

CHAPTER 2.5.

MATHEMATICAL MODELS FOR THE USE OF STERILE INSECTS

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TABLE OF CONTENTS

1. BRIEF OVERVIEW OF MODELLING	148
1.1. Types of Models	148
1.2. Simple Population Models	149
1.3. Host-Parasitoid and Predator-Prey Models	150
2. MODELS OF STERILE INSECT RELEASES	150
2.1. Three Kinds of Control Programmes Using Sterility	150
2.2. Initial Contribution of Knipling to Modelling SIT	151
2.3. Sex Ratio	151
2.4. Residual Fertility of "Sterile Insects"	151
2.5. Competitive Ability of Males	152
2.6. Interactions of Residual Fertility and Competitiveness	153
2.6.1. Residually Fertile Insects Are Fully Competitive	153
2.6.2. Residually Fertile Insects Have Reduced Competitiveness	154
2.7. Mating Patterns	154
2.7.1. Interaction of Polygamy with Competitive Ability	155
2.7.2. Non-Functional Sperm	155
2.7.3. Dominant Lethal Mutations with Fully Competitive Sperm	155
2.7.4. Dominant Lethal Mutations with Reduced Sperm Function	155
2.8. Interaction of Polygamy with Residual Fertility	157
2.9. Population Movement	157
2.9.1. Immigration before Mating	157
2.9.2. Immigration after Mating	158
2.9.3. Large-Scale Population Movement	158
2.10. Combinations of Residual Fertility, Reduced Competitiveness, and Immigration	159
2.11. Density-Dependence of Population Regulation	159
2.12. Age Structure	161
2.13. Population Aggregation	162
2.14. Predation, Parasitism, and Competition	163
2.15. Stochastic Models	163

2.16.	<i>Stability under Various Conditions</i>	164
2.17.	<i>Integration of Control Methods</i>	164
2.17.1.	<i>SIT with Application of Insecticide</i>	165
2.17.2.	<i>SIT with Pheromone Traps for Male Annihilation</i>	165
2.17.3.	<i>SIT with Release of Parasitoids</i>	166
2.17.4.	<i>SIT with Sanitary Measures and Oviposition Traps</i>	166
2.18.	<i>Optimization of Programme Releasing Sterile Insects</i>	167
2.19.	<i>Development of Resistance</i>	168
2.20.	<i>Educational and Instructional Modelling</i>	168
3.	PARAMETER ESTIMATION FOR THE MODELS	168
4.	ASSESSMENT OF SIT MODELLING	169
4.1.	<i>Uses of Models</i>	169
4.2.	<i>Advantages and Limitations of Modelling</i>	169
4.3.	<i>Transient versus Equilibrium Models</i>	170
4.4.	<i>Future Directions and Information Needs</i>	170
5.	REFERENCES	171

SUMMARY

This chapter begins with a consideration of simple population models. The sterility formulation proposed by Knippling is then included into the population models, and these are elaborated in systematic fashion to include the major biological factors that will affect the success of the sterile insect technique (SIT) control programme. These factors include residual fertility, differential competitive ability of wild and sterilized males, mating patterns, immigration, and various combinations of these features. Also examined are density-dependence, age structure, population aggregation, biotic interactions with other species, and then integration of the SIT with other control methods. It was found that combinations of factors are synergistic: combinations of detrimental factors such as residual fertility and inferior competitive ability put severe limits on the probable success of the control programme, while combinations of control methods are much more likely to succeed than single control methods. This is because each control method needs only to account for a smaller proportion of the total mortality when combined with other methods than when acting alone.

1. BRIEF OVERVIEW OF MODELLING

1.1. *Types of Models*

Modelling is the abstraction of processes or states of being. Mathematical models involve equations, graphs or algorithms behind computer code. Virtually all models of the sterile insect technique (SIT) are population models, either analytic (just with equations) or computer models (often called numerical models and in which the equations are usually implicit, rather than being made explicit). Population models keep track of population numbers, and include various features that influence population size and trend, such as birth rate, mortality, age structure, immigration and emigration, competition, etc. Population growth can be either density-independent, in which birth rate and mortality are independent of population size, or density-dependent, in which either or both of birth rate and mortality depend on population size, usually in such a way as to eventually stabilize the population around some long-term mean value.

Mathematical models of populations are typically posed as difference equations or as differential equations. Difference equations are discrete and use some meaningful time step, such as days, years, generations, etc. These are popular with

entomologists, since many insects breed seasonally, such as most temperate forest insect pests (bark beetles, budworms, tent caterpillars, etc.). Differential equations are continuous, involving an infinitesimal time step, and rely on calculus to solve them. They are useful in species that breed continuously within some period of time, such as aphids, stored products pests and animal parasites. However, difference equations do not involve calculus, and generally are easier for the non-mathematician to understand. Another dichotomy is between deterministic models, which always yield the same model result, and stochastic models, which involve randomness. Most of the models of the SIT have so far been deterministic models, involving no random elements.

In this chapter, only models that predict some aspect of system behaviour (population dynamics) will be explored. Thus purely statistical analysis of data, however valuable and relevant that might be to the release programme, will not be considered here. Likewise the derivation of regressions for use in models will not be considered here as SIT modelling. However, a section on model parameter estimation, in which such techniques are mentioned, is included.

