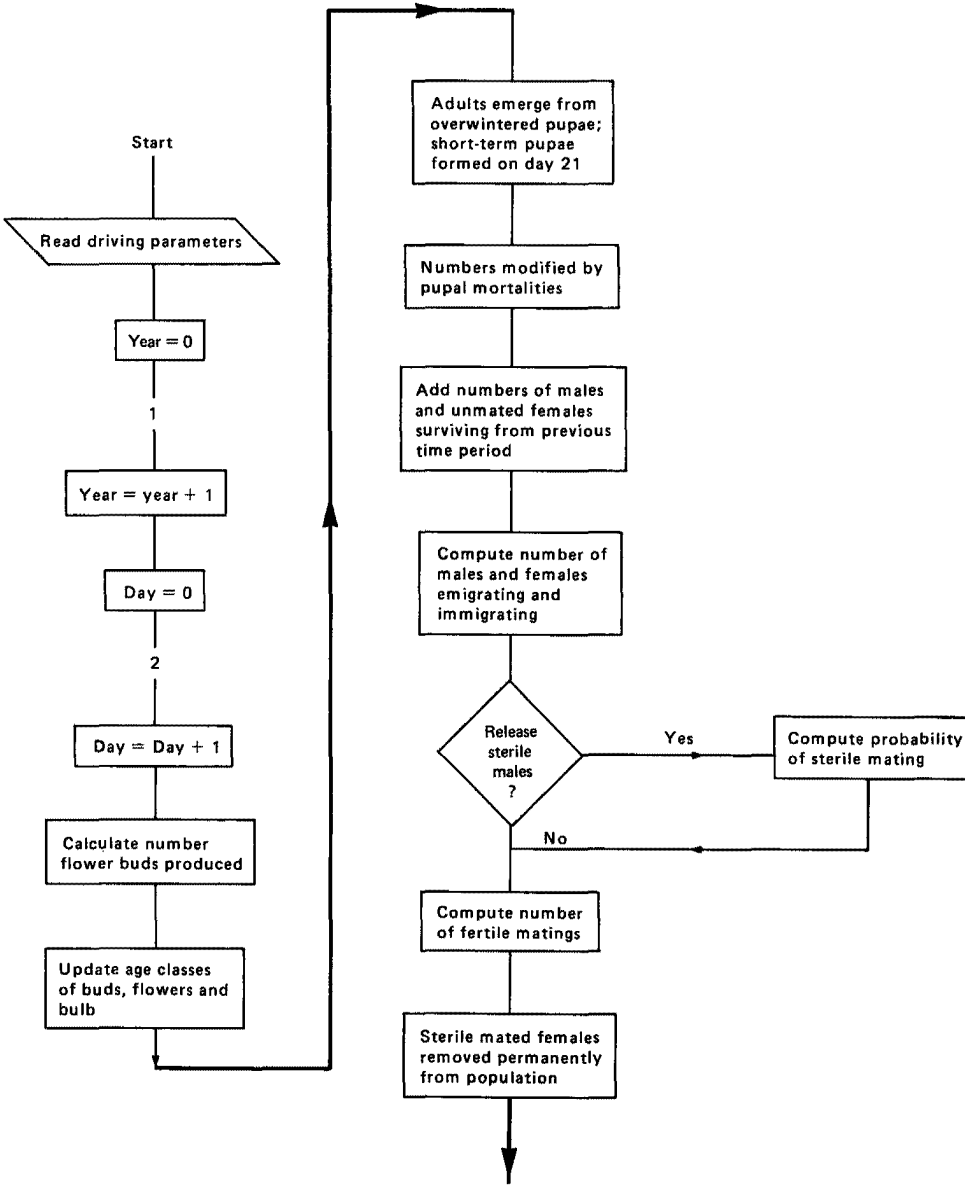


FIG. 1. Biological flow diagram of the bollworm/cotton system (after Murdie and Campion [7]).


Start
Read driving parameters
Year = 0
1
Year = year + 1
Day = 0
2
Day = Day + 1
Calculate number flower buds produced
Update age classes of buds, flowers and bulb
Adults emerge from overwintered pupae; short-term pupae formed on day 21
Numbers modified by pupal mortalities
Add numbers of males and unmated females surviving from previous time period
Compute number of males and females emigrating and immigrating
Release sterile males ?
Yes
Compute probability of sterile mating
No
Compute number of fertile matings
Sterile mated females removed permanently from population

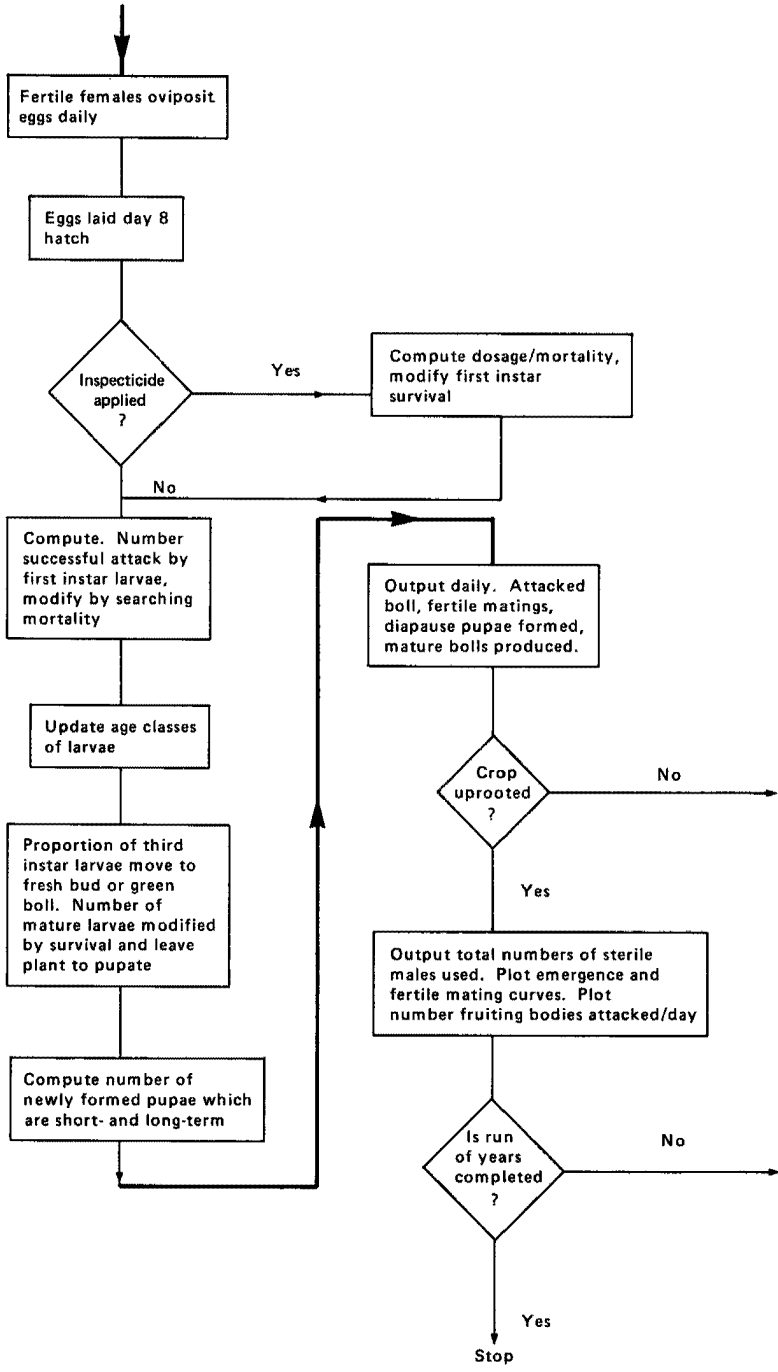


FIG. 2. General computer program.

Whether the population model will produce a significant improvement over the generation model can only be decided at the time of final evaluation. However, the study will provide a useful comparison of the two approaches and perhaps indicate a standard protocol for preliminary experimentation leading to full-scale field trials.

2. THE MODEL

At its present stage of development the model is almost completely deterministic with some stochastic elements in the mating and first instar attack submodels. As further information becomes available, either from

TABLE I. EXAMPLE OF SET OF INPUT PARAMETERS FOR THE COTTON RED BOLLWORM POPULATIONS MODELS

Crop planted	Day 1
First flower bud produced	Day 48
Last flower bud produced	Day 180
Crop uprooted	Day 240
Number of overwintered pupae	8000
First overwintered pupae produce adults	Day 9
Last overwintered pupae produce adults	Day 111
Sex ratio of emerging adults	1 : 1
Number of eggs per fertile female	140
Mortalities:	
Egg	0.56
Searching first instar larvae	0.32
Larvae dying in shed bolls	0.05
Additional larval mortality	0.40
Short-term pupae	0.50
Long-term (overwintering) pupae	0.70
Males/d	0.30
Females/d	0.30
First long-term pupae produced in current season	Day 120
Sterile male release:	
Begin releases	Day 35
End releases	Day 200
Ratio sterile releases to freshly emerged wild males	10 : 1

retrieval of published information or from new field data, the submodels involving density dependence and probabilistic elements will be updated.

The cotton crop is considered central to the pest/crop system (Fig. 1) and is used to initiate and terminate the annual population cycle at the times of planting and uprooting. The bollworm life cycle is considered as rotating around the essential control core, i.e. the plant host, and contains a well-defined sequence of developmental stages (Fig. 2) each subjected to mortalities which are now held constant but will be modified in later models, as indicated above [10].

A typical run uses the driving parameters listed in Table I. The number of parameters used is considered the minimum necessary to build realism into the model but nevertheless illustrates the potential flexibility to modify certain parameters such as age-specific mortalities, timing and rates of releases. For example, effects of pesticide can be simulated by modifying the survival of the first instar larvae as an increasing function of time elapsed from the time of application. Using the parameters given, a single run with no control yielded a long-term pupal count of 9537 per acre at the end of the season and, by releasing 12 450 sterile males, maintaining a ratio of 10 sterile to 1 wild, yielded 122 pupae (Table II).

Daily releases at prescribed ratios assume a good knowledge of daily adult emergences and availability of the necessary numbers of sterilized insects: under these circumstances good control can be predicted (Table II). However, in practice such accurate and up-to-date information will rarely be obtained and more usually estimates of adults would be required one or more weeks in advance of the release date to allow preparation of stocks.

TABLE II. COMPARISON OF SIMULATED DAILY AND WEEKLY RELEASES OF STERILE MALES TO CONTROL RED BOLLWORM DURING ONE COTTON SEASON

Release frequency	Ratio sterile : wild	Total sterile males required	Boll damage (% of control)	Number of overwintering pupae produced (per acre)
Daily	5:1	7021	12	606
	10:1	12451	6	122
	20:1	23023	4	0
Weekly	5:1	8290	20	1387
	10:1	13548	10	215
	20:1	24218	6	31
No releases	-	-	100	9537

This situation was mimicked by simulating weekly releases of numbers (ns_i) of sterile males based on

$$ns_i = 7.0\, ne_{i-6}\, rs$$

where ne_{i-6} is the number of adults emerging 6 d previous to the release day i; r and s are respectively the release and sex ratios, and the factor 7.0 is an adjustment for single weekly releases.

Although the total numbers released are slightly increased (Table II), control was approximately only half as effective as in the daily release scheme. This difference arose from the effective ratio of sterile to wild insects. For example, in the 20:1 regime the ratio varied from about 65 : 1 with the gross overflooding immediately following release to a minimum of about 3 : 1 due to dilution of the sterile males through their mortality and emergences of unsterilized wild adults. Clearly, this situation will occur in the field particularly when the species concerned has a low mating capacity or when the time intervals between releases are long compared with the adult's life expectancy.

It is difficult to compare the outcomes of the population and generation models since the population model does not distinguish between generation yields. However, assuming the same stage-specific survivals as above and using 5 : 1, 10 : 1 and 20 : 1 ratios of releases per generation the expected adult numbers and releases per generation were those listed in Table III.

There are clear differences between the numbers required for sterile releases and the levels of control predicted by the two methods; these differences can be explained by timing and biological factors ignored in the generation model. For example, since a proportion of the overwintered population emerges before buds or bolls are available for attack this proportion does not contribute to the second adult generation and in the population model releases were timed to begin one week before first bud production. The lower numbers produced imply that fewer releases have to be made in the second generation and so on through the season. Other

TABLE III. THEORETICAL TRENDS OF POPULATION DECREASE IN THE RED BOLLWORM FOLLOWING STERILE MALE RELEASE

Generation	Ratio of sterile : wild males					
	5:1		10:1		20:1	
	Adults	Release No.	Adults	Release No.	Adults	Release No.
1	2400	6000	2400	12 000	2400	24 000
2	2388	5969	1302	6 510	682	6 820
3	2375	5938	707	3 535	194	1 940
4	2363	-	384	-	55	-
Total		17 907		22 045		32 760

factors such as decreased rearing sites through boll maturation and fewer emergences through diapause later in the season also contribute to smaller requirements for sterile releases.

However, the releases anticipated by the generation model do have a built-in safety margin of overflooding since they could maximize requirements. On the other hand, serious wastage of sterile material could result which might be critical for many insects difficult to rear in large numbers but perhaps of lesser importance for species such as the Mediterranean fruit fly.

3. DISCUSSION

Sterile male release has great potential for the control or eradication of pest species but with the notable exception of the screw-worm no large-scale successes have been recorded. As a result, the small probability of success would not seem to justify the elaborate and invariably expensive massive rearing and release programs which are necessary to establish the validity of this approach in the field for specific pests.

However, exhaustive investigation of the pest, its biology and ecology would help narrow the gap between the probabilities of failure and success. The experimenter would be provided with more adequate information upon which to base his decision on whether to adopt a single sterile release control strategy or to integrate it with others such as pesticides, cultural methods, sex attractant traps, or biological control [10].

The computer modelling of populations can be easily integrated into the research scheme and offers two major benefits: (1) the critical dissection of population processes and the reconstitution of the segments as a model, which impose a strict discipline on the modeller and lead to a fuller understanding of the system. Subsequent runs on the computer can be used not only to test the program but also to analyse "sensitivity" and thus to determine those key parameters having the greatest effect on population growth and size. The results of the simulated "key factor" analysis [16] could indicate the stage spcific survivals which would most profitably be varied by experimental manipulation to effect control. (2) The second benefit, and the prime concern of the Panel, is that the completed model provides a basis for simulating large field trials and for testing any number of variations of release strategies. Obviously the simulations cannot replace field experiments, neither can they guarantee successful repetitions of laboratory eradications.

The final decision need not necessarily commit the control program to sterile insect release but could also commit it to an alternative single solution or integration of several methods. To this extent the project can be considered as open-ended.

Whether dynamic population models will justify the expense of the extra and time-consuming ecological research when compared with the simpler generation models cannot be determined from present information. However, it must be remembered that even the simple models use parameters for rates of population increase which need to be equally accurate to bear any relation to field conditions which vary with time and space in nature.

ACKNOWLEDGEMENTS

My thanks are extended to Dr. D.G. Campion for reading the manuscript and for his valuable comments. Computing facilities were provided by the University of London Computing Centre on the C.D.C. 6600 through link equipment supported by the Ford Foundation Environmental Resource Management Unit at Imperial College.

REFERENCES

[1] KNIPLING, E.F., The Potential Role of the Sterility Method for Insect Population Control with Special Reference to Combining this Method with Conventional Methods, US Dept. Agriculture, Inf. Bull. ARS-33-58 (Nov. 1964).

[2] KNIPLING, E.F., LAVEN, H., CRAIG, G.B., PAL, R., KITZMILLER, J.B., SMITH, C.N., BROWN, A.W.A., Genetic control of insects of public health importance, Bull. World Health Organ. 38 (1968) 421.

[3] KNIPLING, E.F., "The potential role of sterility for pest control", Principles of Insect Chemosterilisations (LA BREQUE, G.C., SMITH, C.N., Eds), North Holland Publishing Co., Amsterdam (1968).

[4] KNIPLING, E.F., Potentialities and progress in the development of chemosterilants for insect control, J. Econ. Entomol. 55 (1962) 782.

[5] KNIPLING, E.F., Possibilities of insect control eradication through the use of sexually sterile males, J. Econ. Entomol. 48 (1955) 459.

[6] BAUMHOVER, A.H., Eradication of the screw-worm fly, J. Amer. Med. Assoc. 196 (1966) 240.

[7] CONWAY, G.R., A Basic Model of Insect Reproduction and its Implications for Pest Control, Ph. D Thesis, University of California, Davis (1969).

[8] CONWAY, G.R., MURDIE, G., "Population models as a basis for pest control", Mathematical Models in Ecology (JEFFERS, J.N.R., Ed.), Proc. 12th Symp. Br. Ecol. Soc., Grange-over-sands, Lancashire, England (1972).

[9] BERRYMAN, A.A., Mathematical descriptions of the sterile male principle, Can. Entomol. 99 (1967) 858.

[10] MURDIE, G., CAMPION, D.G., The use of computer simulation of cotton red bollworm (Diparopsis castanea Hmps.) populations to investigate the potential value of sterile male release and sex attractants in control programmes, Cotton Growing Rev. 49 (1972).

[11] CAMPION, D.G., LEWIS, C.T., "Studies of competitiveness, chemosterilant persistence and sperm structure in treated red bollworms, Diparopsis castanea (Hmps.)", Sterility Principle for Insect Control or Eradication (Proc. Symp. Athens, 1970), IAEA, Vienna (1971) 183.

[12] PEARSON, E.O., DARLING, R.C.M., The Insect Pests of Cotton in Tropical Africa, Commonwealth Agric. Bureau, London (1958).

[13] TUNSTALL, J.P., Pupal development and moth emergence of the red bollworm (Diparopsis castanea Hmps.) in Malawi and Rhodesia, Bull. Entomol. Res. 58 (1968) 233.

[14] CAMPION, D.G., "Chemosterilisation of the red bollworm Diparopsis castanea (Lepidoptera: Noctindae)", Proc. 13th Int. Congr. Entomol. Moscow, 1968, 3, Publishing House NAUKA, Leningrad (1972) 418.

[15] MUNRO, J.M., An analysis of earliness in cotton, Cotton Growing Rev. 48 (1971) 28.

[16] VARLEY, G.C., GRADWELL, G.R., Key factors in population studies, J. Anim. Ecol. 29 (1960) 399.

THE POSSIBILITIES OF USING THE STERILE MALE TECHNIQUE FOR APHID CONTROL – A THEORETICAL DISCUSSION

A. W. STEFFAN
Institut für Zoologie der Biologischen
Bundesanstalt für Land- und Forstwirtschaft,
Berlin-Dahlem

W. J. KLOFT
Institut für Angewandte Zoologie
der Universität Bonn,
Bonn, Federal Republic of Germany

Abstract

THE POSSIBILITIES OF USING THE STERILE MALE TECHNIQUE FOR APHID CONTROL – A THEORETICAL DISCUSSION.

Aphids are serious plant pests which induce both direct and indirect damage to crops, particularly by transmitting virus diseases. Little attention has been paid to the possibility of utilizing genetic methods, primarily the sterile male technique, for the control of these pests. Reasons for this include the tremendous mass infestations which are observed during the growing season and parthenogenetic reproduction. However, in moderate climates a cyclic change from parthenogenetic to bisexual reproduction occurs. A theoretical discussion on the possibilities of utilizing the sterile male technique for aphid control is presented.

Genetic control of insect pests has found increasing interest. Whether or not such projects can be implemented should be considered carefully before starting any preparatory investigations. Prior to dealing with technical problems such as mass rearing, the sterilization and subsequent field release of treated specimens, biological, physiological and ecological data require analysis. Life cycles and modes of reproduction must be considered first; patterns of population structure and dynamics, especially seasonal fluctuations in distribution, density and dispersal, also are important. Steffan [1, 2] made preliminary tests to determine possibilities of applying genetic control to heterogenetic aphid species. Many members of this insect group undoubtedly are most serious plant pests inducing direct or indirect damage to crops, especially by transfer of economically important virus diseases. Therefore it seems useful to introduce aphids as a subject of discussion for this panel on Computer Models and Application of the Sterile Male Technique. Also, aphids are of general interest, since they usually show heterogenesis, i.e. a cyclic change from parthenogenetic to bisexual reproduction. Thus, aphids could serve as a model for arthropods with both types of reproduction.

Several experiments with sterilizing substances, applied to aphids orally or externally, have been carried out [3-14]. Without considering the particular compounds tested, it might be objected that in these experiments all the species belonged to the Aphididae, and that in all cases the tests were carried out only on parthenogenetic females. However, as will be pointed out, genetic control of aphids can obviously only be applied in cases where, in addition to parthenogenetic reproduction, regular bisexual reproduction also occurs.

In Europe, depending on the particular aphid family, about 20-50% of all species have no bisexual generation and therefore will not be considered here. In subtropical and tropical areas, the percentage of species reproducing parthenogenetically only is higher. Since in heterogenetic species genetic control is limited to sexual forms, it can be applied only during a limited period of the season: most aphid species produce sexuals during late summer or fall after a period of parthenogenetic mass production. Compared with the enormous population density of these parthenogenetic generations – two or three generations may overlap – the number of sexuals is very small. This offers favourable starting conditions for applying genetic control methods.

Usually, the mated sexual female produces one egg only. This diapause egg or, in some cases, the newly hatched first larva of the fundatrix generation, is the overwintering form. This gamogenetic production has to be suppressed. In general, intraspecific incompatibility between aphid strains of different geographical origin cannot yet be excluded. On the other hand, fertile hybridizations between different species of Aphididae are possible [15, 16]. Intraspecific incompatibility within that family would then not be probable.

The production of sterile sexual males with full competitive and mating potency should be possible, since the natural occurrence of such males in Aphis tripolii Laing 1920 is known [17]. For releases of sterile males to be efficient, only the diapause egg or the first larval stage of the fundatrix should hibernate on the primary host. All species in which, besides the gamogenetic hibernation stage, a parthenogenetic generation hibernates on the secondary or also on the primary host (Paracycles), must be omitted from genetic control experiments. This is so because in such cases, some individuals avoid the "check-point" of the sexual generation, and thus are able to build up new populations completing the cycle (Holocycle) the following year. The same holds true whether dealing with heterogenetic-monoecious or heterogenetic-heteroecious species. In the case of the normal holocycle, the sexuparae or sexuals remigrate during the fall from their summer (secondary) hosts to their winter (primary) host, so that the populations on the summer hosts are totally eliminated. The advantage of such an occurrence for genetic control is that the population decreases to a relatively small number of sexuals concentrated on specific host-plants. In numerous heteroecious Aphidina, typically one, several or many species of widespread herbaceous plant(s) may act as secondary host(s) whereas only one woody plant species is the primary host. For a long time, this has been used to advantage in chemical control and might also be useful for genetic control.

One further condition has to be fulfilled: the sterilized sex must have the same appearance, mating behaviour (ability to find and mate with the opposite sex) and competitiveness (including dispersal range) as the normal individual. Males, when sterilized, should have the same or even better viability than fertile females.

According to Steffan [1, 2], four different types of "sexuales" generations can occur in heteroecious aphid species:

(I) Remigrating alates producing on the primary host wingless sexual individuals: $\hat{\sigma}\hat{\sigma}$ (from androparae), $\underset{+}{\varphi}\underset{+}{\varphi}$ (from gynoparae);
(II) Remigrating alate Sexuparae producing on the primary host both sexes which then develop into wingless $\hat{\sigma}\hat{\sigma}$ and $\underset{++}{\varphi\varphi}$.

In types I and II, the dispersal of these very small ♂♂ spans only a few metres. Since precise localized releases of sterile males normally are impossible, the method may prove ineffective in practice.

(III) Remigrating alate Sexuparae producing on the primary host winged ♂♂ and wingless ♀♀.
(IV) Winged sexuales-♂♂ developing on the secondary host and flying to the primary host; winged Gynoparae remigrating and producing wingless sexual ♀♀.

In types III and IV, the ♂♂ have a wide dispersal range allowing the release of sterilized males. In some rare cases the males are apterous, and the sexual ♀♀ can fly. Here of course, the release of sterilized sexuales ♀♀ should also be considered.

Furthermore, remigration to a distinct primary host could become a double "bottle-neck": (1) by reducing the population to a relatively small number of sexuals (as compared with parthenogenetic generations) and (2) by concentrating it on distinct host-plants which, in the case of woody plants such as apple or peach trees, can be surveyed much better than herbaceous plants.

All the types of sexuales-♂♂ and -♀♀ described above can be found in one-host aphid species as well. Thus, in monoecious-holocyclic aphids genetic control might also be possible for types III and IV.

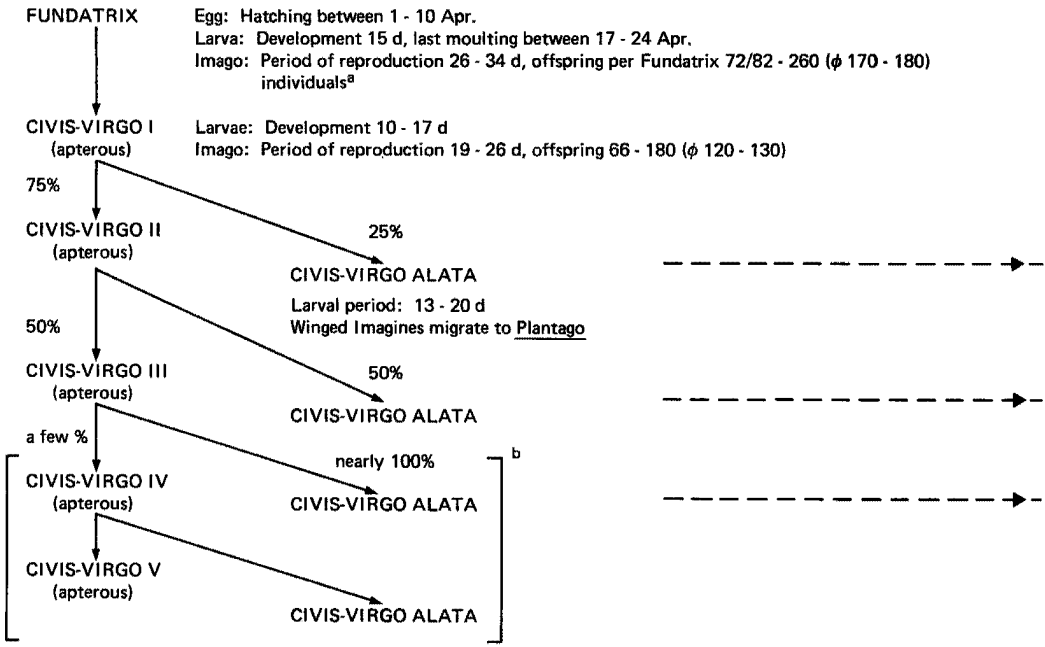
If all these basic requirements are met, a feasible method of mass rearing ♂♂ needs to be developed for the particular species. The production of Sexuparae (Gyno-, Androparae), sexual ♀♀ and ♂♂ can be induced by changing food quality, temperature or photoperiod.

A short-day photoperiod seems to be most important for the determination of Gynoparae, oviparous ♀♀ and, probably, ♂♂ [18, 19]. According to Lees [20, 21], temperature is one of the factors initiating the production of males in Megoura viciae BUCKT. It should be realized, of course, that differences exist between aphid families. In the case of the more "primitive" families, bisexual reproduction seems induced by the host-plant exlusively; here a short day seems to have a supporting effect only. However, in the higher groups of the Aphididae, the aphid family most advanced in evolution, the inducing effect of the photoperiod cannot be neutralized by food quality in the oviparous females nor, probably, in the males. Feeding the Aphididae-species Aphis fabae and Myzus persicae on artifical diets, Tsitsipis [22] got oviparae as well as males under "short-day" conditions only. For further literature, see the reviews of Danilevskii [23], Hille Ris Lambers [24], Lees [25], Kunkel and Kloft [26]. In the case of successful mass rearing under fully programmed external conditions such as temperature and light, either on secondary host-plants or on artificial diets, the winged males could be collected by utilizing their positive phototropism.

Methods of sterilization also need to be developed. Irradiation and application of chemosterilants through membranes or externally might be used. An exact analysis of cytological and cytogenetic peculiarities before and after sterilization should be made, based on the methods and experiments of Steffan [27-31].

Before considering a specific heteroecious-holocyclic aphid species, factors which might influence its population density, structure and dynamics, should be analysed. Some of these are given below.

PRIMARY HOST-PLANT (APPLE)



After reaching the primary host the remigrated Gynoparae produce 3 - 13 (ϕ 7) individuals within 1 - 3 d, most of them within 2 d

SEXUALIS-♀♀ (OVIPARAE)
(apterous)

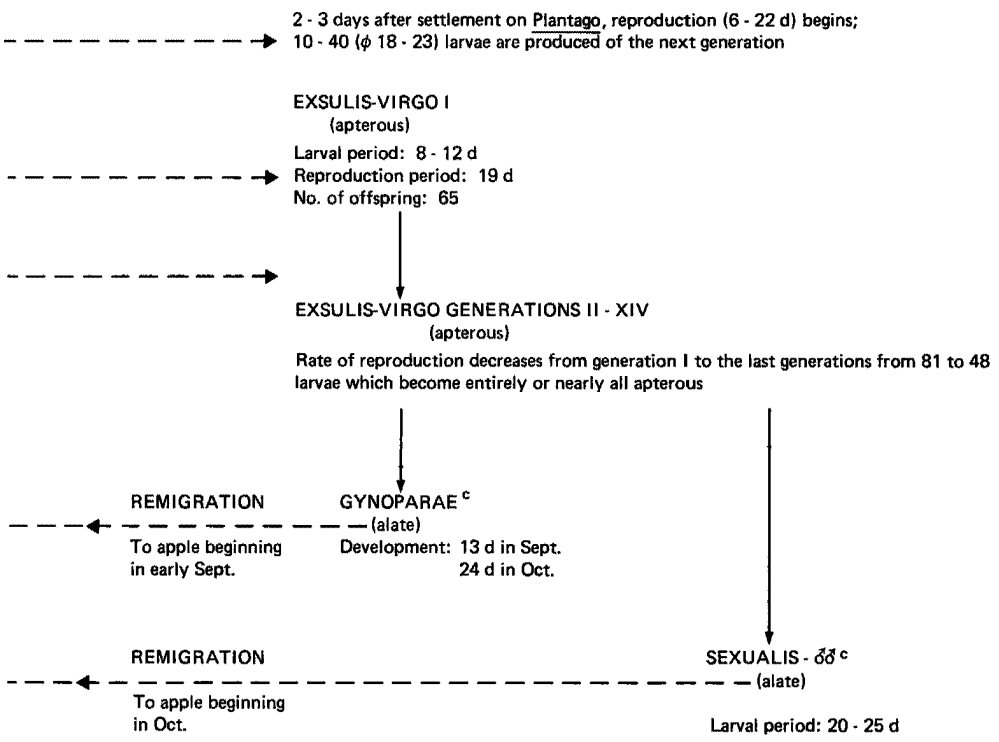
If the Sexualis-♂♂, after arrival on an apple tree, do not find females ready for mating, the Sexualis-♂♂ wait beside the ♀♀ larvae (feeding on the lower side of leaves) until the females reach maturity.

Each Sexualis-♂ can mate several ♀♀;
each ♀ permits only one (?) copulation
Each mated Sexualis-♀ produces
4 - 8 winter eggs (FUNDATRIX - GENERATION)
(only overwintering stage)

[a] ϕ is used as an abbreviation for "average".

[b] Following European authors, only three apterous CIVIS-VIRGO generations are produced per year. United States authors report about five apterous CIVIS-VIRGO generations which possibly might be conditioned by the climate (?).

SECONDARY HOST-PLANT (PLANTAGO)



c The alate aphids appearing during fall are Gynoparae and Sexualis-♂♂. Whether or not these are brothers and sisters is still unknown. (Since they appear at different times, the Gynoparae may be the offspring of generations XII-XIII, and the males of XIII-XIV).

FIG. 1. Life cycle of Dysaphis plantaginea.

Fundatrix generation

Predators and parasites reduce the number of winter eggs. Hatching and survival of larvae are also endangered by weather conditions: sudden frosts, snow, etc. can reduce the number of individuals. The same is true for the larvae of the next generation (Fundatrigeniae). However, dry and warm weather conditions favour this generation and thus permit a good start for building up the population.

Parthenogenetic generations on the primary host (Civis virgo-generations I-V)

Population density is influenced by predators, parasites, weather conditions, growth of the host-plant, seasonal changes in composition of phloem sap (summer minimum, effective especially for generations III-V), trophobiotic relations to ants, and intraspecific group effects. Feedback relations between prior aphid settlement (same species!) and quality or attractiveness of the host-plant or parts of it (based on saliva injection) can reduce the population density. Group effects and food quality, among other factors, have a strong influence on the alate/apterous virgins ratio and are responsible for the time and intensity of migration of the alate individuals to secondary hosts. When migrating alates form within a short period, sudden weather catastrophes during this time can reduce settlement on summer hosts. A warm spring and a summer without heavy rains favour the population density and thermal air currents help even long-range passive migration by air drift.

Parthenogenetic generations on secondary host-plants (Exsulis virgo-generations I-XIV)

The factors already mentioned also affect the population density of these generations. A reduced quality of the food, caused by a slower rate of plant growth and lower temperatures, brakes the development, growth and rate of parthenogenetic reproduction. On the other hand, these same factors, along with changes in the photoperiod, induce the appearance of Sexuparae (Gynoparae, Androparae) or sexual males and influence their rate of production.

Sexuparae or sexuales generation

Remigration to the primary host is greatly influenced by the weather. Early falls in temperature, snow and ice can in some years almost prevent remigration and/or production and development of sexuales on the primary host, as well as mating and deposition of winter eggs. Distances between secondary and primary host-plants, non-contiguity in their aerial distribution, main wind directions, etc. play an important role. In the case of long-range non-contiguity between areas of summer and winter hosts, genetic control can of course be limited to the areas of primary host-plants.

Estimations of relative population densities of migrating aphids in flight can be made with Johnson's air suction traps [32, 33]; for counting the number of individuals on crop plants the methods of Banks can be used [34].

An illustration of a potential candidate for genetic control is the economically important, heteroecious and holocyclic aphid species Dysaphis plantaginea (Passerini 1860) – the Rosy apple aphid. This species occurs in Europe and was introduced to North America and elsewhere. Its primary host is the apple where it causes considerable leaf rolling, inhibition of growth, compression and deformation of young shoots together with crippling of fruits. Its summer hosts are Plantago species, but a part of the parthenogenetic aphids can remain on apples during summer.

Figure 1 gives some specific data on the various life cycles of D. plantaginea in a chart based, among other authors, on Steiner and Baggiolini [35]. These authors also summarized all data on the predator-parasite complex of this species under Central European conditions.

If we admit that, under field conditions and on the secondary host, Gynoparae and Sexuales-♂♂ are produced in the same numerical proportion, a sex ratio of 1 ♂ : 7 ♀♀ can be expected on the primary host-plant. This ratio may change in both directions from year to year, depending on weather conditions during development and migration.

Timing the release of sterilized ♂♂ before the migration of fertile ♂♂ begins could give very effective genetic control of this species.

REFERENCES

[1] STEFFAN, A.W., Möglichkeiten genetischer Bekämpfung von Blattläusen (Homoptera: Aphidina), Z. Angew. Entomol. (1972).

[2] STEFFAN, A.W., Sind mitteleuropäische Blattlausarten genetischen Bekämpfungsverfahren zugänglich? Nachr. Blatt Dtsch. Pflanzenschutzdienst, 2 (1972).

[3] BHALLA, O.P., ROBINSON, A.G., Effect of three chemosterilants on the pea aphid fed on an artificial diet, J. Econ. Entomol. 59 (1966) 378.

[4] BHALLA, O.P., ROBINSON, A.G., Effects of chemosterilants and growth regulators on the pea aphid fed on artificial diet, J. Econ. Entomol. 61 2 (1968) 552.

[5] BONNEMAISON, L., Essais de substances chimiostérilisantes, I. Action sur divers Homoptères et Coléoptères, Phytiat.-Phytopharm. 15 (1966) 59.

[6] BONNEMAISON, L., Essais de substances chimiostérilisantes, II. Action sur divers Homoptères et Coléoptères, Phytiat.-Phytopharm. 15 (1966) 79.

[7] BONNEMAISON, L., Possibilités et conditions générales d'emploi des chimiostérilisants contre les Arthropodes, Compt. Rend. Acad. Agric. France 52 (1966) 137.

[8] BONNEMAISON, L., Action stérilisante du tepa et du D.M.S.O. sur divers insectes, Phytiat.-Phytiopharm. 2 (1968) 105.

[9] EHRHARDT, P., JAYARAJ, S., SCHMUTTERER, H., Die Wirkung verschiedener, über die Pflanze zugeführter Antibiotika auf Entwicklung und Fertilität der Schwarzen Bohnenblattlaus (Aphis fabae), Ent. exp. appl. 9 (1966) 332.

[10] HARRIS, P.H., MATTSON, V.J., Effects of some antibiotics on three aphid species, J. Econ. Entomol. 56 (1963) 412.

[11] HARRIS, P.H., WILES, W.G., Tests of some antibiotics and other chemosterilants on the green peach aphid, J. Econ. Entomol. 59 (1966) 694.

[12] JAYARAJ, S., SCHMUTTERER, H., On the use of certain sulphanilamides against the black bean aphid, Aphis fabae Scop. Z. PflKrankh. PflPath. PflSchutz 73 (1966) 660.

[13] ROBINSON, A.G., Note on fecundity of the pea aphid, Acyrthosiphon pisum (Harris), caged on plants of broad bean, Vicia faba L., treated with various plant growth regulators, Can. Entomol. 91 8 (1959) 527.

[14] ROBINSON, A.G., Effect of maleic hydrazide and other plant growth regulators on the pea aphid Acyrthosiphon pisum (Harris), caged on broad bean, Vicia faba L. Can. Entomol. 92 (1960) 494.