1.2. Simple Population Models

For density-independent population growth, the simplest models are geometric growth for a species with non-overlapping generations, and its continuous counterpart, exponential growth (Box 1). A simple modification to these models, to include resource limitation, puts an upper limit on growth. Many formulations exist for limiting geometric growth; a few were provided by Hassell (1978). This small complication makes some formulations insoluble analytically, and it is a common feature of population models that non-linearities render the models insoluble analytically; it is then necessary to resort to numerical solutions using a computer.

Box 1. Simple Growth Models

Geometric and Exponential Growth

The geometric model is $N_{t+1} = \lambda N_t$. Here N_t is the size of the population at time t , where t is scaled to generations and λ is the rate of increase each generation. In each generation the population size is λ times the size it was in the previous generation. In this model, generations are discrete and non-overlapping. This model is easy to solve. At any time t , $N_t = N_0 \lambda^t$, where N_0 is the size of the population at time $t=0$. The exponential growth model is $dN/dt = rN$. The solution to this model is $N = N_0 \exp(rt)$, where $\exp(rt) = e^{rt}$, e being the base of natural logarithms, r is the instantaneous rate of growth, and N_0 is the initial size of the population at time zero.

Density-Dependent Growth

With density-dependence, the geometric model becomes $N_{t+1} = \lambda N_t \exp(-gN_t)$, in which the exponential term has no real biological meaning, and is simply a convenient device to limit population numbers. The continuous version is the logistic equation: $dN/dt = rN(K-N)/K$, where K is the carrying capacity, imposed by resource limitation.

1.3. Host-Parasitoid and Predator-Prey Models

Modelling host-parasite and predator-prey systems in insect population dynamics has a long history, and the “workhorses” are the Nicholson-Bailey difference equation model and the Lotka-Volterra differential equation model (Box 2). Hassell (1978) described such models, and these models have been used in modelling sterile insect releases for species under the influence of biotic interactions with other species.

Box 2. Predator-Prey and Host-Parasitoid Model

Nicholson-Bailey Model

Without density-dependence $N_{t+1} = \lambda N_t \exp(-aP_t)$; $P_{t+1} = \lambda N_t [1 - \exp(-aP_t)]$ where N_t and P_t are the host and parasite population sizes at time t .

With density-dependence $N_{t+1} = \lambda N_t^{(1-b)} \exp(-aP_t)$; $P_{t+1} = \lambda N_t^{(1-b)} [1 - \exp(-aP_t)]$ where b is a parameter for imposing density-dependence and has no obvious biological meaning, and $\exp(-aP_t)$ is the zero term of a Poisson series, representing those hosts not found each generation by a group of randomly searching parasitoids.

Lotka-Volterra Model

Without density-dependence $dN/dt = rN - bNP$; $dP/dt = P(cN - e)$ in which the first equation gives the rate of change of the prey population (N) in terms of the intrinsic rate of increase, r , and a predation rate per predator, b ; the second equation gives the rate of change of the predator population (P) in terms of the rate of increase per prey, c , and a death rate, e .

With density-dependence $dN/dt = rN(1-aN) - bNP$; $dP/dt = P(cN - e)$, where a is a density-dependent death rate.

2. MODELS OF STERILE INSECT RELEASES

2.1. Three Kinds of Control Programmes Using Sterility

There are three methods of using sterile insects for population control. These are: (1) the standard method of releasing sterile males (or males and females) that have been reared and sterilized; earlier work in modelling of sterile releases was previously summarized by Hamada and Miyai (1985); (2) the treatment of insects with sub-sterilizing doses of radiation or chemosterilants so that the matings are partially sterile, but the offspring of matings involving treated insects are sterile, called inherited sterility (Carpenter et al., this volume); and (3) the deployment of chemosterilants in field traps to sterilize insects that are attracted to the traps. It is mainly the first of these three methods that will be dealt with here. Chemosterilants are seldom used in the field because of their carcinogenic potential, although modelling has been done on this technique by Knipling (1960), Lawson (1967), Staley et al. (1971), Hawkes and Coaker (1977), Barclay (1981a), and Wall and Howard (1994). In addition, although the SIT is usually used for insect control, in some cases the concept can apply to other animals (Klassen et al. 2004).

2.2. Initial Contribution of Knippling to Modelling SIT

Knippling produced a simple numerical model that foreshadowed most future modelling developments (Knippling 1955, 1959). The central feature of Knippling's model, and one found in almost all subsequent models, is the ratio of fertile males to all males in the population: $(M/(S+M))$ where M is the number of fertile males (or females, assuming a 1:1 sex ratio) and S is the number of sterile males. This gives the proportion of the population, under ideal conditions, that results in fertile egg production as a result of some fertile females mating with fertile males. Knippling's (1955) model for the release of sterile insects was a simple modification of the geometric model in Box 1 using the sterility factor above:

$$F_{t+1} = \lambda F_t (M_t / (S + M_t)) \quad (1)$$

where F_t and M_t are again the population size (fertile females and males) at time t , λ is the rate of increase per generation, and S is the release rate of sterile males each generation. This yields a stable steady state at $F=0$ and an unstable positive steady state for F when $S=S^*$, the critical release rate, where $S^*=F(\lambda-1)$, the value of sterile release rate that holds the population at the steady state (Berryman 1967). If $S>S^*$, then the pest population will collapse and be eliminated. If $S<S^*$, then the population in this model will increase indefinitely.