[15] IGLISCH, I., Über die Entstehung der Rassen der "Schwarzen Blattläuse" (Aphis fabae Scop. und verwandte Arten), über ihre phytopathologische Bedeutung und über die Aussichten für erfolgversprechende Bekämpfungsmassnahmen (Homoptera: Aphididae), Mitt. Biol. BundAnst., Berlin-Dahlem, 131 (1968) 1.

[16] IGLISCH, I., Zur Aufstellung eines Verwandtschaftsbildes der "Schwarzen Blattläuse", Aphis fabae Scop. und verwandte Arten, nach biologischen Markmalen (Homoptera: Aphididae), Z. Angew. Entomol. 65 3 (1970) 304.

[17] IGLISCH, I., Zur Morphenfolge von Aphis tripolii Laing 1920 (Homoptera: Aphididae). Ein Beitrag zur Biologie der "Schwarzen Blattläuse", Z. Angew. Zool. 57 (2) (1970) 229.

[18] BONNEMAISON, L., Action inhibitrice d'une longue photopériode et d'une température élevée sur l'apparition des sexupares ailés de Dysaphis plantaginea Pass. (Homoptères, Aphididae), Compt. Rend. 259 (1964) 1768.

[19] BONNEMAISON, L., Facteurs conditionnant l'apparition des mâles chez l'Aphide Dysaphis plantaginea Pass. (Homoptères, Aphididae), Compt. Rend. 260 (1965) 318.

[20] LEES, A.D., The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid Megoura viciae Buckton. II. The operation of the "interval timer" in young clones, J. Insect Physiol. 4 (1960) 154.

[21] LEES, A.D., "Clonal polymorphism in aphids", Proc. Symp. Insect Polymorphism (KENNEDY, J.S., Ed.) 1, Royal Entomological Soc., London (1961) 68.

[22] TSITISIPIS, J.A., MITTLER, T.E., Convenient lighting system for inducing the production of sexual forms of aphids feeding on artificial diets, Ann. Entomol. Soc. Amer. 63 (1970) 1665.

[23] DANILEVSKII, A.S., Photoperiodism and Seasonal Development of Insects, Oliver + Boyd Edinburgh (1965).

[24] HILLE RIS LAMBERS, D., Polymorphism in Aphididae Ann. Rev. Entomol. 11 (1965) 47.

[25] LEES, A.D., The control of polymorphism in Aphids, Adv. Insect Physiol. 3 (1966) 207.

[26] KUNKEL, H., KLOFT, W., "Polymorphismus bei Aphiden (Aphidina, Homoptera)", in SCHMIDT, G.H., Soziale Insekten-Kastenbildung-Polymorphismus, Wiss. Verlagsges. mbH., Stuttgart (1971).

[27] STEFFAN, A.W., Systematik und Evolution der Adelgidae (Homoptera: Aphidina). Eine Verwandtschaftsanalyse auf vorwiegend ethologischer und Karyologischer Grundlage, Zoologica, Stuttg. 115 (1968) 1.

[28] STEFFAN, A.W., Zum Generations- und Chromosomenzyklus der Adelgidae (Homoptera: Aphidina), Verh. Dtsch. Zool. Ges. Heidelberg 1967, Zool. Anz. Suppl. 31 (1968) 762.

[29] STEFFAN, A.W., Zur Karyologie und Chromosomen-Evolution der Blattläuse (Homoptera: Aphidina), Verh. Dtsch. Zool. Ges. Innsbruck 1968, Zool. Anz. Suppl. 32 (1969) 558.

[30] STEFFAN, A.W., Chromosomale Parallelreihen in den Generationszyklen der Fichtengallenläuse (Homoptera: Aphidina: Adelgidae), Umsch. Wiss. Tech. 69 (1969) 843.

[31] STEFFAN, A.W., Die eidonomischen und zytologischen Grundlagen bei der Entstehung anholozyklisch-partheogenetischer Adelgidae-Species (Homoptera: Aphidina), Z. Angew. Entomol. 65 (1970) 444.

[32] JOHNSON, C.G., The changing numbers of Aphis fabae Scop. flying at crop level, in relation to current weather and to the population on the crop, Ann. Appl. Biol. 39 (1952) 525.

[33] JOHNSON, C.G., Ecological Aspects of Aphid Flight and Dispersal, Rep. Rothamsted Exp. St. (1955) 191.

[34] BANKS, C.J., A method of estimating populations and counting large numbers of Aphis fabae Scop., Bull. Entomol. Res. 45 (1954) 751.

[35] STEINER, H., BAGGIOLINI, M., Anleitung zum integrierten Pflanzenschutz im Apfelanbau, Landesanstalt für Pflanzenschutz, Stuttgart (1968).

FIELD STUDIES ON INSECT STERILIZATION WITH MOSQUITOES, HOUSE FLIES AND STABLE FLIES

D.E. WEIDHAAS
Entomology Research Division,
United States Department of Agriculture,
Agricultural Research Service,
Gainesville, Fla.,
United States of America

Abstract

FIELD STUDIES ON INSECT STERILIZATION WITH MOSQUITOES, HOUSE FLIES AND STABLE FLIES.

Field tests on the release of radiation or chemosterilized mosquitoes, stable flies and house flies are reviewed with particular emphasis on the potential of the method, reductions in density and reproductive success of the populations under stress of total population control. The results with house flies include experiments with sterility utilizing chemosterilant baits. Insects of reputed high biotic potential were shown to have low rates of reproductive success under given environmental conditions.

Over the past 15 years there has been a considerable amount of research devoted to the study of sterility induced in mosquitoes, house flies and stable flies by radiation and chemosterilants. Much of this research has been in the form of laboratory studies designed to show that insects could be successfully sterilized, and to develop the necessary background data and information required for developing the sterile male or insect release technique. In addition, a considerable amount of research has been devoted to studying the effects of radiation and chemicals on the insects themselves.

I do not intend to discuss any of these developments in laboratory research for they are outside the subject of this panel. I prefer to review the data available on the field evaluation of insect sterility. Emphasis will simply be given to results indicating the feasibility of the sterilization approach. Emphasis will also be given to interpreting the data obtained in these studies in terms of the dynamics of the field populations on which this technique was used. Little detail of experimental procedures and design will be given. However, these details are available in the list of references presented at the end of this paper.

The first field release of sterile mosquitoes was carried out in Florida in the late 1950s [1]. Males of Anopheles quadrimaculatus Say were reared in the laboratory, sterilized by exposing pupae of mixed ages to gamma radiation and released in the field in two different locations. The males that were released were affected by the radiation treatment and were not fully competitive with untreated males. It was not only impossible to demonstrate that the released males had any significant influence on the density of populations into which they were released, but there was no appreciable degree of sterility obtained in females of the wild population. Subsequent field studies [2] led to the conclusion that the males of the

colonized strain were somehow incapable of effectively mating with wild females under field conditions and that the colonized and wild strains differed in some behavioral trait. Incidentally, this conclusion was reached and substantiated by the use of sterility as a tag. Virgin, colour-tagged colony females and virgin, colour-tagged wild females were released along with sterilized colony males into a naturally infested mosquito area. Wild, fertile males competed with sterile colony males in mating both types of females. The types of matings were identified by the sterility tag.

Another release of sterile male mosquitoes was conducted in Florida with Aedes aegypti L. [3]. Again, males were reared in the laboratory and sterilized by gamma radiation. The feasibility of the sterile male release technique with this species was not demonstrated.

In India in the mid-1960s, radiation-sterilized males of Culex fatigans Wiedemann were released into a natural population [4]. A small percentage of sterile egg rafts was recovered, but males were not released in sufficient numbers to reduce density.

Although none of the release experiments demonstrated the feasibility of the sterile male release technique, they did develop useful data and methods on rearing, sterilization, sexual separation and release.

In general, in these early experiments the males sterilized by radiation were not equally competitive with normal, untreated males. Consequently, the emphasis switched from radiation to chemicals as sterilizing agents. Chemically sterilized males were shown to be equally competitive with untreated males. More recently, the competitiveness of radiation-sterilized male mosquitoes has been much improved by irradiating older pupae.

The next field releases of sterile males were made on Seahorse Key, near Cedar Key, Florida, with Culex p. fatigans in 1968 and 1969 [5,6]. Males were reared outdoors at the laboratory in Gainesville, Florida; pupae were harvested and the males separated by size; the males were sterilized by exposure of adults to tepa or pupae to thiotepa. I should like to review the results of these studies in general since they were the first experiments to demonstrate the validity of the concepts behind the sterile male release technique in research with mosquitoes under actual field conditions, and also they demonstrated the usefulness of the technique in determining the dynamics of field populations of one species of mosquito.

These experiments were conducted under the ideal field conditions of a small, essentially isolated island. The island was Seahorse Key, off the Gulf Coast of Florida, which was only 1 mile by 1/8 mile in size. However, the island had a naturally occurring population of Culex p. quinquefasciatus (= fatigans). All of the breeding sites for the immature stages of this mosquito occurred within an area about 130-160 yd in diameter. Males were released daily at one location; thus, they did not have to travel over 60 - 80 yd to get together with females for mating. The first year (1968) the release of chemosterilized males over an 8-week period (4 generations) resulted in a degree of sterility that increased from 0 to 85% by the 4th generation. Density was reduced by about 68%. Reproductive success of the population increased from 1x at the start of the experiment to about 10x in the 3rd and 4th generations. The experiment was terminated before essential elimination of the population occurred.

However, the experiment was repeated in the same location the following year (1969). In this experiment the release of sterile males and the removal

of egg rafts resulted in suppression and essential elimination of the population in a 12-week period (6 generations). There was a reduction of 96% in the density of the population as measured by egg raft collection and a reduction in the fertility of the egg rafts of 99.8%. Again the reproductive success of the population increased from 1x to 10x during the experiment. Weidhaas and co-workers [7] have correlated estimates of the survival in adult females (related to egg deposition) and survival in immature stages to the reproductive success of the population under stress of total population control through the release of sterile males.

In a study on the release of chemosterilized stable flies, Stomoxys calcitrans (L.), conducted in Gainesville, Florida at a dairy farm, sterility levels in the wild population reached 77% and reductions in density were noted, indicating that reproductive success of the population was limited [8]. Further studies are needed with this insect.

In research with the house fly, Musca domestica L., work was not concentrated on the sterile male release technique, but rather on the use of chemosterilant baits. High levels of reduction in density may have been demonstrated with reproductive success of the population studied limited to values of 11x or less [9].

REFERENCES

[1] WEIDHAAS, D.E., SCHMIDT, C.H., SEABROOK, E.L., Field studies on the release of sterile males for the control of Anopheles quadrimaculatus, Mosquito News 22 3 (1962) 283.

[2] DAME, D.A., WOODARD, D.B., FORD, H.R., WEIDHAAS, D.E., Field behavior of sexually sterile Anopheles quadrimaculatus males, Mosquito News 24 1 (1964) 6.

[3] MORLAN, H.B., McCRAY, E.M., Jr., KILPATRICK, J.W., Field tests with sexually sterile males for control of Aedes aegypti, Mosquito News 22 3 (1962) 295.

[4] KRISHNAMURTHY, B.S., RAY, S.N., JOSHI, G.C., A note of preliminary field studies of the use of irradiated males for reduction of Culex fatigans Wied. populations, Vector Control, WHO Bulletin, Suppl. to Vol.29, Geneva (1963).

[5] PATTERSON, R.S., FORD, H.R., LOFGREN, C.S., WEIDHAAS, D.E., Sterile males: Their effect on an isolated population of mosquitoes, Mosquito News 30 1 (1970) 23.

[6] PATTERSON, R.S., WEIDHAAS, D.E., FORD, H.R., LOFGREN, C.S., Suppression and elimination of an island population of Culex pipiens quinquefasciatus with sterile males, Science (US) 168 (1970) 1368.

[7] WEIDHAAS, D.E., PATTERSON, R.S., LOFGREN, C.S., FORD, H.R., Dynamics of a population of Culex pipiens quinquefasciatus Say., Mosquito News 31 2 (1971) 177.

[8] LaBRECQUE, G.C., MEIFERT, D.W., RYE, J., Jr., Control of stable flies, Stomoxys calcitrans (L.) with the release of chemosterilized adults, Can. Entomol. (1972) (in press).

[9] WEIDHAAS, D.E., LaBRECQUE, G.C., Studies on the population dynamics of the housefly, Musca domestica L., Bull. World Health Organ. 43 (1970) 721.

THE CONSEQUENCES OF CONTROL OF AFRICAN TRYPANOSOMIASIS

J. FORD
Hope Department of Entomology,
University Museum, Oxford,
United Kingdom

Abstract

THE CONSEQUENCES OF CONTROL OF AFRICAN TRYPANOSOMIASIS.

The importance of agricultural insect pests can be assessed by calculating the amounts by which they depress market yield. More difficult to evaluate are disease vectors, for human suffering is not easily measured although estimations of mortality, the lowering of reproduction rates or of work time lost through morbidity can be attempted. Tsetse flies, or rather the several trypanosomes they transmit, affect the lives of human communities in all these ways, both by increasing the difficulties of farming as well as by severely affecting, to the point of death, the lives not only of people but of all their domestic animals. They also exclude large areas of land from any kind of productive use. They are therefore intimately involved in the maintenance of stable states in tropical African ecosystems. Because of this it is not easy to predict the consequences of their control or elimination, for this may, in turn, remove controls on numerous elements in these ecosystems and not always with results beneficial to the human community. This paper draws attention to the results of some former control schemes and suggests that planning of sterile male release programs ought to include assessments of the ecological consequences of success as well as of the mere elimination of tsetses.

1. TSETSE ELIMINATION

Three methods of tsetse elimination or control are currently in use: (1) bush-clearing to destroy the habitat; (2) animal slaughter to remove the food hosts; (3) direct destruction of the flies with insecticides. Neither the first nor second method need be total and insecticide spraying is usually selective and, in any case, uses quantities much smaller than are needed for crop pests. Nevertheless, each method may have undesirable side effects tending to reduce resource potential. Sterile male release should not directly diminish natural resources. But it will upset the balance of ecosystems: indeed it will be used with this intention, as are other methods of control.

Observations of long-term consequences of trypanosomiasis control by the first three methods mentioned, as well as by therapeutic and prophylactic attacks on the trypanosomes, show that very often they have sequels of a kind not anticipated by their promoters. It should also be noted, in passing, that in some environments human population expansion, in the distant past as well as during the last 30 years, has eliminated Glossina over far greater areas than have the operations of applied entomologists.

2. POPULATION EXPANSION

Such population expansion has had this result in Sukumaland in Tanzania and has been followed by proliferation of domestic livestock. Cattle population growth is limited by (a) tsetse-infested peripheral woodlands which are being destroyed by expanding agriculture. The area of disease-free pasture is thus continually increasing. However (b), the cattle population increase outstrips grass growth so that periodically large numbers of animals die of starvation. (c) Reduction of grazing pressure following high cattle mortality is followed by unusually high grass growth which permits the tick, Rhipicephalus appendiculatus, to extend its range, leading to epizootics of theileriosis among the recovering herds. Infected calves acquire a life-long immunity if they survive so that, in due course, the grass cover is again reduced, ticks disappear, and the cycle recommences. Large-scale elimination of peripheral tsetse-belts will not reduce but will lead to the magnification of this wasteful cycle. What is needed (and the appropriate authorities are not inactive in these matters) is the development of a fully commercialised industry for livestock farming, combined with pasture conservation. These are old problems still not solved.

3. TRYPANOSOMIASIS CONTROL

Control of trypanosomiasis, even in intensively managed ranches run by sophisticated businesses, may not lead to vegetation impoverishment, as in Sukumaland, but give rise to other changes which also reduce livestock productivity. Successful control of cattle trypanosomiasis by drugs in East African coastal bush was followed by multiplication of palms, acacias and thicket plants, with consequent reduction of grass cover. This led to weight loss and falloff in productivity of ranch cattle. One cannot add a large biomass of cattle to an ecosystem already carrying a near-capacity biomass of wildlife without provoking adjustments that are disadvantageous. In other words, no amount of tsetse extermination can make two blades of grass grow where one grew before and it is this which is the basic problem in the African livestock industry.

4. AREA OF TSETSE INFECTION

The area of tsetse infestation in tropical Africa is about 4.5×10^6 square miles. There are very few areas where Glossina can be eliminated without risk of reinfestation. Some kind of barrier is necessary; but it is common experience that barriers are not fully efficient. Failures lead to what is called "defence in depth" – a barrier to protect a barrier and so on.

In 1949 Uganda began a 10-year program of tsetse elimination. Some 5000 km^2 were reclaimed. Such operations tend to lengthen the periphery to be defended and increase distance from administrative and supply centres. Expenditure to maintain the position achieved continued to increase and the tsetse-free area was enlarged to 8000 km^2. There has been, of course, a marked response in the stock population which rose from 2.5×10^6

to 3.8×10^6 between 1950 and 1968. But there has been no change in the number of treatments for trypanosomiasis proportional to total cattle population (66% in 1950 and 67% in 1968, though with fluctuations from 33 to 109% in the interim).

Limits to further reclamation are imposed by international boundaries or by National Parks. Still unreclaimed is the Busoga fly belt, focus of the worst human epidemic ever known. The National Parks were originally evacuated because of sleeping sickness and there are recent indications that trypanosomes are still active. Similarly, on the edge of the Serengeti Park in Tanzania recent tourist infections have revived interest in the Ikoma focus first identified in 1925.

5. HUMAN TRYPANOSOMIASIS

Persistent natural foci of human trypanosomiasis have been strikingly manifest in the Zaire Republic (formerly Democratic Republic of Congo). The Belgian working hypothesis held that transmission of the parasite (T. gambiense) was solely between humans via tsetses of the Palpalis group. The very severe epidemic originating at the end of the 19th century was eventually attacked by curative and prophylactic drugs. Removal of the trypanosomes from the human hosts should, it was believed, render the vectors harmless. In roughly 40 years, infection incidence was reduced to very low levels and many areas were declared free of infection.

Within two years of the Belgian withdrawal infection incidence, in areas where surveys could still be undertaken, had returned to the levels of 1925. Not only this, but the trypanosomes were now resistant to curative drugs formerly in use and were showing characteristics generally associated with those known to be derived from wild animals (rhodesiense type). Most startling, however, was that this epidemic resurgence was appearing in precisely those places which had been the most fearful foci of infection in the early days of the Congo Belge, including some which, for years, had been free of clinical disease. The basic transmission cycle on which the natural foci of infection depended was from wild animal to wild animal through species of tsetse not belonging to the Palpalis group. Moreover this became evident because prolonged prophylaxis had deprived the populations at risk of those naturally acquired antibodies which, in pre-colonial days, must have offered considerable protection against acute infection.

6. CONCLUSIONS

What do these examples (which could easily be multiplied) suggest in the context of the present discussions?

(a) The approach must be ecological: that is, the definition of the problem must be made in the context of factors contributing to the maintenance of the whole system of which the infection is a component.
(b) Final models should attempt to predict consequences (economic, conservational) of removal of any key factor in terms of the populations from which control due to disease will be lifted. Immunological changes

in such populations when removed from natural sources of infection must not be overlooked. This is of great importance with cattle, from the viewpoints both of their own survival if barriers break down and also of their potentialities as amplifier populations for human trypanosomes.