2.3. Sex Ratio

One question asked early in the use of sterile release programmes was, "Is there an optimal sex ratio for the insects being released?" It was initially thought that the release of females would be counterproductive. This question was addressed by Ailam and Galun (1967) and by Lawson (1967); using probabilistic models of mating, they found that the release of females is never detrimental (assuming they are all fully sterile), and in fact may assist the control programme if males are limited in their mating ability, in which case some fertile females might not get mated. However, there are limited field data to support this suggestion.

2.4. Residual Fertility of "Sterile Insects"

If some of the treated insects are not completely sterilized, then the situation becomes more complicated. Klassen and Creech (1971) constructed a simple numerical model in which a certain proportion of the released males remained fertile. They found an upper limit to this "residual fertility" that was compatible with the success of the release programme. Their model can be put into algebraic form and generalized. When there is incomplete sterilization of the released insects, a fraction, q , of males remains fertile. In that case, Knippling's model can be modified as in Box 3. The critical sterile release rate is then only finite for $q<1/\lambda$. If $q>1/\lambda$, then the population is not controllable by sterile releases. Thus, for example, if the rate of increase, λ , is 10, then q must be less than 0.1, i.e. the released males must be

greater than 90% sterile in order for control by the SIT to be possible. Also, if the residual fertility is more than about three-fourths of the limiting value, then the required rate of sterile releases is much higher than with complete sterility (Fig. 1).

If both males and females are released and neither sex is completely sterile, then the fertile male X fertile female matings can be modelled as in Box 3. If residual fertility exists in both sexes following release, it becomes impossible to eliminate the pest population by sterile releases alone; the best that can be done is to suppress it to a low level with continuing sterile releases. In addition, control is impossible unless $q_m < F/\lambda(F + q_f S_f)$, where q_m and q_f are the residual fertilities of males and females, respectively. This value of q_m is smaller than that without the release of females (Fig. 2). Thus less residual male fertility can be tolerated with the release of residually fertile females (Barclay 2001).

Box 3. Residual Fertility of "Sterile Insects"

Here Knippling's model becomes: $F_{t+1} = \lambda F_t (M_t + q S) / (M_t + S)$, where it is assumed that either only males (M_t) are released or that released females are completely sterile and only males display residual fertility. This model has a stable steady state at $F = M = 0$, and an unstable positive steady state for F and M when $S = S^*$, the critical release rate, where $S^* = M(\lambda - 1) / (1 - \lambda q)$. Here, S^* is only finite for $q < 1/\lambda$.

If both males and females are released and neither sex is completely sterile, then the fertile male X fertile female matings can be modelled by the equation: $F_{t+1} = \lambda (F_t + q_f S_f) (M_t + q_m S_m) / (M_t + S_m)$, in which F_t is the number of wild fertile females in generation t , q_m and q_f are the proportions of treated males and females, respectively, that remain fertile, and S_m and S_f are the number of treated males and females, respectively, that are released each generation (Barclay 2001). So far there is no restriction on the sex ratio. If we assume a one-to-one sex ratio (where $M_t = F_t$ and $S_m = S_f = S$), then we obtain a quadratic equation: $\lambda q_m q_f S^2 - [1 - \lambda(q_m + q_f)]FS + (\lambda - 1)F^2 = 0$ which gives two roots when solved for either S or F . The upper root of F is unstable, and represents the size of the population before initiating sterile releases. The lower root of the equation for F is stable, and is the value at which the population would be maintained by residual fertility after collapse due to suppression by sterile releases. Thus it is impossible to eliminate the pest population by sterile releases alone; also control is only possible if $q_m < F/\lambda(F + q_f S_f)$. The relationship between the maximum values of q_m and q_f is hyperbolic (Fig. 2).

2.5. Competitive Ability of Males

The ability of sterile males to compete with wild males for mates can be affected by sterilization through the debilitating effects on either sperm competition or the behaviour of the adults (Calkins and Parker, this volume; Lance and McInnis, this volume). This problem was modelled by Berryman (1967), Bogyo et al. (1971), Berryman et al. (1973), Itô (1977), and Barclay (1982a). Their models are summarized by the model in Box 4. All of their models show that the critical release rate increases as the competitive ability of sterilized insects decreases.

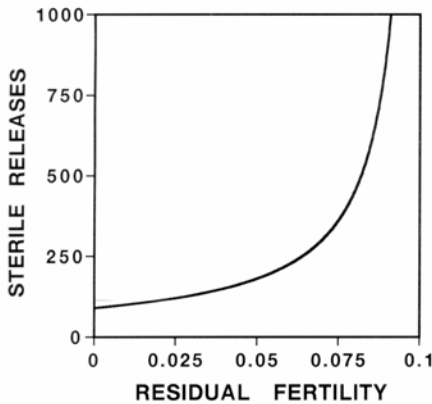


Figure 1. The critical sterile release rate, S^* , as a function of residual fertility, q . $\lambda = 10$.

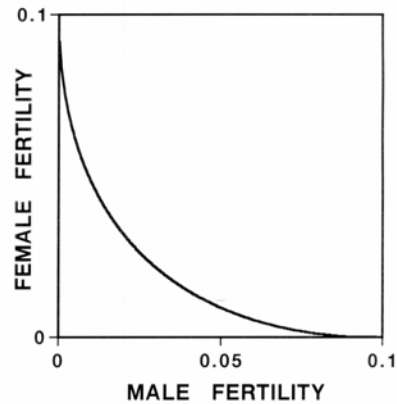


Figure 2. Allowable residual fertility when it is in both males and females. $\lambda = 10$.

Box 4. Competitive Ability of Males

We define c as a coefficient of competitive ability, with 0 being completely non-competitive and 1 being fully competitive. Then $F_{t+1} = \lambda F_t (F_t / (F_t + cS))$. This model has a stable steady state and $F=M=0$ when $S>0$. The positive (unstable) steady state for F occurs when $S=S^*$, the critical value, where $S^*=(\lambda-1)F/c$, which is greater than $(\lambda-1)F$, with full competitive ability (Itô and Yamamura, this volume).

2.6. Interactions of Residual Fertility and Competitiveness

In this model only males display residual fertility; females are either completely sterilized or not released.

2.6.1. Residually Fertile Insects Are Fully Competitive

Here the insects that remain fertile after treatment are fully competitive with wild insects (Box 5). The allowable residual fertility of males is an almost linear function of the competitive ability of released sterile males (Fig. 3A, solid line), unless λ is very small. Also, for a given degree of residual fertility, S^* becomes larger as c becomes smaller (Fig. 3B). Thus the extent of residual fertility, and lack of competitive ability, compatible with control are each more restricted in the presence of the other (Barclay 2001).

Box 5. Residual Fertility and Competitiveness

If residual fertile insects are fully competitive, $F_{t+1} = \lambda F_t(F_t + qS)/(F_t + qS + cS(1-q))$, then this model has a stable steady state at $F=M=0$ when $S>0$. The positive (unstable) steady state occurs when $S=S^*=(\lambda-1)F/(c(1-q)-q(\lambda-1))$, and S^* is finite only if $q < c/(\lambda-1+c)$.

If residual fertile insects are of reduced competitiveness, then the model becomes $F_{t+1} = \lambda F_t(F_t + cqS)/(F_t + cS)$. If there is no residual fertility, there is a stable steady state at $F=M=0$, if $S>0$, and a positive unstable steady state when $S=S^*=(\lambda-1)F/c$.

If there is both residual fertility and unequal male competitive ability, the steady state for F is at $S^*=(\lambda-1)F/(c(1-q\lambda))$, and this is finite only if $q < 1/\lambda$.

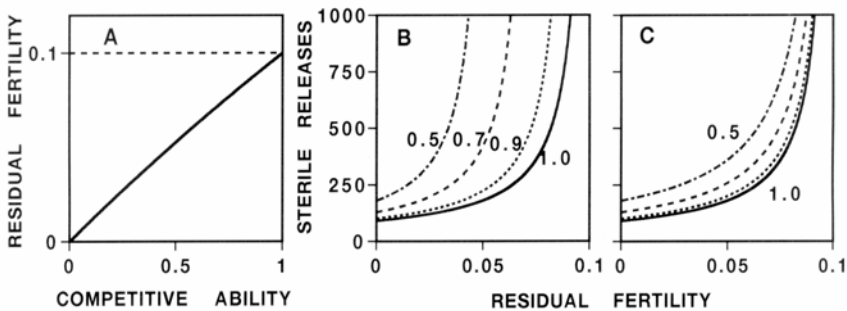


Figure 3. A: Changes in allowable residual fertility with changes in competitive ability of sterile males. Residually fertile insects are of reduced competitive ability (broken line) or are fully competitive (solid line). B and C: Critical sterile release rates for residual fertility (0 to 0.1) and competitive ability (0.5, 0.7, 0.9, 1.0). In B, residually fertile insects are fully competitive, and in C, residually fertile insects are of reduced competitive ability. $\lambda = 10$ in all cases. (Figure from Barclay 2001, reproduced with permission.)

2.6.2. Residually Fertile Insects Have Reduced Competitiveness

Here the insects that remain fertile after treatment are not fully competitive with wild insects (Box 5). The critical sterile release rate in this case (Fig. 3C and Box 5) is not as large as the corresponding value when residually fertile insects are of full competitive ability (Fig. 3B).

2.7. Mating Patterns

Another question asked early in the use of sterile releases was, "Should the females of the target species in a sterile release programme mate once or more than once?" The question has been addressed by Knippling (1964), and in the models of Berryman (1967), Lawson (1967), Zouros (1969), and Barclay (1984). The answer appears to be that female remating (polygamy) is quite compatible with the SIT, as long as mating is random, with sterilized males being fully competitive. In addition, in polygamous species, it doesn't matter whether sperm is diluted, replaced or excluded

after the first mating, again as long as mating is random, and sterile males are fully competitive (Lance and McInnis, this volume).