(c) Where multivector transmissions are implicated – as in persistent natural foci of infection – more permanent results may be achieved by an attack on vectors responsible for transmission between natural hosts (wildlife) than on the vector responsible for spread of the parasite through the human population. (Peridomestic populations of Glossina tachinoides which rarely bite man may provide an exception.) In general, to attack the man-to-man vector (usually Palpalis group flies) while wildlife-feeding Morsitans or Fusca group remain untouched, is to leave the main reservoir of human infection in being.

(d) In barrier situations or in areas such as National Parks consideration should be given to the possibilities of maintaining vector populations at low densities rather than aiming at rapid extermination. The object would be to prevent disruptive epidemics or epizootics while sustaining a maximum ecological equilibrium combined with some degree of natural antibody formation in neighbouring human and domestic animal communities.

(e) Present discussion is directed towards promotion of pilot schemes to yield significant results in two years. The main object will be to try out the application of Knipling-derived models in the field. The opportunity should be taken to involve as many disciplines as possible in modelling the anticipated results of success. These disciplines should include entomology, parasitology, immunology, demography, wildlife conservation and economics. The value of different types of ecological and/or epidemiological models for application to such disease systems should also be explored. There are currently a number of research teams at work in these different fields of knowledge. There is a need to begin to integrate their work if new control methods are not to repeat the failures of the past.

RESUME OF REQUIREMENTS FOR A STERILE INSECT RELEASE PROGRAM EXCLUSIVE OF BASIC LABORATORY AND FIELD CAGE STUDIES

B.A. BUTT
Entomology Research Division,
Agricultural Research Service,
United States Department of Agriculture,
Yakima, Wash.,
United States of America

Abstract

RESUME OF REQUIREMENTS FOR A STERILE INSECT RELEASE PROGRAM EXCLUSIVE OF BASIC LABORATORY AND FIELD CAGE STUDIES.

A sterile insect release program requires a dependable production and release of high-quality sterile insects into the field. The ecology, numbers and distribution of the target insect should be known before mass field releases begin.

1. INTRODUCTION

In recent years, entomologists have conducted laboratory experiments on the sexual sterilization of many insect species and have also conducted large-scale experimental and/or commercial control programs with several insects. This discussion is limited to the requirements for large-scale sterile insect release programs.

2. REARING

Rearing facilities and methods must be adequate to consistently produce large numbers of vigorous insects. A reduction in insect production, even for a short time during critical periods of the release program, may result in partial or complete failure in control of the target pest because releases must not fall below the minimal required number (or ratio) at any time.

3. COMPETITIVENESS OF RELEASE STERILE INSECTS

The released male insect should be vigorous and healthy and must be competitive with native males in seeking out and mating with native females. Damage to the released insects by irradiation, handling, marking, and release must be kept to a minimum. The released insect must be able to survive in the release environment. Often unique situations are encountered by released insects that are not common to native insects, such as being dropped from high-flying aircraft through cold air into tropical valleys or chilled insects being released onto bare ground during hot summer months.

In either case, the released insect may die before it reaches proper shelter. Also, many released insects may fall in non-host areas.

The insect must not be laboratory adapted to the extent that it is not active in mildly adverse weather such as wind or cold, while the native insects are still active. The released insects must be "in phase" with the native insects. To be effective, the released insects must fly and mate at the same time as the native insects.

Slightly reduced competitiveness may be compensated for by releasing greater numbers of sterile insects.

4. RELEASE

Ground and/or air release methods should be developed which allow flexibility in the numbers of insects released per hectare and which will do minimum damage to the released insects. Releases should begin before the first spring emergence of the target insect and continue throughout the season. If releases are withheld until target insects are trapped, some natives may already have mated. Also, early "shakedown" releases are always desirable. Releases of insects that are not strong fliers should be spaced at close intervals or be continuous, and insects with a short life-span must be released frequently.

5. POPULATION STUDIES PRIOR TO RELEASE OF STERILE INSECTS

Before the release program begins, the following information must be known.

(a) The target insect population in the release area and the distribution of that population through space and time. Total numbers of released insects per hectare or average ratios for the season can be meaningless. There must be adequate numbers of released insects in the areas of high native populations; also, there must be an adequate ratio of sterile to native insects during the highest population periods. To achieve a satisfactory ratio, for example, a 40:1 ratio at all locations at all times, an average seasonal ratio of several hundred to one may be required. This must be considered in determining the required laboratory production of sterile insects for a release area.

(b) The target insect populations adjacent to the release area and the movement of native and released insects into and out of the release area. Gravid monogamous females moving in from adjacent areas can disrupt an otherwise successful program.

6. POPULATION SUPPRESSION PRIOR TO RELEASE OF STERILE INSECTS

The degree of suppression by sterile insects is dependent on the ratio of sterile to native insects. Therefore, it is advantageous to reduce the native population to the lowest practical level before the actual release of sterile insects. Insecticide applications, hosts removed, and other cultural methods are often very effective in reducing high native populations to a level which can easily be overflooded with sterile insects.

7. MONITORING THE RELEASE PROGRAM

Effective methods of monitoring the release program throughout the season must be developed. One of the most common methods of determining sterile-to-native ratios in the field is to trap marked, released and native insects in sex-attractant, light, or other lure traps. Although sex-attractant trap catches may not indicate the actual sterile-to-native ratios in the field, they do indicate the ratios of those responding to females. The males not responding to traps would probably not respond to females. The percent fertility of eggs collected from oviposition sites in the field or from field-collected native females also indicates the effectiveness of the release program, as does the number of new infestations by the target pest in the release area.

8. EVALUATION OF STERILE INSECT RELEASE PROGRAMS

Evaluation of the control program is usually finalized at the end of the season. The program is successful if the target insect population is eradicated or suppressed to an acceptable level, but if the population increases at a normal rate the program is not effective. The evaluation of intermediate levels of control is difficult because the experiment is usually conducted in a large unreplicated plot with a low population and often other population suppression methods have been used simultaneously or immediately preceding the sterile insect releases.

Final evaluation of a release program is often determined by insect counts, host damage, or by determining overwintering populations following the release program.

9. IMPACT OF THE RELEASE PROGRAM ON OTHER ARTHROPOD SPECIES

The impact of a release program on the ecosystem must be evaluated. The release of large numbers of insects may result in an increase in predators which feed on the released individuals and if sterile but ovipositing females are released, there may be an increase in egg parasites. The absence of pesticides normally used to control the target insect should result in an increase in parasites and predators which in turn may control other pests; however, there may also be an increase in other pest populations which were previously suppressed by pesticides used to control the target insect. Also, the eradication of the target insect may make a niche available in the ecosystem for another species.

10. PRIORITIES

Most workers begin sterile insect release programs in the laboratory by studying the effects of irradiation or chemosterilants on a certain insect. Unfortunately, field and rearing studies are often delayed until the laboratory studies are completed even though rearing, population and

ecological problems are usually more difficult and require more time to solve. Rearing and field studies should begin early in the research program. If laboratory data show that the subject insect cannot be sexually sterilized without excessive damage, the information developed in the field studies will still be applicable to most present and future pest control methods.

SOME BIOLOGICAL OBSERVATIONS RELATED TO CODLING MOTH CONTROL BY THE STERILITY PRINCIPLE*

M.D. PROVERBS, D.M. LOGAN, Bernice E. CARTY
Research Station,
Canada Department of Agriculture,
Summerland, British Columbia,
Canada

Abstract

SOME BIOLOGICAL OBSERVATIONS RELATED TO CODLING MOTH CONTROL BY THE STERILITY PRINCIPLE.

Although the female codling moth Laspeyresia pomonella (L.) is polygamous, most of the eggs are laid before the second mating. Consequently, if transfer of irradiated sperm elicits normal oviposition, it will not be a serious handicap to control if the sperm is noncompetitive. Unlike fully sterile sperm (40 krad dose), partially sterile sperm (25 krad) induced normal oviposition, satisfied the mating instinct of the wild female, and evidently was only slightly less competitive than untreated sperm. Release of mixed sexes for suppression of reproduction is often stated to be as efficient as or superior to release of sterile males only. This may not be so for the codling moth because, when the wild moth population was low, the rate of sterile male dispersal (and consequent chance of mating with wild females) was more rapid in the absence of sterile females. Estimates of adult codling moth populations, by release-recapture procedures, are influenced by the method used for capturing the insects. With female-baited traps the ratio of laboratory to wild males captured was smaller with untreated wild females than with laboratory reared females treated with 40 krad of gamma radiation. With black-light traps the ratio of males to females captured during the first night of trapping was approximately 7:1 for sterile laboratory-reared moths but only 2:1 for naturally occurring wild moths. Rate of population increase per generation is most variable and even more difficult to predict. Increase per generation in field cages averaged 6-fold, but there was considerable variation (2- to 28-fold). More detailed information is needed on the behaviour of wild and irradiated laboratory-reared codling moths before an accurate mathematical model can be constructed to simulate the sterile moth release method for control of this insect.

1. INTRODUCTION

In recent years publication of mathematical models to describe various aspects of the sterile insect release method has focused attention on a number of parameters which should be carefully investigated for successful implementation of this technique of population management. The models have not only indicated which are the more important parameters, but they have made many researchers acutely aware that for most insect species the biological information needed for construction of accurate models is woefully inadequate. One of the main reasons for the inadequate or even misleading data is that in many instances precise methods have not been developed for measuring certain parameters.

This paper examines certain biological habits of the codling moth, Laspeyresia pomonella (L.), which influence the success of the sterile insect release method of control, and points out certain weaknesses in some of the techniques used to obtain data required for model construction with this insect.

---

* Contribution No.337 of the Research Station.

2. SEXUAL ATTRACTIVENESS AND RATE OF EGG LAYING

In most apple-growing areas of British Columbia the female codling moth may mate more than once. However, dissection of reproductively old females collected in apple orchards suggests that the moths usually deposit most of their eggs before they mate for a second time. If this is so, the female is essentially monogamous, and the importance of releasing males with competitive sterile sperm may be of less significance than previously believed. Of course, noncompetitive sperm should be capable of either inducing normal egg laying or satisfying the mating instinct of the female. If the mated female fails to oviposit and her mating instinct is not satisfied she will probably soon copulate with a normal male (which is capable of successful sperm transfer to four or more females) and commence laying a normal complement of hatchable eggs.

Studies of the importance of sperm competitiveness and the related problems of sexual attractiveness and rate of egg laying were initiated with Dr. B. Nagy in 1970 at the Hungarian Research Institute for Plant Protection. The work was later continued in British Columbia.

The relationship between sexual attractiveness and oviposition rate in females mated with untreated or irradiated males was investigated by the following procedure. Untreated virgin female moths, no more than 24 h old, were mated in small jars, one pair of moths per jar. As soon as the copulating moths separated, the mated females were placed in sex traps. Some traps were baited with virgin females. These were used as an index for comparing male response since virgins are much more attractive than mated females. The traps were made from 4- and 1-pint cylindrical cardboard containers. Two-thirds of the lid and bottom of the larger container were cut away, and the cylindrical wall lined with polyethylene-coated paper smeared with Stikem® adhesive to capture attracted males. The lid and bottom of the smaller container were replaced by fibre glass screen, and the cylindrical wall lined with paper. The females, which were confined in the smaller container, laid most of their eggs on the paper liner. The smaller container was placed inside the larger one to complete the trap assembly. On the day of mating the traps were suspended from branches of apple trees in one or two orchards. The trap position was randomized and changed daily to reduce the influence of uncontrollable variables. Every other day 1000-1500 marked moths of each sex, reared on an artificial diet [1], were released from up to 16 ground release stations dispersed uniformly throughout each orchard. As a rule, the released moths were not irradiated. The numbers of male moths (wild and laboratory-reared) trapped and the numbers of eggs laid by the confined females were usually recorded daily until most of the females were dead or moribund. New traps were used for every experiment because the walls of the inner cylinder became impregnated with sex pheromone.

2.1. Untreated laboratory females mated with untreated laboratory males

As was stated earlier, dissections of field-collected codling moths indicated that the females deposit most of their eggs before they mate for a second time. The purpose of this first experiment was to obtain evidence to support this observation. It was assumed here, and in the subsequent two experiments, that if no or very few males were captured in the sex

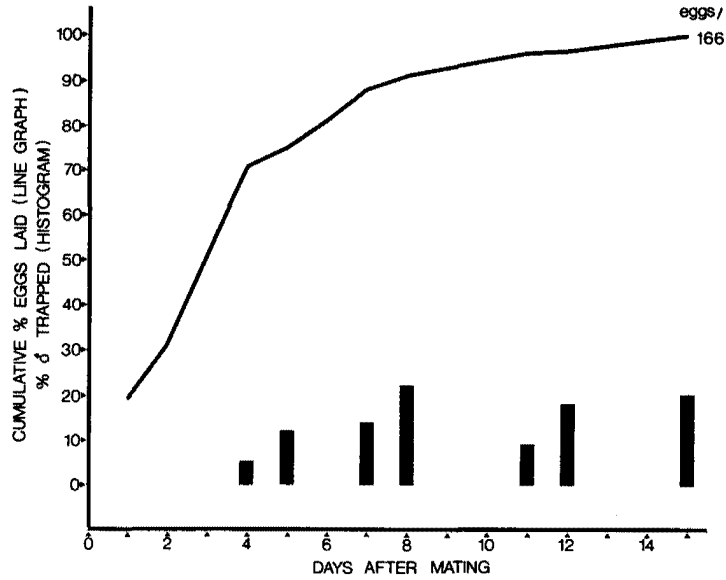


FIG. 1. Males trapped and cumulative eggs laid by female laboratory-reared codling moths after mating with untreated laboratory males. Trapped males are expressed as a per cent of those trapped by untreated virgin laboratory females. Sixteen traps per type of female, five females per trap.

traps, the females were producing no or very little sex pheromone, and consequently were unlikely to mate. Because of a shortage of wild moths, the traps were baited with laboratory-reared insects. Nevertheless, the results (Fig. 1) do support the evidence obtained from dissection of wild females. Not until the fourth day after mating did the females show any attraction. Even then the level of attraction was very low, for the number of males trapped was only 5% of that captured in traps baited with virgin females, and by this time the mated females had deposited 71% of the total number of eggs that they eventually laid in the 15-d trapping period. After the fourth day the attractiveness of the mated females increased, indicating that they would likely mate again. However, at no time did their attractiveness approach that of virgin females. The greatest number of males captured on any day was never greater than 22% of that captured in traps baited with virgin females, and of the total males captured (1822) in 15 d only 9.7% were taken in traps baited with mated females.

2.2. Untreated laboratory females mated with untreated or irradiated laboratory males

Although the previous experiment showed that mating with an untreated male induced the female to deposit most of her eggs before she regained her sexual attractiveness, there was no guarantee that this would be true for females mated with irradiated males. Consequently, attractiveness and oviposition rate were next established for laboratory females mated with untreated laboratory males, or with males exposed to 40 or 25 krad of

gamma radiation. The higher dose induces almost complete sterility – 40-krad male × untreated female results in about 3% egg hatch – and the lower dosage induces partial sterility – 25-krad male × untreated female results in about 15% egg hatch.

Traps baited with untreated virgin females captured numerous moths on days 1-7, none on day 8, and several on day 9 (a total of 1678 for the 9-d period), indicating good male activity in the orchard except for day 8. During the following eight days the weather was unseasonably cool and only 50 males were captured. This was unfortunate, for differences between the three types of females might have been apparent when the females became older.

In the first experiment each trap was baited with three females, whereas in the present experiment there was only one female per trap. This may explain why traps baited with females mated to untreated males captured proportionately more males per day in the first experiment than in the second. However, this difference should not appreciably affect the comparison of results within experiments.

The degree of sexual attractiveness and rate of egg laying were essentially the same for females mated with untreated or 25-krad males, whereas females mated with 40-krad males exhibited slightly greater

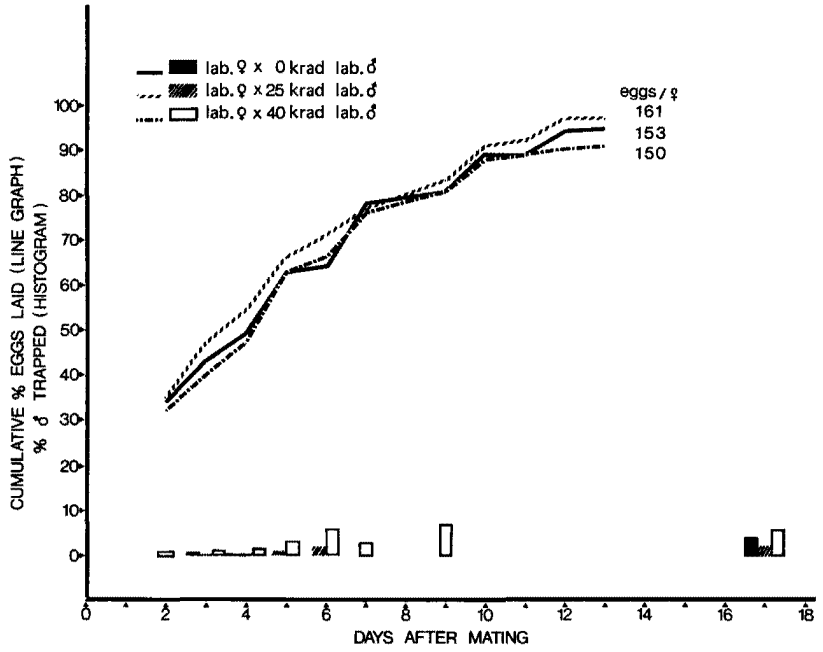


FIG. 2. Males trapped and cumulative eggs laid by female laboratory-reared codling moths after mating with untreated or irradiated laboratory males. Trapped males are expressed as a per cent of those trapped by untreated virgin laboratory females. Eggs laid are expressed as a per cent of those laid by untreated laboratory females mated with untreated laboratory males. Sixteen traps per type of female, one female per trap.

attractiveness but the same rate of egg laying (Fig. 2). The attractiveness of females mated with 40-krad males generally increased slowly, reaching a maximum on day 9. Even then the level of attraction was rather low, for the number of males captured on day 9 was only 7% of that in traps baited with virgin females. By this time the mated females had deposited 81% of the total number of eggs that were laid over the 17-d trapping period. It may be concluded that even with females mated with virtually sterile males (40-krad dose), only a small percentage of these laboratory-reared females are likely to remate before depositing most of their eggs.

2.3. Untreated wild females mated with untreated wild males or with irradiated laboratory males

Because the behaviour of laboratory-reared moths may be different from that of the wild insect, the previous experiment was repeated with wild females that were collected in the field as larvae and reared out in an insectary to the adult stage. The females were mated once with 25- or 40-krad laboratory males or with untreated wild males. Untreated wild virgin females were used as an index for comparison of sexual attractiveness.