2.7.1. Interaction of Polygamy with Competitive Ability

If sterile males are equally competitive for mates with fertile males, sterile sperm is fully competitive with fertile sperm, and there is no residual fertility, then the effects of polygamy (multiple female mating) are simply to reshuffle the sperm at each mating, and polygamy has essentially no effect. On the other hand, if sterilization is incomplete, and/or sterilized males (or their sperm) are of inferior competitive ability, then the situation is more complex. The work of Berryman (1967) (also addressed by Zouros (1969)) is particularly insightful in this matter. If only the first mating of a female results in sperm retention, or if all of the sperm of previous matings is replaced at each successive mating, and if all matings occur before oviposition begins, then the effective number of matings is just one. If the sperm from all matings mixes and is retained, then the effect of multiple matings depends on sperm competition as well as on competition between sterile and fertile males for mates. Berryman (1967) addressed this important problem, and it is worthwhile revisiting his results, making appropriate changes in his notation to make it consistent with the development above. Berryman considered three cases, depending on sperm action (Box 6).

2.7.2. Non-Functional Sperm

If the sperm of sterilized adults is either nonexistent or immotile, then a female mating m times will only produce sterile eggs if all the matings were with sterile males. The resulting critical values (Box 6) of the sterile release rate, S^* , are shown in Fig. 5 for several values of M , the maximum number of matings, values of the adult competition coefficient from 0.5 to 1.0, two values of the probability of mating, and assuming a binomial distribution of mating frequencies.

2.7.3. Dominant Lethal Mutations with Fully Competitive Sperm

If sterility is caused by dominant lethal mutations, and the sperm of sterilized adults is fully competitive with that of fertile adults, then it can be shown that the probability that an egg is fertilized by a sterile sperm is independent of the number of matings, and the results from section 2.5. on competitive ability still hold with polygamy, and correspond to the case of $M=1$ in Fig. 5.

2.7.4. Dominant Lethal Mutations with Reduced Sperm Function

If sterility is caused by dominant lethal mutations, and the sperm of sterilized adults is of reduced competitive ability compared with that of fertile adults, then it can be shown that the probability that an egg is fertilized by sterile sperm depends on the number of matings. The values of the critical release rates, S^* , in Box 6, are shown in Fig. 4A and B against the adult sterile competitive ability, c_a , and for the sperm competitive ability, c_s . In addition, the values of c_a and c_s are shown for given values of the critical release rate (250, 500), S^* , when it is held constant (Fig. 4C).

Box 6. Mating Patterns

Interaction of Multiple Female Mating and Competitiveness

The probability of a fertile female mating with a sterile male is defined as $P_s = c_a S / (F_t + c_a S)$, and the probability of a fertile female mating with a fertile male as $P_f = F_t / (F_t + c_a S) = 1 - P_s$, where c_a is the competitive ability of sterile adults (equivalent to c in Box 4). Berryman (1967) considered the joint distribution of the number of matings, and the number of sterile matings, as a sequence of marginal distributions of the number of sterile matings given the number of matings. Thus a female can mate from zero to M times, and for a given number, m , of matings the number of sterile matings is binomially distributed. If ${}_m C_n$ is defined as the number of combinations of m things taken n at a time ($= m! / n!(m-n)!$), then the conditional probability that a given female mates with n sterile males, given that she mates m times, is $P(n|m) = {}_m C_n P_s^n P_f^{m-n} = {}_m C_n P_s^n (1 - P_s)^{m-n}$. This is one term of a binomial distribution that describes the number of sterile matings given the number of matings, and there will be $M+1$ such distributions, including one for no matings. Berryman considered three cases, dependent on sperm action.

Non-Functional Sperm

If the sperm of sterilized adults is either nonexistent or immotile, then a female mating m times will only produce sterile eggs if all the matings were with sterile males. The probability of this occurring is P_s^m , and so the probability of at least one fertile mating is $(1 - P_s^m)$. Then the probability of at least one fertile mating, over the range of mating frequencies, is $\sum P_m (1 - P_s^m)$ for $m = 1, 2, 3, \dots, M$, and so the population equation becomes $F_{t+1} = \lambda F_t \sum P_m (1 - P_s^m)$ for $m = 1, 2, 3, \dots, M$, where P_m is the probability of mating m times.

Dominant Lethal Mutations

In the binomial expansion of the probabilities of m matings, where m goes from 0 to M , each of the terms representing mixed fertile and sterile matings will be weighted by a factor, c_s , representing the competitive ability of sterile sperm. Thus the probability of an egg being fertilized by a sterile sperm, taken over all mating frequencies, will be $P(e) = P_s^m + c_s((m-1)/m) {}_m C_{m-1} P_s^{m-1} (1 - P_s) + c_s((m-2)/m) {}_m C_{m-2} P_s^{m-2} (1 - P_s)^2 + \dots + (0/m) {}_m C_0 (1 - P_s)^m$, which can be reduced to $P_s^m + c_s P_s (1 - P_s^{m-1})$, where $P_s = c_a S / (F_t + c_a S)$, as above. We can write the equation as $F_{t+1} = \lambda F_t \sum P_m [1 - (P_s^m + c_s P_s (1 - P_s^{m-1}))]$ for $m = 1, 2, 3, \dots, M$. The values of the critical release rates, S^* , are shown in Fig. 4A and B against the adult sterile competitive ability, c_a , and for the sperm competitive ability, c_s . In addition, the values of c_a and c_s are shown for given values of the critical release rate (250, 500), S^* , when it is held constant (Fig. 4C).