It is known (e. g. see Table I) that laboratory males are less attracted to wild virgin females than to virgin laboratory females. This was reflected in the relatively low numbers of males (487) captured in traps baited with wild virgin females during the 12-d period of the experiment. The numbers of males attracted to mated wild females were correspondingly low and consequently the numbers of moths trapped are, as a rule, shown for 2-d periods in Fig. 3.

The most outstanding difference between this experiment with wild females and the previous experiment with laboratory females is that wild females mated with 40-krad laboratory males regained much of their sexual attractiveness on the fifth day after mating. Although their attractiveness then declined it never fell to the level recorded for

TABLE I. UNTREATED LABORATORY-REARED AND NATURALLY OCCURRING WILD CODLING MOTHS CAPTURED IN SEX TRAPS (BAITED WITH VARIOUS TYPES OF VIRGIN FEMALES) AFTER RELEASING EQUAL NUMBERS OF MALE AND FEMALE LABORATORY INSECTS. THREE FEMALES PER TRAP; FOUR TRAPS PER TYPE OF FEMALE.

Type of female	Radiation dose to female (krad)	Trapped males	
		Total	Laboratory : wild
Wild	0	180	2.9:1
Laboratory	0	535	3.8:1
Laboratory	25	263	3.5:1
Laboratory	40	277	4.8:1

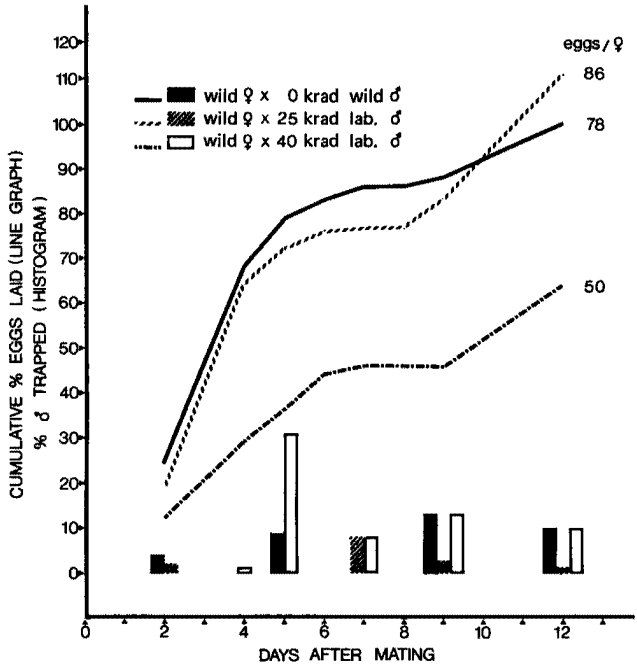


FIG. 3. Males trapped and eggs laid by wild female codling moths after mating with irradiated laboratory males or untreated wild males. Trapped males are expressed as a per cent of those trapped by untreated wild virgin females. Eggs laid are expressed as a per cent of those laid by untreated wild females mated with untreated wild males. Four traps per type of female, three females per trap.

laboratory females mated with 40-krad laboratory males. On day 5, wild females mated with 40-krad laboratory males had laid only 36% of the total number of eggs that were laid by wild females mated with wild males during the 12-d trapping period. Also, the total eggs laid in the 12-d period was only 64% of that laid by wild females mated with untreated wild males.

Wild females mated with 25-krad laboratory males were usually less attractive than wild females mated with untreated wild males, though rate of egg laying was slightly slower with the former during the first 9 d. It was not until the seventh day that the females mated with 25-krad males regained any appreciable measure of attractiveness and by that time they had deposited 74% of the total number of eggs laid in the 12-d experiment by females mated with untreated wild males.

The results of this experiment suggest that mating with a virtually sterile (40-krad) laboratory male will not satisfy the mating instinct of a wild female, and she will likely remate before many eggs are laid. If the second mating is with an untreated wild male, then virtually all eggs laid thereafter will hatch, for fully sterile sperm cannot compete with normal sperm [2, 3]. On the other hand, mating with a partially sterile (25-krad) laboratory male will satisfy the mating instinct of a wild female

as effectively as if she were mated with an untreated wild male, and she will deposit most of her eggs before she remates.

The difference in results between laboratory females mated with 40-krad laboratory males in the second experiment and wild females mated with 40-krad laboratory males in the third experiment illustrates how serious errors can occur in mathematical models if the initial data are based solely on laboratory-reared insects. It must also be pointed out that although the procedures used in the foregoing experiments yield more reliable results than laboratory procedures, it is unreasonable to expect that moths confined in sex traps in the field will behave in an identical manner to nonconfined moths. The general trends are almost certainly correct, but the magnitude of behavioural differences between the various types of mated females could be measurably different for nonconfined moths. Improved techniques will be needed to ascertain the magnitude of these behavioural differences.

3. SPERM COMPETITIVENESS

The previous experiments indicated that mating with an untreated or a partially sterile male (25 krad) induces the female moth to deposit most of her eggs before she mates for a second time. However, since the female lays some eggs after the second mating, it should still be advantageous if sperm from partially sterile males can compete with sperm from normal males.

Sperm competitiveness was investigated by mating virgin females first with an untreated male and then with a 25-krad male, or in the reverse order. Females were also mated twice with untreated males as a control.

On the basis of the per cent egg hatch (Table II) it is evident that the second mating, whether with an irradiated or normal male, was the important one. However, the effect of the first mating evidently was not completely lost. Where the first mating was with a 25-krad male and the second with an untreated male, the per cent egg hatch was somewhat lower than where both matings were with untreated males. Also, where the first mating was with an untreated male and the second with an irradiated male, the egg hatch (21%) was slightly higher than normally occurs when a female is only mated by a 25-krad male (about 15% hatch).

TABLE II. EGGS LAID AND PER CENT HATCH AFTER FEMALE CODLING MOTHS WERE MATED TWICE, FIRST WITH AN UNTREATED AND THEN WITH AN IRRADIATED (AT 3 ± 2°C) MALE, OR VICE VERSA.

1st mating with	2nd mating with	No. of females mated	Eggs per female	Av. % hatch
Untreated ♂	25-krad ♂	30	64	21
25-krad ♂	Untreated ♂	43	42	69
Untreated ♂	Untreated ♂	31	73	80

In a recent theoretical paper by Bogyo and co-workers [4] a graph dealing with sperm competitiveness indicates that if a female insect mates more than once, then it is unnecessary to have competitive sperm provided the sperm is utilized from the first or last mating only. Evidently the authors assume that sterile sperm will induce oviposition. For if oviposition does not commence, and a subsequent mating is with a fertile male, then the female will lay a normal complement of viable eggs. The codling moth could be included as a fairly typical candidate for Bogyo's graph provided the male is partially sterile (25-krad dose). With such males, the sperm or accessory gland fluid induces normal oviposition, and it is the sperm from the last mating which is primarily utilized in fertilization. However, with fully sterile males (40-krad dose), the rate of oviposition in wild females is appreciably reduced (Fig. 3), and once a female is mated by a fertile male she immediately commences and continues to lay mostly viable eggs whether or not she has already mated or later mates with a fully sterile male [2, 3].

4. DISPERSAL OF STERILE MALE MOTHS

It is often stated (e. g. Ref. [5]) that in the sterility principle of insect control, release of sterile males plus sterile females is just as effective, and often more effective, than release of sterile males alone. However, this may not be true for the codling moth. Both in laboratory and in field cage tests the addition of sterile males alone to untreated male and female moths has suppressed reproduction more effectively than the addition of sterile males plus sterile females [2, 3, 6] . Hathaway and co-workers [7] have speculated that the superiority of sterile males alone may be due to harassment of the females because of the high ratio of males to females. They showed that in small laboratory cages a high ratio of males to females results in a considerable reduction in the life span of the female moths, but it seems much less likely that this would occur with nonconfined moths in the field. Certainly very good control has been achieved in field experiments both by release of sterile males alone and by release of mixed sexes [8-12] , but because of many uncontrollable variables in such field experiments we cannot definitely say at this time which is the better procedure. However, it seems reasonable to believe that rate of male dispersal in the field is an important factor in the degree of control exercised by the two types of releases.

Rate of sterile male dispersal was estimated in a number of apple orchards in which the wild codling moth population was either relatively high or relatively low. Males alone were released from a single point at one end of each orchard, and males plus females from a point at the opposite end of each orchard. The direction of the prevailing winds was at right angles to an axis joining the two release points. Before release, all moths were sterilized by exposure to 50 krad of gamma radiation in carbon dioxide and then marked for subsequent identification. Three or four days after release, sex traps, each baited with 10 virgin females, were suspended from every tree. The numbers of moths trapped in one night were recorded. As a rule, each experiment was repeated about two weeks later, but this time males alone were released at the point

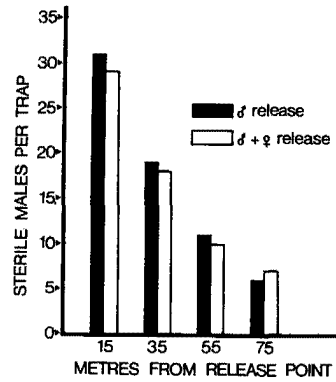


FIG.4. Sterile male codling moths captured in sex traps (each baited with 10 virgin females) on the fourth day after releasing sterile (50 krad in CO_2) males plus sterile females at one end of an apple orchard and sterile males only at the other end. Equal numbers of sterile males released at each end of the orchard. Sex ratio of 1:1 where males plus females released. Sixty-four trees; one trap per tree. Relatively high wild population (2.5 males per trap).

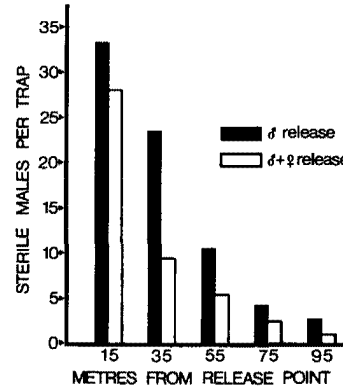


FIG.5. Sterile male codling moths captured in sex traps (each baited with 10 virgin females) on the third day after releasing sterile (50 krad in CO_2) males plus females at one end of an apple orchard and sterile males only at the other end. Equal numbers of sterile males released at each end of the orchard. Sex ratio of 1:1 where males plus females released. Eighty-seven trees; one trap per tree. Relatively low wild population (0.2 males per trap).

used previously for males plus females, and vice versa. Figures 4 and 5 are typical examples of the results obtained in two orchards, one with a relatively high and one with a relatively low wild population.

Where the wild moth population was relatively high (Fig. 4), release of males plus females or release of males alone resulted in very similar rates of male dispersal. In contrast, where the wild population was low (Fig. 5), release of males plus females generally resulted in a much slower rate of male dispersal than when males alone were released.

The efficiency of sex traps is reduced if there are large numbers of females present (unpublished results from the Summerland Research Station). Consequently, it might be argued that where the wild population was low (Fig. 5), the smaller numbers of males trapped with the mixed sex release were due, not to decreased rate of male dispersal, but to reduced trap efficiency in the presence of sterile females. However, if this were so, we would expect traps immediately adjacent to the male plus female release point to capture considerably fewer males than traps located near the sterile male release point. But the difference in numbers of males captured 15 m from the two release points was only 16%, whereas the difference at the four more distant trapping sites varied between 44 and 64%. The difference in numbers of captured males at the 15-m trapping site probably represents differences in trapping efficiency, whereas differences at further trapping distance largely represent differences in rate of male dispersal. There is some evidence [13] that in pome fruit orchards female moths remain close to the point of release and consequently the released sterile females would not materially affect trapping efficiency at the more distant trapping sites.

The wild codling moth population in apple and pear orchards is, or should be, very low before initiating programs of sterile moth release. Because such a population is far from uniform and is usually limited to a few "hot-spots" (the locations of which are often unknown), it should be advantageous to release sterile males only, because of their relatively rapid rate of dispersal. The slower male dispersal observed when sterile males and sterile females are released together probably occurs because the sterile males do not have to seek out wild mates, but simply copulate with nearby sterile females. In fact such matings were frequently observed within a few hours after releasing mixed sexes. Unfortunately, no truly effective method has been developed for rapidly sexing codling moths, and consequently it would be impractical at this time to conduct a sufficiently large-scale field experiment to determine conclusively whether release of sterile males alone would effect better control than release of mixed sexes.

5. ESTIMATING CODLING MOTH POPULATIONS

Various workers have estimated codling moth populations by banding tree trunks to capture the mature larvae, by examining fruit for larval injury, and by using sex or black-light traps in conjunction with release of marked adults. None of these procedures is entirely satisfactory. Some of the shortcomings of sex- and black-light traps are considered below.

5.1. Sex traps

Until the recent introduction of synthetic sex pheromone, the use of sex traps for monitoring and estimating codling moth populations was limited to traps baited with living virgin females. It is known that traps baited with wild females capture fewer male moths than those baited with laboratory-reared females. However, we could find no published data to indicate whether the ratios of wild to laboratory males captured were

the same with the two types of females. To investigate this, traps baited with virgin laboratory-reared females (untreated or irradiated) or with untreated wild virgin females, were set out in a randomized manner in a small apple orchard in which the codling moth infestation (based on numbers of injured fruit) was reasonably uniform. Wild females were reared from infested apples collected in the field; laboratory females were also reared on apples. The location of each trap was changed daily to minimize the effects of uncontrollable field variables. Equal numbers of untreated male and female moths, reared in the laboratory on an artificial diet [1], were released from several points in the orchard on the day the traps were set out and on every second day thereafter for the duration of the experiment. Trapped laboratory (marked) and wild (unmarked) males were recorded daily.

As was expected, traps baited with wild females captured fewer males than traps baited with untreated or irradiated laboratory females (Table I). However, the ratio of laboratory to wild males captured was appreciably smaller for traps baited with wild female moths than for those baited with 40-krad laboratory females. The question that immediately arises is: which type of female is giving the true ratio of laboratory to wild males? From the standpoint of controlling a wild population by release of sterile laboratory males, we are primarily interested, not in the true or absolute ratio of laboratory to wild males, but rather in the effective ratio. Laboratory moths which are not attracted to wild females would be of little or no value in a control program and should not be considered in arriving at the effective ratio. The ratio obtained with traps baited with wild females is likely to represent a truer picture of the effective ratio, and probably should be used in estimating the size of native populations.

From a practical standpoint a supply of wild female codling moths is seldom available for population estimation or for the constant monitoring of the ratio of sterile to wild males as required in sterile insect release programs. Consequently, laboratory-reared females are normally used in sex traps and the females are routinely irradiated to avoid the possibility of starting an infestation, which could happen if some of the females are inadvertently mated before they are placed in the traps. (Nonirradiated mated females lay fertile eggs in the traps, and the hatched larvae readily attack nearby fruit). Fortunately, the present results, though based on small numbers of insects, indicate that the ratios of wild to laboratory males captured are not appreciably different for wild and 25-krad laboratory females. Therefore, if the radiation dose is kept to the minimum level required for female sterilization (about 25 krad), the use of sterile laboratory females will probably give fairly reliable results.

Synthetic sex pheromone is likely to replace living females as the attractant in sex traps, but it will still be necessary to establish whether the ratio of sterile to wild males trapped is the same with synthetic pheromone as with wild virgin females.

5.2. Black-light traps

In the course of an experiment on dispersal of codling moth adults some pertinent information was revealed on the comparative response of the male and female to black light. Equal numbers of male and female moths, reared on apples in the laboratory, were exposed to 50 krad of gamma

TABLE III. MALE LABORATORY-REARED CODLING MOTHS CAPTURED IN NINE BLACK-LIGHT TRAPS AFTER IRRADIATING (50 krad IN CO_2) AND RELEASING EQUAL NUMBERS OF MALES AND FEMALES ON 8, 9, 10, AND 11 AUG. 1967.

Trapping date	% males trapped[a] after indicated days of release							
	1	2	3	4	5	6	7	8
12 Aug.	88	87	86	86	-	-	-	-
14 Aug.	-	-	62	58	46	41	-	-
15 Aug.	-	-	-	42	53	39	25	-
16 Aug.	-	-	-	-	46	48	41	25

[a] Males + females = 100%.

TABLE IV. IRRADIATED LABORATORY-REARED AND NATURALLY OCCURRING WILD CODLING MOTHS CAPTURED IN NINE BLACK-LIGHT TRAPS AFTER RELEASING THE IRRADIATED (50 krad IN CO_2) LABORATORY MOTHS (σ:♀ = 1:1) ON 8, 9, 10, AND 11 AUG. 1967.

Trapping date	No. of males and females trapped		Per cent male	
	Laboratory-reared	Wild	Laboratory-reared	Wild
12 Aug.	2020	724	87	67
14 Aug.	996	643	53	65
15 Aug.	291	580	43	66
16 Aug.	102	406	44	61

radiation in carbon dioxide, marked, and released from several points in a small apple orchard that was severely infested with wild codling moths. The procedure was repeated for the following 3 d, using a different coloured marker each day. Fifteen-watt black-light traps were operated in the orchard on the fifth, seventh, eighth and ninth day. Trapping results are shown in Tables III and IV.

With laboratory-reared moths, many more males than females were captured during the first trapping night. The per cent recovery of the laboratory moths was inversely proportional to the age of the moths, but age had no effect on the proportion of males to females trapped (Table III). On the second trapping night the proportion of males to females dropped very appreciably (probably because 20% of the released males were trapped the first night), continued to decline on the third night, and generally was about the same on the fourth night as on the third.

In contrast to the results with laboratory moths, it was found with naturally occurring wild moths that the proportion of males to females

captured was about the same for each trapping night (Table IV). But the most important point was that this proportion (61-67% males) was much lower than that for laboratory moths (87%) on the first trapping day. On the other hand, the average proportion of males to females was not too different when based on the total numbers of moths captured over the entire experiment, that is, 65% males for wild and 72% males for laboratory moths.

It is obvious that if mathematical models are based on population estimates derived from males captured on the first night, the results will be appreciably different from those based on estimates derived from males captured over the entire trapping period. The latter is likely to be more reliable. However, the population of naturally occurring wild codling moth adults can increase very rapidly, even from day to day, at certain times of the year. When a control program is in progress it is essential that changes in the proportion of sterile (laboratory-reared) to wild males be determined very rapidly so that if extra sterile males are required they can be released without delay. If it takes several days to determine these changes, it will then be too late to start releasing the necessary extra sterile insects.

One possible danger in using light traps for estimating the ratio of sterile laboratory males to wild males is that the stimulus for attraction may not be related to sexual behaviour. Possibly a number of males which respond to a light stimulus may not be attracted to or mate with females. In contrast, sex traps, particularly those baited with wild females, employ a sexual stimulus for attraction and consequently should give a much better indication of the effective ratio of sterile to wild males.

6. POPULATION INCREASE PER GENERATION

Several authors (e. g. Refs [4, 14]) have illustrated by mathematical models that the size of population increase per generation is one of the most important parameters affecting the results of sterile insect release. For most insects, including the codling moth, this parameter is not only difficult to measure accurately, but it varies considerably from one generation to another. Also, it is most difficult to predict with any degree of accuracy since it is affected by many uncontrollable variables, notably weather.

In field cage experiments with codling moths over a number of years it was found that the increase per generation varied from 2- to 28-fold, with an average increase of 6-fold. In each experiment these results were usually based on a single introduction of known numbers of moths into cages over dwarf apple trees carrying small numbers of fruit. At best, these findings serve only as a guide to the likely increase per generation with nonconfined moths. It should also be noted that the increase in larval numbers during the second generation is three or more times that of the first generation, but the numbers of second-generation larvae that develop to the moth stage the following spring may be drastically reduced by predators, parasites and low winter temperatures, particularly if there is little or no snow cover. In a control program by sterile insect release, the larval population capable of fruit injury is very important, whereas

in an eradication program it is only the larvae that develop into adult moths that are of primary concern.

The potential for high population increase was illustrated in two apple orchards in which sterile moth release programs were conducted [9, 10]. When the programs were discontinued, the codling moth population in the two orchards had been reduced to extremely low levels, for less than 0.09% of the fruit were attacked by larvae that were capable of overwintering. By the following autumn fruit injury had increased to about 10%, and 1 yr later to at least 80%. This was the approximate level of infestation in these unsprayed orchards at harvest prior to their preparation for sterile moth release.

7. CONCLUDING REMARKS

The limited observations on codling moth behaviour reported in this paper show that much of the present data is still very incomplete. The experiments were based, in some instances, on relatively small numbers of insects; the work was limited to certain times of the year; trials were conducted with one laboratory strain of codling moth; and the observations were made in a very limited geographical region. Changes in these and other factors will modify the results, some more so than others. Nevertheless, some of the information is sufficiently reliable to construct useful, though tentative, mathematical models. More detailed experiments are needed to establish the variability of the important parameters, particularly rate of increase per generation. When this is known, mathematical calculations then can be applied to estimate how over- or underestimating these parameters is likely to affect the outcome of sterile moth release.

The problem of "hot-spots" of infestation is one of the most serious drawbacks to commercial implementation of the sterile insect release procedure for codling moth control. It should be possible to develop mathematical procedures that tell more precisely the importance of these hot-spots, but first it will be necessary to accumulate more detailed information on the flight behaviour of both sexes of the wild and sterile laboratory-reared moth. And, of course, improved methods must be developed to quickly identify and delineate hot-spots so that additional sterile moths can be released in these areas without delay.

REFERENCES

[1] BRINTON, F.E., PROVERBS, M.D., CARTY, B.E., Artificial diet for mass production of the codling moth, Carpocapsa pomonella (Lepidoptera: Olethreutidae), Can. Entomol. 101 (1969) 577.

[2] HATHAWAY, D.O., Laboratory and field cage studies of the effects of gamma radiation on codling moths, J. Econ. Entomol. 59 (1966) 35.

[3] PROVERBS, M.D., NEWTON, J.R., Some effects of gamma radiation on the reproductive potential of the codling moth, Carpocapsa pomonella (L.) (Lepidoptera: Olethreutidae), Can. Entomol. 94 (1962) 1162.

[4] BOGYO, T.P., BERRYMAN, A.A., SWEENEY, T.A., "Computer simulation of population reduction by release of sterile insects. I. A study of the relative importance of the parameters of a mathematical model", Application of Induced Sterility for Control of Lepidopterous Populations (Proc. Panel Vienna, 1970), IAEA, Vienna (1971) 19.

[5] BERRYMAN, A.A., Mathematical description of the sterile male principle, Can. Entomol. 99 (1967) 858.
[6] PROVERBS, M.D., NEWTON, J.R., Suppression of the reproductive potential of the codling moth by gamma irradiated males in caged orchard trees, J. Econ. Entomol. 55 (1962) 934.
[7] HATHAWAY, D.O., BUTT, B.A., LYDIN, L.V., Reduction of sexual aggressiveness of male codling moths treated with tepa or gamma irradiation, J. Econ. Entomol. 63 (1970) 1881.
[8] BUTT, B.A., HATHAWAY, D.O., WHITE, L.D., HOWELL, J.F., Field releases of codling moths sterilized by tepa or by gamma irradiation, 1964-67, J. Econ. Entomol. 63 (1970) 912.
[9] PROVERBS, M.D., NEWTON, J.R., LOGAN, D.M., Orchard assessment of the sterile male technique for control of the codling moth, Carpocapsa pomonella (L.) (Lepidoptera: Olethreutidae), Can. Entomol. 98 (1966) 90.
[10] PROVERBS, M.D., NEWTON, J.R., LOGAN, D.M., Autocidal control of the codling moth by release of males and females sterilized as adults by gamma radiation, J. Econ. Entomol. 60 (1967) 1302.
[11] PROVERBS, M.D., NEWTON, J.R., LOGAN, D.M., Codling moth control by release of radiation-sterilized moths in a commercial apple orchard, J. Econ. Entomol. 62 (1969) 1331.
[12] WHITE, L.D., HUTT, R.B., BUTT, B.A., Releases of unsexed gamma-irradiated codling moths for population suppression, J. Econ. Entomol. 62 (1969) 795.
[13] WILDBOLZ, T., BAGGIOLINI, M., Über das Mass der Ausbreitung des Apfelwicklers während der Eiablageperiode, Mitt. Schweiz. Entomol. Ges. 32 (1959) 241.
[14] KLASSEN, W., CREECH, J.F., Suppression of Pest Populations with Sterile Male Insects, US Dept. Agric., Agric. Res. Serv., Misc. Publ. No.1182 (1971).

PRELIMINARY STUDIES OF MEDITERRANEAN FRUIT FLY Ceratitis capitata Wied. POPULATIONS IN CYPRUS

C. SERGHIOU, J. ZYNGAS, A. KRAMBIAS
Ministry of Agriculture and Natural Resources,
Nicosia, Cyprus

Abstract

PRELIMINARY STUDIES OF MEDITERRANEAN FRUIT FLY Ceratitis capitata Wied. POPULATIONS IN CYPRUS.

Surveys conducted in Cyprus in the years 1969 - 1971 showed that Mediterranean fruit fly Ceratitis capitata Wied. populations were very low in winter and spring, increased in summer and reached peak populations in the fall. In a test for the evaluation of different types of traps baited with trimedlure, best results were obtained with the McPhail glass trap, the metal sticky trap and the Steiner trap. Data collected in 1971 in a preliminary field trial for the control of the Mediterranean fruit fly by the use of the sterile insect release method and related data of laboratory tests and of tests under cages in the field are discussed.

1. INTRODUCTION

The Mediterranean fruit fly or medfly, Ceratitis capitata Wied. is a serious pest of citrus, peaches, apricots, plums, figs, pomegranates and many other hosts in Cyprus.

The present method of medfly control is based on malathion bait sprays which are practised systematically in the case of citrus groves.

In recent years interest has developed in the suppression or eradication of medfly by the use of the sterile insect release method.

This paper presents data on medfly population dynamics collected in the years 1969-1971 in different hosts and localities of Cyprus. These data will be useful in programs for the control of this fly by the use of sterile insects. In addition, data are presented of a preliminary test for the control of medfly by the use of sterile insects, of related laboratory tests and of competitive tests in cages in the field.

2. MEDFLY POPULATION FLUCTUATION IN DIFFERENT LOCALITIES AND HOSTS

This study was conducted during 1969-1971 and covered several localities of Cyprus, such as citrus-producing areas in Limassol and Morphou and stone-fruit-producing areas in Solea and Deftera. The survey was conducted using plastic traps baited with trimedlure which were serviced at approximately 15-d intervals. The number of traps placed in each locality and host varied from 1 to 10 and a total of 54 traps were used.

Results are presented in Tables I and II for 1969 and 1970-71, respectively.

Medfly populations were generally very low from January through May, increased in the months June, July and August, reached peak populations

TABLE I. MEAN NUMBER OF MEDITERRANEAN FRUIT FLIES Ceratitis capitata Wied. CAPTURED IN PLASTIC TRAPS BAITED WITH TRIMEDLURE ON DIFFERENT HOSTS AND LOCALITIES IN CYPRUS, 1969

Location	Host	No. of traps used	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Morphou	Grapefruit	10	6.7	154.1	85.5	127.6	55.7	39.8	8.9
Solea	Peach	7	0.3	4.4	1.0	47.6	271.7	68.7	56.0
Solea	Apple	5	0.0	6.2	11.0	72.6	239.4	52.0	52.8
Solea	Plum	2	0.5	3.5	8.5	39.0	439.5	79.0	80.5
Deftera	Peach	3	7.3	7.3	26.7	23.0	233.7	53.3	0.0
Deftera	Apricot	7	16.7	21.8	67.1	733.8	1191.6	1257.6	412.8
Deftera	Fig	4	22.0	35.7	44.7	708.2	1442.7	1222.5	466.2
Deftera	Olive	1	0.0	0.0	3.0	10.0	1016.0	585.0	126.0
Limassol	Grapefruit	3	315.0	38.3	0.3	0.0	0.0	3.0	-
Limassol	Jaffa	2	7.0	0.5	0.0	0.0	16.5	13.0	-
Limassol	Fig	4	22.0	35.7	44.7	708.2	1442.7	1222.5	466.2
Nicosia-Limassol Road	Carob	4	0.0	0.0	0.0	1.0	40.0	17.3	-
Nicosia-Limassol Road	Pine	2	0.0	0.0	0.0	1.0	2.0	0.5	-

TABLE II. MEAN NUMBER OF MEDITERRANEAN FRUIT FLIES, Ceratitis capitata Wied. CAPTURED IN PLASTIC TRAPS BAITED WITH TRIMEDLURE ON DIFFERENT HOSTS AND LOCALITIES IN CYPRUS, 1970-1971

Location	Host	No. of traps used	Apr. 1970	May 1970	Jun. 1970	Jul. 1970	Aug. 1970	Sep. 1970	Oct. 1970	Nov. 1970	Dec. 1970	Jan. 1971	Feb. 1971	Mar. 1971	Apr. 1971	May 1971	Jun. 1971	Jul. 1971
Morphou	Grapefruit	10	0	2	9	58	58	29	19	6	2	0	0	0	0	0	-	-
Solea area	Peach	7	-	0	0	9	31	65	114	140	23	0	0	0	0	0	-	-
Solea area	Apple	5	-	0	0	7	14	256	478	221	11	0	0	0	0	0	-	-
Solea area	Plum	2	-	0	0	12	8	252	834	277	8	0	0	0	0	0	-	-
Deftera	Peach	3	-	0	7	22	291	26	11	33	0	0	0	0	0	0	0	4
Deftera	Apricot	7	-	0	15	51	79	1128	269	691	33	0	0	0	0	0	0	1
Deftera	Fig	4	-	0	13	158	336	1202	736	932	30	0	0	0	0	0	0	1
Deftera	Olive	1	-	0	0	0	0	77	71	160	7	0	0	0	0	0	0	8
Limassol	Grapefruit	3	0	1	32	1	0	0	48	13	1	0	0	0	0	0	0	-
Limassol	Jaffa Orange	2	0	0	10	2	1	1	7	32	4	0	0	0	0	0	0	-
Limassol	Fig	4	0	0	0	0	0	18	78	141	4	0	0	0	0	0	0	-
Nicosia – Limassol Road	Carob	4	0	0	1	0	0	1	1	6	0	0	0	0	0	0	1	-
Nicosia – Limassol Road	Pine	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	-
Nicosia – Limassol Road	Olive	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	-

TABLE III. NUMBER OF MEDFLIES CAPTURED PER NADEL TRAP IN THE MORPHOU AREA, 1970[a]

Location	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Karavostasi	25	0	3	2	5	13	24	24	71	10	24	27
Pendayia	-	-	-	0	1	0	5	5	1	1	4	1
Prastio Morphou	0	0	0	0	5	23	86	956	207	64	2	3
Syrianochori	1	0	0	0	1	7	6	1	0	2	1	0
Zodhia	2	0	4	1	23	99	250	320	115	17	5	2

[a] Figures in the table are the mean of four traps.

TABLE IV. NUMBER OF MEDFLIES CAPTURED PER NADEL TRAP IN THE MORPHOU AREA, 1971[a]

Location	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.
Karavostasi	2	0	0	1	1	13	2	1	14	45
Pendayia	0	0	0	0	0	0	0	26	90	3
Prastio Morphou	0	0	0	0	0	18	16	215	227	13
Syrianochori	0	0	0	0	1	1	6	9	1	2
Zodhia	0	0	0	0	9	15	337	458	148	10

[a] Figures in the table are the mean of four traps.

from September through November, and then declined in December. Very low catches were observed in traps placed on non-hosts (carob and pine) located in areas where no hosts were grown; contrasted are the high catches on fig, a very susceptible host.

3. MEDFLY POPULATION STUDIES IN THE MORPHOU AREA

This survey, which was conducted in 1970 and 1971, aimed at establishing the medfly population fluctuation pattern in the Morphou area, which is the largest of the three main citrus-producing areas of the island. Nadel traps baited with trimedlure were placed on citrus trees in five villages of the area at the rate of four traps per village; flies were counted weekly.

Results are presented in Tables III and IV for 1970 and 1971, respectively.

There were differences in the number of flies captured in the various locations, with high catches at Prastio and Zodia and low catches at Pendayia, Syrianochori and Karavostasi. The medfly population fluctuation is more clearly shown in the areas with high medfly catches. In those areas, the medfly population was very low from April through May, increased in June and July, reached a peak in August and September, and began declining in October. The decline in October was probably related more to control practices than to climatic conditions.

4. MEDFLY POPULATION STUDIES IN THE KARPASS PENINSULA

This is currently the leading candidate area for the initiation of a large-scale pilot project for the eradication or suppression of medfly by the use of the sterile insect release method. It was, therefore, considered essential to study its medfly population. The survey was conducted during 1970-1971. Ten 1-ft^2 metal sticky traps baited with trimedlure were placed in each of five villages in the area. Traps in each location were placed on 10 different host plants. Seven traps were placed within village

TABLE V. NUMBER OF MEDFLIES CAPTURED PER METAL STICKY TRAP BAITED WITH TRIMEDLURE IN KARPASS. Host-plant classification

Host		Apr. 1970	May 1970	Jun. 1970	Jul. 1970	Aug. 1970	Sep. 1970	Oct. 1970	Nov. 1970	Dec. 1970	Jan. 1971	Feb. 1971	Mar. 1971
English name	Latin name												
Pomegranate	Punica granatum	15	23	58	238	361	545	825	723	202	18	0	0
Apricot	Prunus armeniaca	4	30	196	394	144	938	1062	713	173	10	0	0
Sycamore fig tree	Ficus sycomorus	23	25	43	46	106	568	797	419	153	9	0	0
Loquat	Eriobotria japonica	19	44	206	298	209	654	751	777	230	18	0	0
Fig	Ficus carica	3	2	5	147	343	1329	532	711	72	9	0	0
Orange	Citrus sinensis	63	93	55	202	233	805	514	618	330	57	1	0
Prickly pear	Opuntia vulgaris	14	5	2	16	71	505	596	447	150	9	0	0
Lentisc tree	Pistacia lentiscus	0	0	1	1	5	16	15	40	21	0	0	0
Carob	Ceratonia siliqua	0	0	1	3	1	2	13	45	22	0	0	0
Pine tree	Pinus halepensis	0	0	1	3	1	2	7	19	6	0	0	0

TABLE VI. NUMBER OF MEDFLIES CAPTURED PER METAL STICKY TRAP BAITED WITH TRIMEDLURE IN KARPASS. Location classification

Location		Apr. 1970	May 1970	Jun. 1970	Jul. 1970	Aug. 1970	Sep. 1970	Oct. 1970	Nov. 1970	Dec. 1970	Jan. 1971	Feb. 1971	Mar. 1971
Rizokarpason	Host	28	43	56	221	254	477	596	576	179	20	0	1
	Non-host	0	0	1	0	0	1	9	14	10	1	0	0
Leonarissos	Host	14	22	151	348	342	965	668	508	133	14	0	0
	Non-host	0	0	0	1	1	2	3	5	1	0	0	0
Ayios Andronicos	Host	14	9	44	234	134	843	1025	496	130	26	0	0
	Non-host	0	0	0	2	1	3	18	55	36	0	0	0
Yialousa	Host	11	21	122	105	137	900	715	1082	396	18	0	0
	Non-host	0	0	3	6	2	6	14	76	25	0	0	0
Koma tou Yialou	Host	30	61	34	55	183	632	622	486	100	14	0	0
	Non-host	0	0	0	3	7	17	14	24	9	0	0	0

TABLE VII. MEDFLY CATCHES FROM DIFFERENT TYPE TRAPS AT PRASTIO MORPHOU IN 1969

Month	Type of trap				
	Israel old-type trap	Triangular sticky trap	Steiner trap	McPhail glass trap	Metal sticky trap
Feb.	2	0	2	3	5
Mar.	0	0	1	1	2
Apr.	1	0	1	2	2
May	6	4	16	43	31
Jun.	69	105	173	220	141
Jul.	86	134	307	522	142
Aug.	21	149	111	287	255
Sep.	21	100	97	145	153
Oct.	1	65	70	90	137
Nov.	8	59	77	108	143
Dec.	1	7	8	13	16
Total	216	623	863	1434	1027

limits where many susceptible hosts were grown and three on non-hosts in the forest area surrounding the villages, where few or no medfly hosts were grown. Observations were made at 15-d intervals.

Results are presented in Tables V and VI as the mean number per host plant and mean number per village respectively. In Table VI, catches from the seven hosts and the three non-hosts are grouped separately.

There were practically no medfly catches in February and March, medfly population increased rather steadily from April through August, reached peak population levels from September through November, declined in December and reached low levels in January.

As was to be expected, there were pronounced differences between medfly catches within the village limits, where many susceptible hosts were grown, and outside the villages, where very few hosts were found.

5. EVALUATION OF THE CAPTURING EFFICIENCY OF DIFFERENT TYPES OF TRAPS

A test was conducted in 1969 to evaluate the efficiency of five different traps in capturing medflies. Traps tested were the (a) Israel old-type trap (b) triangular sticky trap (c) Steiner trap (d) McPhail glass trap and (e) metal sticky trap.

TABLE VIII. NUMBER OF MEDFLIES RELEASED, ADULT EMERGENCE IN THE LABORATORY AND IN THE FIELD, AND MALE STERILITY OF IRRADIATED MEDFLIES SENT FROM SEIBERSDORF

Date	No. medflies released[a]	Adult emergence in the laboratory[b] (%)	Adult emergence in the field[c] (%)	Egg hatch from crosses of 9-krad treated males with untreated females in a 1:1 ratio (50 male-female pairs)[d] (%)
29 May	830 000	-	85	0
5 Jun.	350 000	93	75	0.4
16 Jun.	100 000	83	15	3.1
26 Jun.	150 000	-	55	-
3 Jul.	150 000	86	65	1.3
10 Jul.	150 000	85	60	1.0
21 Jul.	150 000	60	53	2.3
28 Jul.	150 000	64	48	3.0
4 Aug.	350 000	3	58	0.7
14 Aug.	350 000	86	27	2.0

[a] Measured volumetrically.
[b] Based on samples of 100 pupae.
[c] Based on samples of 500 pupae examined one week following release.
[d] Egg hatch data were based on three samples totalling 300-450 eggs collected the 2nd, 4th and 6th day after beginning of oviposition.