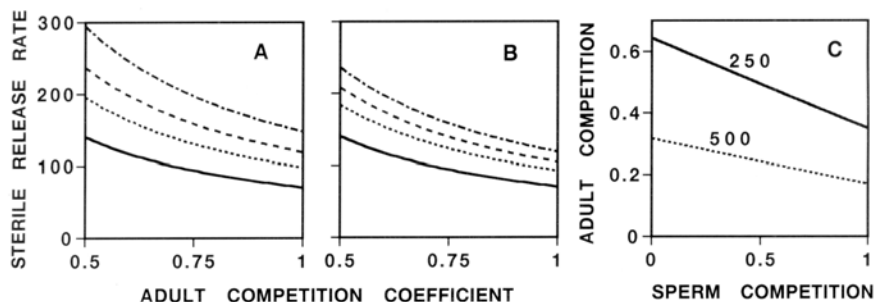


Figure 4. A and B: Values of the critical release rates, S^* , for values of adult sterile competitiveness, c_a , four mating frequencies (1,2,4,8), and two probabilities of mating — A: 0.6, B: 0.8. C: Limits on adult sterile competitiveness compatible with control of the pest population; these are shown for a range of values of sperm competitiveness and two values of sterile releases (250,500). (Figure generated from equations, Berryman 1967.)

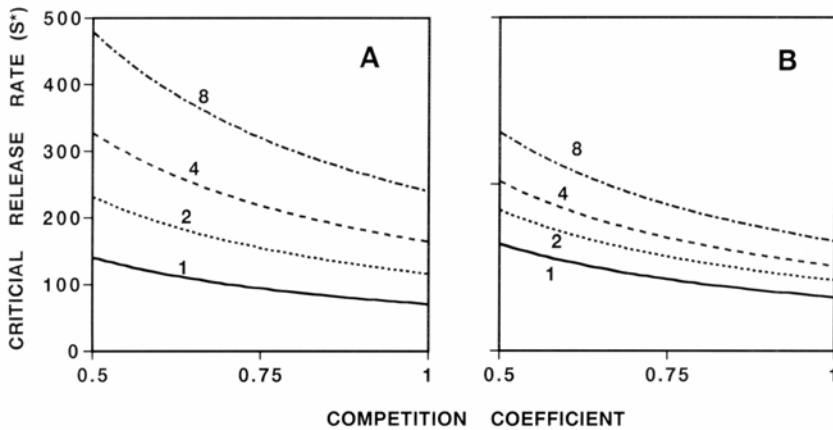


Figure 5. Critical sterile release rates when sterile males produce non-functional sperm. The maximum possible number of matings, M , is 1,2,4,8, and the probability of mating in A is 0.8, and in B is 0.9. The adult competition coefficient ranges from 0.5 to 1.0. $\lambda=10$ in all cases. (Figure generated from equations, Berryman 1967.)

2.8. Interaction of Polygamy with Residual Fertility

A similar analysis on residual fertility (not shown) can be performed. Starting with the equation for residual fertility, and assuming that sterile sperm are fully functional, one proceeds as with the case of dominant lethal mutations and fully functional sperm. The result is that the probability that a female will mate with a sterile male is independent of the number of matings (Barclay 2001), and the probability that an egg will be fertilized by a sterile sperm is also independent of the number of matings. Thus multiple female mating (polygamy) and residual fertility have no interaction, and the results derived above for residual fertility alone apply both to monogamy and polygamy.

2.9. Population Movement

The release of sterile insects, together with immigration from outside the control area, can be modelled by a simple modification of the model in Box 4 (Dietz 1976, Prout 1978). Following Prout, two cases must be accommodated here: (1) immigration before mating, and (2) immigration after mating. In these two models it is assumed that all sterilized insects that are released are completely sterile.

2.9.1. Immigration Before Mating

Assuming that V males and V females immigrate each generation prior to mating, the female immigrants are thus available for mating with the released sterile males

as well as the wild males, and the male immigrants are available for competing with the sterile males. The model (Box 7) has two positive roots for F , with the upper one being unstable (the population as it existed just prior to sterile releases) and the lower one being stable. This lower steady state represents a population in a state of collapse due to sterile releases, but which is replenished each generation by immigrants. Note that zero is not a steady state solution here. The required sterile release rate grows rapidly with V , but there is no value of immigration that disallows control by sterile releases. The values of S^* depend only modestly on V , if the immigration rate each generation is only a small proportion of the total population.

Box 7. Immigration

Immigration Before Mating

If we include immigration into the model, we obtain $F_{t+1} = \lambda(F_t + V)(F_t + V)/(F_t + S + V)$. Solving for steady state, we obtain the quadratic: $(\lambda - 1)F^2 - [S - (2\lambda - 1)V]F + V^2 = 0$ which has two positive roots for F , with the upper one being unstable and the lower one being stable. Note that zero is not a steady state solution here.

The critical release rate is $S^* = [(\lambda - 1)F + \lambda V](F + V)/F$.

Immigration After Mating

The equation here is $F_{t+1} = [\lambda F_t^2 / (F_t + S)] + \lambda V$. Note that, if the wild population is reduced to zero, it will be reconstituted the following generation, as then $F_{t+1} = \lambda V$. Again solving for steady state, we obtain $(\lambda - 1)F^2 - [S - \lambda V]F + \lambda VS = 0$.

The critical sterile release rate is given by $S^* = F[(\lambda - 1)F + \lambda V]/(F - \lambda V)$, and sterile releases can only control the population if $V < F/\lambda$.