The test was located in a citrus orchard at Prastio Morphou. The experimental design was a randomized complete block with five replications. Traps were baited with trimedlure, serviced every three weeks and medflies counted weekly.

Results are presented in Table VII.

Best results were obtained with the McPhail glass trap, the metal sticky trap and the Steiner trap.

6. DATA COLLECTED IN A PRELIMINARY TEST FOR THE CONTROL OF MEDFLY BY THE USE OF STERILE INSECTS

Data presented concern the second release site which was a 3.5-acre peach orchard situated at Morphou and belonging to the Government. This orchard had poor medfly isolation. The first release site, a privately owned farm growing different medfly hosts, had to be abandoned because

TABLE IX. DATA ON FERTILE STINGS, INFERTILE STINGS AND EGG HATCH BASED ON WEEKLY SAMPLES OF 100 FRUITS PICKED FROM THE RELEASE AND CONTROL SITES AT MORPHOU

Release site

	14 Jun.	21 Jun.	28 Jun.	5 Jul.	12 Jul.	23 Jul.	30 Jul.	6 Aug.	13 Aug.	20 Aug.
No. infertile stings	396	736	132	106	69	6	10	10	12	27
No. fertile stings	-	-	-	15	40	20	20	24	169	184
No. eggs hatched	-	-	-	94	179	76	116	108	214	808
No. eggs unhatched	-	-	-	2	23	16	76	37	39	265
No. larvae	-	-	-	0	82	48	34	104	376	892
Per cent egg hatch	-	-	-	98	89	82	60	74	85	75

Control site

	12 Jul.	23 Jul.	30 Jul.	6 Aug.	13 Aug.	20 Aug.
No. fertile stings	3	3	14	121	72	186
No. eggs hatched	17	14	58	272	493	710
No. eggs unhatched	0	0	1	4	25	126
No. larvae	11	0	24	363	116	843
Per cent egg hatch	100	100	98	98	95	85

of a rather severe infestation of early maturing loquat fruits (Eriobotria japonica) with infertile stings.

Weekly releases in the Government farm began at the end of May and were continued until the middle of August. Sterile medflies, reared and irradiated at the IAEA Seibersdorf Laboratory, were sent to Cyprus by air. Pupae received a radiation dose of 9 krad, 1-2 d before emergence. Upon arrival in Cyprus, flies still in the pupal stage were measured volumetrically, placed in brown paper bags and transferred to the release site.

Adult emergence of irradiated flies was determined in the laboratory based on a sample of 100 pupae from each shipment, and in the field from a sample of 500 taken one week after each release.

Male sterility was evaluated in the laboratory based on egg hatch of crosses of irradiated males with untreated females.

Weekly samples of 100 fruit were picked from the release and a control site, and brought into the laboratory, where the number of infertile and fertile stings was determined. Eggs were collected from the infested fruit, placed on a moist cloth in petri dishes and hatchability was determined 4-5 d later. Larvae present in fruits were allowed to complete their development and pupate and then were counted. Since it was impossible to locate eggs in fruits with developing larvae, these larvae, though counted, were ignored when determining the per cent egg hatch.

Results are presented in Tables VIII and IX.

Adult emergence was consistently (with a single exception) higher in the laboratory than in the field. Male sterility was very high as evidenced from the egg hatch from crosses of irradiated males with untreated females, which was never higher than 3% (Table VIII).

There was only a slight decrease in egg hatch in the release site compared to the control site (Table IX). The limited success was probably due to poor medfly isolation of the release site and poor quality of the released flies.

7. COMPETITIVE TESTS IN CAGES IN THE FIELD IN 1971

Test No. 1. This was an unreplicated test under a cage covering a single peach tree. Irradiated medflies of the Seibersdorf strain sent from Vienna were combined with untreated medflies of the Cyprus strain reared in Cyprus in a ratio 500 sterile males: 500 sterile females: 100 normal males: 100 normal females. Irradiated flies emerged and were sexed on 26 June; untreated flies emerged and were sexed on 27 June. Flies were released on 27 June and an 18-fruit sample was picked on 6 July.

Test No. 2. This was similarly an unreplicated test under a cage covering a single peach tree. Irradiated and untreated flies were of the Seibersdorf strain and were used in the same ratio as in the previous test. Flies emerged, were sexed and transferred to the field on 10 July, and a 50-fruit sample was picked on 20 July.

Test No. 3. This test had two replications; a single apricot tree under a cage formed a replicate. Irradiated medflies of the Seibersdorf strain were combined with untreated medflies of the Cyprus strain in a ratio 150 sterile males: 150 sterile females: 50 normal males: 50 normal females. Irradiated flies emerged and were sexed on 26 June; untreated

TABLE X. CORRECTED FERTILE-TO-INFERTILE STING RATIO AND EGG HATCH IN TESTS UNDER CAGES IN WHICH MALE AND FEMALE MEDFLIES IRRADIATED WITH 9 krad WERE COMBINED WITH UNTREATED MALES AND FEMALES IN A 5 : 5 : 1 : 1 RATIO

	Fertile stings	Infertile stings	Corrected fertile to--infertile sting ratio	Eggs hatched	Eggs unhatched	% hatch
Test 1	35	46	3.8	49	222	18.1
Test 2	75	109	3.4	98	260	27.3

TABLE XI. CORRECTED FERTILE-TO-INFERTILE STING RATIO AND EGG HATCH IN TEST UNDER A CAGE IN WHICH MALE AND FEMALE MEDFLIES IRRADIATED WITH 9 krad WERE COMBINED WITH UNTREATED MALES AND FEMALES IN A 3 : 3 : 1 : 1 RATIO

	Fertile stings	Infertile stings	Corrected fertile-to-infertile sting ratio	Eggs hatched	Eggs unhatched	% hatch
Replication I	161	132	3.6	146	540	21.3
Replication II	171	91	5.6	170	564	23.2
Mean	166	111	4.6	158	552	22.2

flies emerged and were sexed on 28 June. The test was initiated on 30 June and a 50-fruit sample from each replicate was picked on 8 July.

Results of tests No. 1 and No. 2 are given in Table X and of test No. 3 in Table XI.

Since these tests were mostly unreplicated, and also since flies often differed in age and strain, no definite conclusions can be drawn. It may nevertheless be noted that the corrected fertile-infertile sting ratio varied from 3.5 to 5.5 and that the egg hatch from crosses of irradiated males and females with untreated males and females in the ratio of 5 : 5 : 1 : 1 and 3 : 3 : 1 : 1 varied from 18.1% to 27.3%.

THE USE OF SIMULATION IN THE CHOICE OF AN OPTIMUM RADIATION DOSE FOR CONTROL OF Glossina morsitans

C.F. CURTIS
Tsetse Research Laboratory,
Langford, Bristol,
United Kingdom

Abstract

THE USE OF SIMULATION IN THE CHOICE OF AN OPTIMUM RADIATION DOSE FOR CONTROL OF Glossina morsitans.

A computer simulation method was devised to determine the dose of irradiation which, when given to male tsetse flies, would be optimum for both sterility and effectiveness in suppressing a wild population. A deterministic model was used; the assumptions included non-overlapping generations, an initial insecticide treatment and releases of males only. Among treatments of 12, 17 and 30 krad, 17 krad was calculated to cause the most rapid population decline and to be most efficient as regards the numbers to be released for achieving a given population reduction.

Compared with other Diptera, tsetse flies (Glossina spp.) are very resistant to radiation sterilization and, at the doses needed for a high percentage dominant lethality, a considerable reduction in adult male life-span occurs [1, 2]. Survival is improved if an atmosphere of nitrogen is used during irradiation but, even so, 100% dominant lethality cannot be achieved without reduction in male life-span and the induction of behavioural abnormalities which may imply a reduction in mating competitiveness in the wild [3]. The question therefore arises as to what dose would produce males with optimum effectiveness in suppressing a wild population, and a computer simulation method has been adopted to try to answer this.

A deterministic model was used and, for simplicity, the generations were assumed to be non-overlapping. Experience with a model of a tsetse population with overlapping generations [4] suggests that, for the present purpose, the simpler non-overlapping assumption is an adequate approximation. The flow chart of the model is shown in Fig. 1; one cycle around the chart represents one generation.

Stimulated by the results of Dr. J. Itard with G. tachinoides, Langley and I at Langford and Mews and Offori at Seibersdorf have been studying the F_1 from irradiated male G. morsitans. The sex ratio is biased towards males, presumably because, as in Drosophila, X-chromosome sperms present a larger target for dominant lethal induction than do Y-chromosome sperms [5]. A large proportion of the F_1 males and females show semi-sterility and Miss P. Pell has confirmed cytologically that this is due to the induction of chromosome translocations. The simulation model must therefore take into account that semi-sterile translocation heterozygotes (T/+) will continue to appear in the population for several generations after a release of irradiated males, and that some double translocation heterozygotes (DT) will be generated.

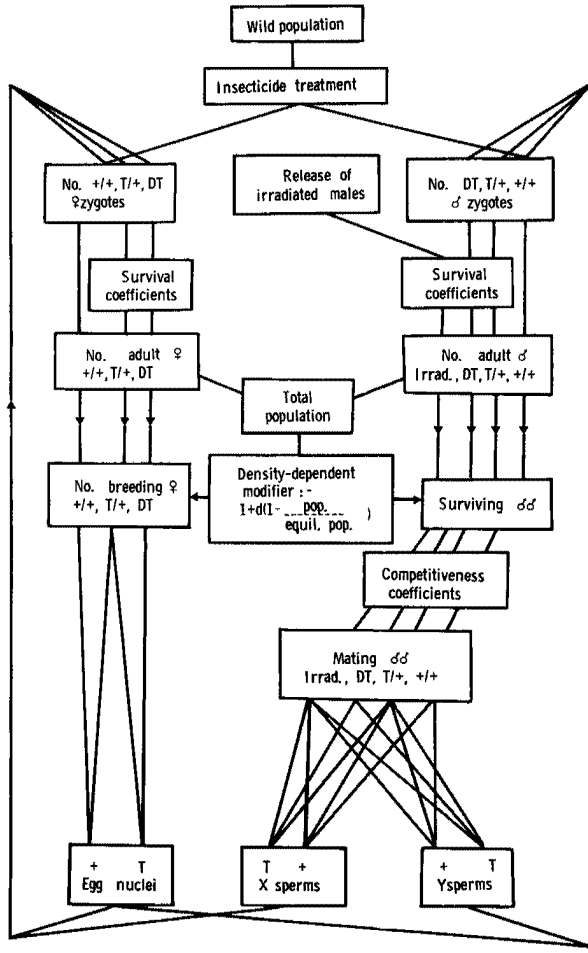


FIG. 1. Flow chart of the computer model.

The model assumes that males only are released; this is both practicable and desirable in tsetse [3]. The numbers of the different types born or released into the population are adjusted for their probabilities of survival. The translocation heterozygotes have been assigned survival values corresponding to those found for a translocation in G. austeni [6]. For the survival of males irradiated at various doses the data of Curtis and Langley [3] have been used; it is desirable that these are replaced by field data when they become available.

In considering the question of the optimum dose for population suppression, it is essential to give some thought to the density-dependent regulation (resilience) of the population. Artificial reduction of a Culex pipiens population gave it a tendency to tenfold increase per generation [7].

In such a case, a treatment which left 10% residual fertility would obviously be inadequate to drive the population to extinction, however many males were released. In view of their viviparity and other evidence, it seems unlikely that a tsetse population could show more than a twofold increase per generation as a result of extreme density reduction. This upper limit has been incorporated into the model by using a value of 1.0 for d in the density dependence modifier term, by which the population size is multiplied, as indicated in Fig. 1. In tsetses, competition could only occur at the adult stage and the strength of density-dependent action is assumed to depend on the density of the total adult population (including released males) relative to the equilibrium density at the carrying capacity of the environment.

The mating competitiveness of males is certainly one of the most important factors in determining the optimum treatment to use, but the available data are seriously inadequate. Based on laboratory data for G. austeni [6] the translocation heterozygotes were assumed to have normal competitiveness. An unreplicated field cage experiment with G. morsitans at one radiation dose indicated 50% of normal competitiveness [8], and this figure has been used for the irradiated males at all doses. It is important that field data on competitiveness should be collected by relating the sterile:fertile male ratio to the proportion of females with sterile inseminations.

In simulating fertilizations between numerous types of males and females it is simpler not to consider all the possible types of mating, but rather to compute the contribution of each type of parent to the pool of each type of gamete and then to consider the frequencies of the types of zygote which arise by combining the male and female gametes. Irradiated sperm in G. austeni is known to be fully competitive for fertilization [9], so random fertilization of gametes has been assumed. Only the viable types of gamete and zygote (i.e. those without dominant lethals or chromosome imbalance) need to be explicitly considered. The contribution of the various types of parent to the pools of normal (+) and translocation (T) gametes is determined by coefficients not shown in Fig. 1. The T/+ parents contribute 25% of their gametes to the + and T pools and the remainder are inviable. The fertility and gamete production of double translocation heterozygotes may be influenced by various factors. In the model the double heterozygotes have been given the properties of an example that has been studied in Drosophila [10]. Males irradiated at a particular dose are made to contribute to the pools of the various types of sperms according to laboratory data on the numbers of F_1 males and females at that dose and the proportion showing semi-sterility.

Figure 2 shows the results of some simulations with the model. It is assumed that an initial insecticide treatment is used, and therefore the population density is well below the carrying capacity of the environment throughout the period of the releases. After the insecticide treatment, the resilience of the population causes a partial recovery before the irradiated males begin to take effect. Figure 2 shows laboratory data, or interpolations from them, for three radiation treatments and the computed effects on the population of repeated releases of standard numbers of males treated at each dose. It is shown that 17 krad causes the most rapid population decline of the three and it would also be the most efficient in terms of the numbers required to be released to achieve a specified population reduction. To get an idea of the importance of the F_1 sex-ratio distortion

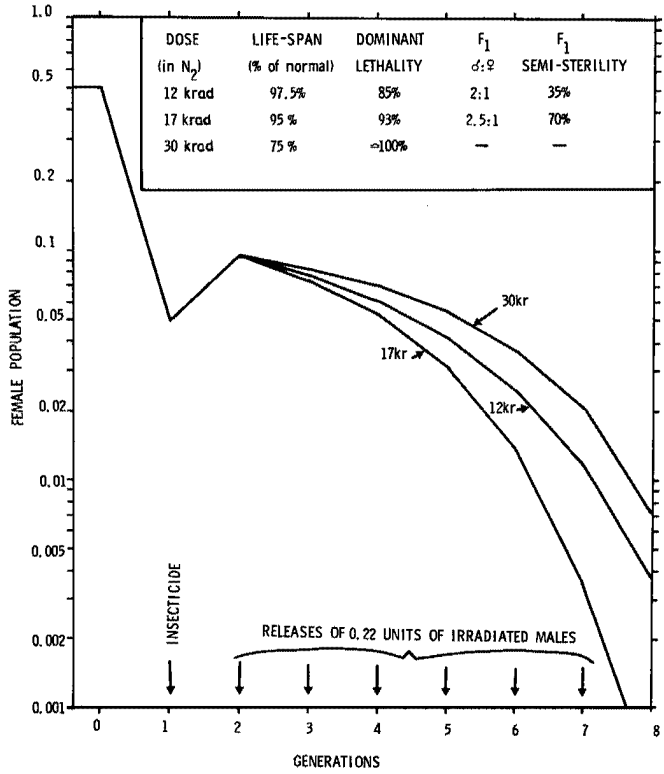


FIG.2. Results of simulations using the data indicated. Population size and numbers of irradiated males released are expressed in the same unit.

and semi-sterility, a simulation was run of 17 krad with the F_1 effects removed: the result resembled that shown in Fig. 2 for 12 krad.

The superiority of 17 krad could probably have been guessed, without the use of the computer, by inspection of the data. However, as better data become available, especially on competitiveness in the wild, it seems likely that computer simulation will be of real value in optimizing the treatment to be used.

REFERENCES

[1] ITARD, J., Stérilisation des mâles de Glossina tachinoides Westw. par irradiation aux rayons gamma, Rev. Élev. Méd. Vét. Pays Trop. 21 (1968) 479.

[2] DEAN, G.J., WORTHAM, S.M., Effects of gamma radiation on the tsetse fly Glossina morsitans Westw., Bull. Entomol. Res. 58 (1969) 505.

[3] CURTIS, C.F., LANGLEY, P.A., Use of nitrogen and chilling in the production of radiation induced sterility in the tsetse fly Glossina morsitans (in press).

[4] CURTIS, C.F., HILL, W.G., Theoretical and practical studies of a possible genetic method for tsetse fly control, Isotopes and Radiation in Entomology (Proc. Symp. Vienna, 1967), IAEA, Vienna (1968) 233.
[5] CATCHESIDE, D.G., LEA, D.E., The rate of induction of dominant lethals in Drosophila melanogaster by X-rays, J. Genet. 47 (1945) 1.
[6] CURTIS, C.F., SOUTHERN, D.I., PELL, P.E., CRAIG CAMERON, T.A., Chromosome translocations in Glossina austeni (in press).
[7] WEIDHAAS, D.E., PATTERSON, R.S., LOFGREN, C.S., FORD, H.R., Bionomics of a population of Culex pipiens quinquefasciatus Say, Mosquito News 31 (1971) 177.
[8] DEAN, G.J., DAME, D.A., BIRKENMEYER, D.R., Field cage evaluation of the competitiveness of male Glossina morsitans orientalis Vanderplank sterilised with tepa or gamma radiation, Bull. Entomol. Res. 59 (1969) 339.
[9] CURTIS, C.F., Radiation sterilization and the effect of multiple mating of females in Glossina austeni, J. Insect Physiol. 14 (1968) 1365.
[10] ROBINSON, A.S., CURTIS, C.F., Crossing over in a double translocation in Drosophila, Can. J. Genet. Cytol. 14 1 (1972) 129.

RECOMMENDATIONS

1. GENERAL RECOMMENDATIONS

In view of the potential hazards of environmental pollution accompanying the injudicious use of toxicants, insect resistance to chemicals and the inadvertent side effects of toxicants on non-target organisms, entomologists have been looking for alternative methods of control. On the economic plane, the increasing legal restrictions to international trade of agricultural commodities with pesticide residues have added urgency to this problem. The sterile insect release method represents an alternative pest control method which does not suffer from any of these drawbacks.

This method is now well established as a form of control technology and its use has led to several successes. Among these are the eradication of the screw-worm in Curaçao and in the southeast of the United States and control in the southwest United States; suppression of the medfly; eradication of the oriental fruit fly; the establishment of biological barriers to the migration of the Mexican fruit fly and demonstration of the control of the codling moth. Promising field experiments have also been carried out with the tsetse and mosquitoes, as well as a large number of other insects.

The need now arises for improving the reliability and economy of the method so that it can be extended to these and other major agricultural and medical pests.