For a given immigration rate, the required sterile release rate is much higher if immigration is after mating than before mating.

2.9.2. Immigration After Mating

In this case it is assumed that V males and V females immigrate each generation after mating. The female immigrants are thus not available for mating with the released sterile males or the wild males, however the male immigrants are available for competing with the sterile males. Thus, immigrating females remain fully fertile. Note that, if the wild population is reduced to zero, it will be reconstituted the following generation, as $F_{t+1} = \lambda V$. For a given value of immigration rate, the required sterile release rate, S^* , is much higher if immigration is after mating than before mating, due to the fully fertile nature of the immigrating females.

2.9.3. Large-Scale Population Movement

The problem of large-scale population movement was addressed by Manoranjan and van den Driessche (1986), Lewis and van den Driessche (1993), Plant and Cunningham (1991), and Marsula and Wissel (1994). They showed, using diffusion equations, that dispersal of insects, coupled with non-linear growth terms, can result in waves of invasion or extinction. Both the velocity and direction of these waves depend critically on the rate of release of sterile insects. With low rates of release, the travelling wave advances as an invasion; when the density of sterile insects exceeds a critical density, the wave recedes, giving rise to local extinction. This is

likely to have considerable relevance to programmes releasing sterile insects such as the New World screwworm *Cochliomyia hominivorax* (Coquerel) eradication programme in the southern USA, Mexico and Central America, in which the pest population has been pushed back to Panama and a sterile insect buffer zone created. Matlock and associates are pursuing this approach with the screwworm, assessing the size of the buffer zone needed to ensure that insect invasion into the eradicated area does not occur (R. B. Matlock, Tulane University, personal communication).

2.10. *Combinations of Residual Fertility, Reduced Competitiveness, and Immigration*

Four models can be considered, being the four combinations of: (1) those sterilized insects that show residual fertility can be either of reduced competitive ability (reduced) or fully competitive (equal) with the wild insects, and (2) insects can immigrate either before mating or after mating.

Barclay (2001) provided equations for the four cases, and the values of the limiting residual fertilities are shown in Table 1 and Fig. 6. In Table 1, the allowable residual fertility for the case of residually fertile insects being of reduced competitive ability is the same as for the case involving sterile insects being fully competitive and immigration occurring. The other two cases yield more stringent limits on allowable residual fertility than with no immigration. It is apparent that there is a strong interaction among residual fertility, competitive ability, and immigration, with the feasible limits on each factor becoming much more restrictive in the presence of the other factors.

Table 1. Limits on residual fertility (q) when competitive ability of "sterilized but residually fertile insects" is either reduced or equal to that of wild fertile insects, and immigration is either before, or after, mating

	Reduced	Equal
Before	$q < F/\lambda(F + V)$	$q < cF[\lambda(F + V) - F(1 - c)]$
After	$q < (F - \lambda V) / \lambda F$	$q < c(F - \lambda V)[\lambda F - (1 - c)(F - \lambda V)]$

2.11. *Density-Dependence in Population Regulation*

Density-dependence in a population has been shown by modelling to predispose it to control by sterile releases (Miller and Weidhaas 1974, Itô 1977, Prout 1978, Barclay and Mackauer 1980a). There are several formulations that include density-dependence in a model of a population, and all yield the same qualitative results. The two distinct ways that density-dependence assists the SIT are: (1) reduces the

effective biotic potential of a species by increasing the natural mortality at higher densities, and (2) introduces a bifurcation (splitting of one root of the equation into two) into the model whereby the population suddenly collapses as the sterile insect release rate is increased above the level required at the bifurcation (Fig. 7). This avoids the necessity of the high levels of release needed to reduce the population below the unstable steady state in the model with no density-dependence. This bifurcation occurs in all the models involving density-dependence, and appears to result from the interaction of the depressing effects of density-dependence and the unstable equilibrium created by the SIT formulation in section 2.2., which results in the release of sterile insects being more effective at low density than at high population density, and thus the efficiency of the SIT increases as the population declines. The sudden collapse of a population under attack by sterile insect releases has indeed been observed in the programme against the melon fly *Bactrocera cucurbitae* (Coquillett) in Okinawa, Japan (Iwahashi 1977). Thus this predicted bifurcation appears to be a robust result, and one that apparently mimics nature.

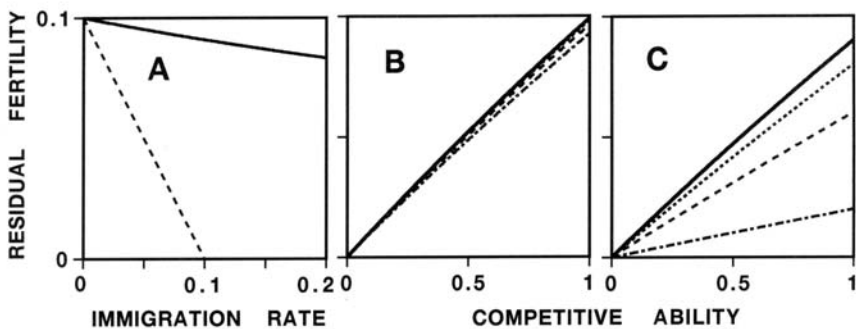


Figure 6. A: The allowable residual fertility (q) when the released insects that are fertile are also fully competitive with wild insects. Immigration occurs before mating (—); immigration occurs after mating (----). B and C: Allowable residual fertility as a function of competitiveness of released insects. Immigration occurs at 1% (—), 2% (.....), 4% (----), and 8% (-.-.-) of the wild population size F . B: Immigration occurs before mating. C: Immigration occurs after mating. (Figure from Barclay 2001, reproduced with permission.)