The feasibility of the sterile male technique alone or integrated with other methods of control ultimately depends on an understanding of the dynamics of controlled and non-controlled populations. To predict the behaviour of such populations when submitted to the sterile male technique, mathematical formulation incorporating several biological parameters is required. Computer simulation entails writing a program representing the relationships between the components of a system. Various sets of initial conditions (such as possible sterile male release strategies) are then introduced and the consequences of each are computed. While computer simulation has proved its value in other fields, the Panel believes that simulation is also an extremely useful tool, in conjunction with field-population studies, for accelerating the development of the sterile male technique.

The Panel reviewed models of the control of various pests by the sterile male technique in relation to available biological data. It is recognized that for each species and even within a species separate models may be required.

The Panel recognizes the inherent hazard of using models based on assumptions in the absence of pertinent data. Such models will not reveal results of practical use with a sufficient degree of certainty. However, the elaboration of models has focused attention on some of the most important parameters for which actual data need to be measured.

In addition, simulation with assumed parameters has delineated the relative importance of some of the parameters involved. These parameters are:

(a) Size of population
(b) Growth potential when the population is submitted to control

(c) Migration patterns
(d) Survival patterns of released and wild insects
(e) Mating behaviour and competitiveness.

The Panel recognized several problems related to the development of computer simulations for use in studying population dynamics and sterile male control programs, including:

(a) The complexity and number of biological parameters.
(b) The lack of complete quantitative field data on biological parameters and their interactions, particularly as they vary from species to species and within species over time and space.
(c) The need for exchanging models.

Consequently the approach to the development of the sterile insect release method should include the encouragement and support, where possible, of the following:

(a) The determination, storage and analysis of data on biological parameters of insect populations as they exist naturally over time intervals or generations for periods of at least one year. In pursuit of this objective, encouraging the development of standard sampling techniques and uniform reporting of results.
(b) The Panel recommends that, for greatest success, the implementation of sterile male release programs and the construction of models be treated as continuing and complementary activities. Certainly, the predictive ability of models should improve as experience in applications is acquired. In turn, better models will enable the design of more efficient insect control strategies.
(c) The expansion of simplified models and standardization of more complex models for use in simulations of population dynamics and total population suppression by sterile male releases and combinations of sterile male releases and other new, conventional or potential methods of control.

In addition to the sterile male technique, the Panel recognized other methods of control (pesticides, predators, parasites, genetic factors, pathogens, cultural methods, pheromone traps) some of which are most useful at high population densities, whereas others are most useful at low densities.

The Panel recognized that the integration of these various methods of control is highly desirable and that computer simulation would be of great benefit for their optimal integration. This is particularly so in the case of translocations and conditional lethals where population genetics of some complexity are involved.

The application of the sterile male technique alone or in combination with other methods requires the cooperation of an interdisciplinary team. In this connection, biologists with a working knowledge of modelling would be extremely useful. The Panel therefore recommends that the Joint Division encourage training in the basic principles of modelling for biologists involved in the sterile male technique. This can be done by supporting 2-3 week courses in modelling. In addition, it is recommended that consideration be given to a brief introduction to modelling to be presented at future sterile male technique training courses.

The meeting divided into five committees dealing with specific groups of pests. The comments and recommendations of these committees follow.

2. RECOMMENDATIONS OF THE "COMPUTER" GROUP

2.1. Regarding the use of models

The main objectives of models are the following:

(a) To help study and help understand the dynamics of populations in order to control them more effectively.
(b) To help formulate effective release strategies.
(c) To help in calculating the economics of sterile release programs.

2.2. Regarding the use of computers

(a) Because of the complexity of natural systems it is felt that the use of computer simulation is highly desirable for most species.
(b) To achieve cooperation, the aim should be to use programs that can be used on both small and large computers of different makes. As far as possible one should avoid making programs machine-dependent. Modern simulation languages should be considered.
(c) There is a lack of understanding among scientists even in developed countries of the possibilities computers can offer. Assistance in computer education and use in model studies should be initiated, particularly in developing countries.
(d) The collection and establishment of a possible library of programs by the Agency is recommended. A collection of suitable subroutines which can be put together differently for different programs, or at least a catalogue with write-ups of existing programs, should be considered.

3. CODLING MOTH

The group recognizes the need for a computer model to simulate the complex sterile moth release control program for the codling moth. The model would first be used to investigate factors which have specific effects on control and thus would affect the control strategy selected. These factors include the effects of:

(a) Releasing moths with different levels of sterility and competitiveness.
(b) Releasing moths of one or both sexes.
(c) Releasing moths of both sexes together but which have been mated before the time of release.
(d) Varying the distance between release lines.
(e) Varying the time between releases.
(f) Residual diapausing populations which either do not emerge in the first season after entering diapause or are formed from first brood larvae.

The model would be used to simulate variations in the parameters implicit in the factors listed above and to determine the rates of releases which would be required to effect control or eradication within an acceptable

period. The strategy adopted would depend to a large extent on prior measurement of the overwintering larvae and the production capabilities of the factory. Given that factory production could not be altered significantly in a short period, chemical control of the first brood might be indicated to reduce the maximum population expected to a size which could be overflooded to the required effective ratio of sterile to wild moths.

Information from measurements of field ratios at any time during the control program should be used in additional simulations. Projection of the expected scale of damage would be obtained and appropriate supplementary control measures could be used if the damage forecasted was unacceptable.

3.1. Data required for a simple model

(a) Size of spring flight
(b) Rates of increase for first and second generations
(c) Mating habits of adult moths of the first and second generations
(d) Quality of released individuals
(e) Recovery potential of population throughout the year.

Information on dispersal would be essential for decisions relating to distances between release lines and the degree of isolation required.

3.2. Data needed in preparing a simple model of isolated population

(a) Codling moth populations 50 pairs/acre.
(b) Two generations per year.
(c) Rate of increase: generation 1 × 3x (range of x: 1-3½)
generation 2 × 10x (range of x: 5-25)
(d) Competitiveness unknown but some measure could be obtained from field cage trials where a ratio 10:1 maintained population; and a 40:1 ratio reduced numbers by 90%. (Both sexes were released together in a ratio of 1:1 with males 95% sterile and females 100% sterile. The values do not correct for diapausing individuals which would not appear in post-treatment flight.)
(e) Diapause: generation 1: 10% of pupae
generation 2: 90% of pupae
} (variation unknown)
(f) Variation of flight distances unknown. 95% of females remain within 400 m of release point. Individual males trapped up to 10 km from release point.

3.3. Analysis of residual infestations

Insufficient information is available on the methodology of sampling and releasing sterile insects to control "hot spots". This problem should be the subject of an additional model, and to attempt to include this component in the general model would be unrealistic. Such a model cannot be developed until information on the range of effect and efficiency of traps is available.

4. MOSQUITOES

The group recognizes that modeling and computer simulation of mosquitoe control programs utilizing the sterile make technique is advantageous. How-

ever, actual computer simulation of a sterile male release program would be more meaningful after additional specific and quantitative data is available.

Thus, emphasis should be placed, through encouragement and support, if possible, on the identification, collection and accumulation of biological and ecological data essential to a thorough understanding of population dynamics and the use of computer simulation of control programs. The particular parameters of most importance include population size in terms of absolute and relative densities per unit area and time or generation over at least a one-year interval; sex ratio; survival of adults; survival during the immature stages, average and range of the number of eggs per oviposition, time intervals at which egg clutches are layed during the gonotrophic cycle, and migration and dispersal patterns of both adult males and females.

Although computer simulation of an actual field control program is not considered immediately feasible, because of lack of biological data, such simulations would be extremely helpful to the development of the sterility method of control and should be undertaken as soon as possible. Computer modelling can be useful in other ways to the development of the sterile male approach. Thus, the committee cites the following examples where computer simulation would be recommended:

(a) Computer simulations of sterile male control programs.

It is recommended that a comprehensive model be developed and standardized for population dynamics research and for simulations of sterile male control programs. When the standard model and sufficient biological data are available, simulations should be made to determine (1) optimal timing for releases, (2) optimal patterns of releases, (3) optimal numbers to be released, (4) optimal costs, (5) optimal time to initiate releases, (6) optimal time to end releases, and (7) the influences of variations of parameters on both population dynamics and control.

(b) Computer simulations of the effectiveness of different methods of control, alone or in combination.

In this type of simulation assumptions can be made for parameters such as population size, survival patterns, growth rates, degree of control of reproduction, and any other parameters needed for a simple or complex model and held constant to compare the effectiveness of different methods of control when used alone or integrated. Various assumed levels representing high, low and medium values can be assumed. It is recommended that simulations be conducted to compare the effectiveness of:

(1) Sterile males vs. known translocations
(2) Sterile males plus various translocations
(3) Insecticides plus sterile males.

Biological information exists on the following, albeit piecemeal and somewhat incomplete and in some cases developed under laboratory conditions:

Length and survival of aquatic stages:

Egg hatching
Larval instars
Pupal period
Pupal sex ratio.

Emergence, mating and primary dispersal:

Emergence pattern
Male terminalia rotation
Male and female sexual maturity
Swarms and behaviouristic sex ratios
Percentage of female fertilization before the first bloodmeal.

Length of life and oviposition:

Male and female daily survival pattern and life pattern
Gonotrophic cycles and their variation
Average number of eggs per raft or clutch
Age-grading techniques and determination of parous-nonparous ratios
Secondary dispersal.

Information also is available on:

Different sterility systems
Competitiveness under cage and field conditions
Mass rearing and costing.

5. TSETSE FLY

Computer simulation has already been useful in research on the following aspects of tsetse control by the sterile insect release method:

(a) Conversion of data on survival and fecundity of laboratory-reared tsetse to prediction of the productivity of mass-rearing plants.
(b) Comparison of the efficiency of the use of translocations with that of sterile males.
(c) Choice of irradiation dose which gives an optimum combination of male survival, competitiveness, dominant lethality, and sex ratio distortion and semi-sterility in the F_1.

The main parameter which needs to be determined to improve (b) and (c) is the resilience of tsetse populations to reduction in density. A preliminary estimate of the resilience may come from the rate of recovery of populations incompletely eradicated by insecticides. A more accurate estimate should come from a preliminary SIRM program in which the proportion of wild females which have sterile matings is recorded.

A SIRM project against tsetse could be planned using simple non-computer models of the wild population with data on population density, competitiveness of release males and population resilience. It is probable that release strategies could be improved if a more realistic and complex computer model were available and it is recommended that one be elaborated. Tsetse generations are strongly overlapped and a model assuming discrete generations will be inadequate for simulating the size and timing of releases or for interrelating predictions of the model and field data as the release

project proceeds. An overlapping generation model for tsetse has been constructed but it is recommended that it be improved by inclusion of the effects of non-uniformity of the environment and of release patterns. This is especially important if a large population is to be treated by advancing sterile male releases on a broad front or if sterile males are to be used as a barrier to re-invasion of a reclaimed area. A realistic model of the situation would require data on the flight range of tsetse. Some data on this parameter are available but it needs to be refined by feedback from properly monitored preliminary sterile male release projects.

Released tsetse sterile males can transmit trypanosomiasis and the possible danger from this must be considered in formulating release strategies. Computer simulation may help in assessing the dangers, given data on the relation of population density to disease transmission rate.

The long-term effects of tsetse eradication are complex. In the future, computer simulation may prove valuable in predicting the effects and benefits or disadvantages of various policies, but much more ecological, sociological and economic data are needed before this could be useful. Data required for a simplified computer simulation model of G. morsitans (with estimates of actual values) are:

Male density (5000/(mile)^2, 18-fold fluctuation in different years)
Survival after release of artificially reared but unsterilized stock (normal)
Survival of irradiated flies in captivity (0.95 of normal at about 95% sterility)
Survival of sterilized flies in the wild (unknown)
Competitiveness in captivity (normal)
Competitiveness in large field cage (about 50% of normal)
Competitiveness in wild (less than 50% of normal)[1]
Resilience (2-fold recovery of very low-density population/generation, upper limit)[1]
Sperm irradiated at 12 krad is fully competitive for fertilization so that details of multiple mating and sperm precedence may be ignored.

Additional data required for a more complex computer model (with estimates of actual values) are:

Mean male life span (30 d)
Pupal period (30 d, range 20-80)
Pupal survival (40%)[1]
Mean female life span (50 d)
Larval survival in utero (100%)
Migration within tsetse habitat (200-700 yd per week)[1]
Immigration from outside habitat (unknown)
Dominant lethality (93% at 17 krad in nitrogen)
F_1 semi-sterility (70% at 17 krad in nitrogen).

[1] Based on guess work, with little or no actual data available.

6. MEDITERRANEAN FRUIT FLY (MEDFLY)

The Panel noted that considerable experience has already been acquired with sterile insect releases to suppress the medfly. Basic rearing technology, radiation biology and release techniques and the bionomics in some areas are at a relatively advanced stage of development.

Simulation can significantly assist in the suppression programs for the medfly even though the values of some important parameters have not been measured. By using actual values where available and by estimating unknown values of key parameters preliminary models can be established and used to plan preliminary field trials. From the results of these trials estimates of the parameter values can be refined. Subsequently, a more realistic model can be developed from which it should be possible to determine whether sterile releases alone would be effective, acceptable or economical or whether complementary control methods (bait sprays, male annihilation) would have to be used in conjunction with sterile releases to suppress target populations. In any case, a program strategy could be designed by simulation which would minimize cost and maximize effectiveness. In addition, the simulation would provide the basis for computing the rearing-plant capacity, release strategy, the size of the release area and the cost of the complementary control methods.

The Panel believes that estimates of the following key parameters would be sufficient to permit reliable simulation:

(a) Total population size (including numbers for all life stages) at time of initiation of program
(b) Number of adult progeny produced per fertile female
(c) Developmental time from egg to adult and adult longevity
(d) Detailed map of likely medfly population concentrations
(e) Number of inseminated female migrants, into the target area per unit time
(f) Mating habits – time course of egg production and age-specific fecundity
(g) Competitiveness at various temperatures and level of sterility of released flies
(h) Field behaviour and effective longevity of steriles (dispersal rates and pattern, rhythm of activity).

The above parameters when used in simulation would permit computation of the economy and acceptability of the release strategy, the optimal combinations of sterile male releases with other suppressive measures, and permit comparison with conventional control programs.

As point of departure, simulation could be used to develop a program for a 2000 square mile area such as might be encountered on the Karpass peninsula of Cyprus. Initially an experiment might be restricted to the period from January to June in order to cover the end of the apricot harvest and to permit evaluation of the program.

The following parameters and values could be used in simulation for Cyprus:

TABLE I. POSSIBLE SIMULATION PARAMETERS AND VALUES FOR CYPRUS

Parameter	Known values	Assumed values	
		Reasonable assumption	Guess
1. Initial field population			100 000 flies
2. Adult emergence pattern – time			25 d
3. Adult emergence pattern – No. flies			4000/d
4. No. adult progeny per fertile mating of untreated x untreated			20 flies (at all densities throughout season)
5. Residual hatch at 9 krad of untreated female x treated male	3%		
6. No. of adult progeny per mating of untreated female x treated 9-krad male			0.6 fly (3% x 20)
7. No. adult progeny per mating of treated female x untreated male	0		
8. No. adult progeny per mating of treated female x treated male	0		
9. Av. competitiveness value		0.5	
10. Av. adult longevity (early season)		40 d	
11. Av. egg-laying period (early season)		30 d	
12. Period when 90% of eggs deposited		14 d	
13. No. times males mate over time			once/d over 20 d
14. Degree of fertility of untreated males throughout mating period			Constant
15. No. times females mate in field		Once	
16. Distribution of flies			
a. In discontinous commercial plantations			10% in 30 plantations
b. In populated areas			80% in 20 populated areas
c. In remaining areas			10%
17. Rhythm of activity of released flies compared with wild flies			Synchronous
18. Does migration occur in target area?			No

The Panel recommends the following to the Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture.

1. All assumed values of parameters should be determined experimentally in appropriate field and laboratory studies, including sterile releases.
2. Developing countries should be encouraged to incorporate the use of models in their medfly control programs involving sterile medflies and other methods.

LIST OF PARTICIPANTS

PANEL MEMBERS

Bogyo, T. P.	Statistical Services, College of Agriculture, Washington State University, Pullman, Washington 99163, United States of America
Butt, B. A.	Entomology Research Division, USDA, ARS, 3706 W. Nob Hill Boulevard, Yakima, Washington 98902, United States of America
Cuéllar, C. B.	Ross Institute of Tropical Hygiene, London School of Hygiene and Tropical Medicine, University of London, Keppel Street (Gower Street), London, WC1E 7HT, United Kingdom
Curtis, C. F.	Tsetse Research Laboratory, University of Bristol, Langford House, Langford, Bristol, BS18 7DU, United Kingdom
Ford, J.	Hope Department of Zoology (Entomology), University of Oxford, University Museum, Oxford, United Kingdom
Frissel, M. J.	Association Euratom-Ital, Institute for Atomic Sciences in Agriculture, P. O. Box 48, Wageningen, The Netherlands
Haniotakis, G. E.	UNDP/SF Project GRE 25(458) on the Control of Olive Pests and Diseases, P. O. Box 6, Kifissia, Athens, Greece

Klassen, W.	Office of the Administrator, USDA, ARS, Washington, D. C. 20250, United States of America
Kloft, W. J.	Institut für Angewandte Zoologie, Universität Bonn, An der Immenburg 1, 53 Bonn, Federal Republic of Germany
Moore, I.	Volcani Centre of Agricultural Research, Bet Dagan, Israel
Murdie, G.	Imperial College Field Station, Silwood Park, Ascot, Berks., United Kingdom
Proverbs, M. D.	Canada Department of Agriculture, Entomology Section, Summerland, B. C., Canada
Serghiou, C.	Agricultural Research Institute, Ministry of Agriculture and Natural Resources, Nicosia, Cyprus
Steffan, A. W.	Institut für Zoologie, Biologische Bundesanstalt für Land- und Forstwirtschaft, Königin Luise-Strasse 9, Berlin-Dahlem, Federal Republic of Germany
Wehrhahn, C. F.	University of British Columbia, Institute of Animal Resource Ecology, Vancouver 8, B. C., Canada
Weidhaas, D. E.	Entomology Research Division, USDA, ARS, P. O. Box 1268, Gainesville, Florida 32601, United States of America
Wijnands-Stäb, K. J. A.	Association Euratom-Ital, Institute for Atomic Sciences in Agriculture, P. O. Box 48, Wageningen, The Netherlands

Yasuno, M.	WHO/ICMR Research Unit on Genetic Control of Mosquitoes, 2-3 Ring Road, Kilokri, New Delhi 14, India

INTERNATIONAL ATOMIC ENERGY AGENCY

Fried, M.	Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture
Ouye, M. T.	Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture
Mews, A. R.	Division of Research and Laboratories
Offori, E. D.	Division of Research and Laboratories
Nadel, D.	Division of Research and Laboratories
Ahmed, M.	Division of Research and Laboratories
Lewis, B.	Division of Scientific and Technical Information

SCIENTIFIC SECRETARIES

Lindquist, D. A.	Joint FAO/IAEA Division of Atomic Energy, in Food and Agriculture, International Atomic Energy Agency
Monro, J.	Division of Research and Laboratories, International Atomic Energy Agency

EDITOR

Mautner Markhof, F.	Division of Publications, International Atomic Energy Agency