The exact behaviour of the SIT under density-dependence appears to depend sensitively on the biology of the system. Lawson (1967) and Berryman et al. (1973) pointed out that overcrowded populations may deplete their resources sufficiently such that survival to the adult stage is low. In this case, killing some of them (or lowering egg production) might actually result in a higher survival to the adult stage, making the use of the SIT counterproductive in such a situation. Another situation might be encountered in the case of an insect species wherein egg production is much higher than the resource allows, e.g. the olive fruit fly *Bactrocera oleae*

(Gmelin) in which one egg per fruit is laid. If sterile eggs did not deter insects from laying further eggs in a fruit already containing a sterile egg, then reduction in fertile egg production would have to be substantial before any effect would be noticed.

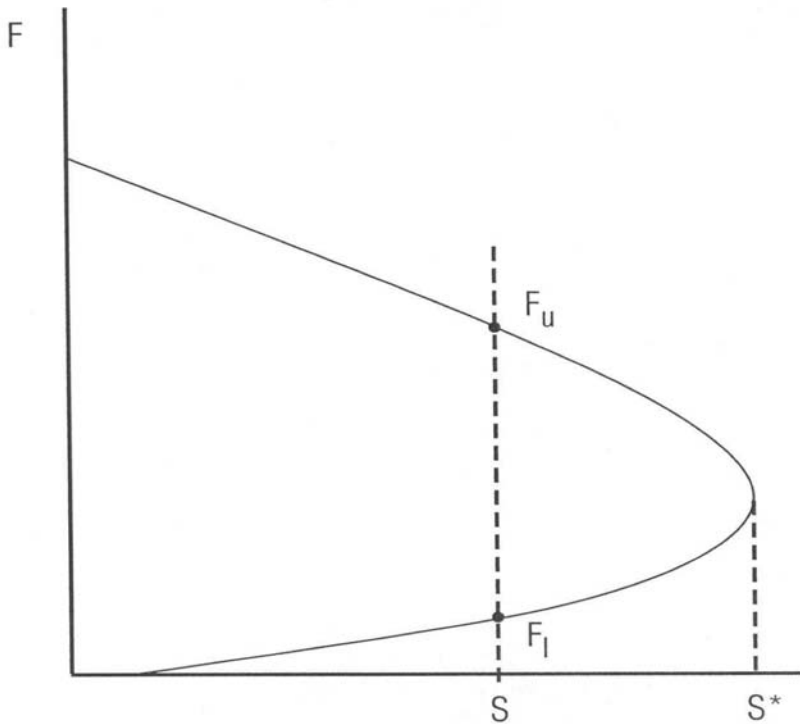


Figure 7. Isoclines formed by setting the equations for sterile insects (S , vertical line) and fertile insects (F) to zero; where they cross are the two steady states. The upper one is stable, and the lower one unstable. As sterile releases increase, the sterile isocline moves to the right. The bifurcation is at the point where the isoclines are tangent to each other. Larger values of sterile insect releases result in a sudden collapse of the population.
(Figure generated from equation 12, Barclay 2001.)

2.12. Age Structure

The existence of two or more life stages of a species complicates the dynamic responses of a population to mortality factors, especially if the two stages are ecologically different, as they are in mosquitoes and other pest species in which the two active stages occupy different habitats. If density-dependence is strong in one stage and weak or absent in the other stage, then the density-dependent stage is strongly buffered against mortality factors and tends not to vary greatly, while the

other stage may vary more but the mean size is a linear function of the buffered stage. As such, somewhat different responses to mortality affecting mainly one stage would be expected, and indeed this appears to be the case. In the case of the SIT, the sterile insects released always affect the adult stage, reducing fertile egg production.

Prout (1978) modelled the SIT for species with identifiable age structure and subject to immigration. His results indicated that, if the larval stage caused the pest problem, a higher level of immigration of mated adults was tolerable.

Barclay (1980b) showed that the critical release rate (S^*) is a larger proportion of the larval equilibrium size when density-dependence is in the larval survivorship than when density-dependence is in the adult survivorship. Thus, relative to a given larval equilibrium, the population requires fewer sterile insect releases when density-dependence is in the adult stage.

2.13. *Population Aggregation*

In nature most populations are not dispersed evenly over the available habitat. Some processes, such as territoriality, result in dispersion patterns that are more regular than one would expect of a random spatial distribution. However most populations will tend to have a somewhat aggregated dispersion pattern. Aggregation is the most difficult pattern to deal with in making sterile insect releases, as one has to know where the clumps are located.

Modelling of spatial aggregation has been done by Wehrhahn (1973) and Barclay (1992a). Wehrhahn used a mosaic of patches, inhabited by differing numbers of insects, and compared the required release rates for various patterns of aggregation. He used Monte-Carlo simulation, which introduces random numbers to allow stochastic variation, in this case, of migration rates among patches. Wehrhahn pointed out that the control programme itself will probably change the nature of the spatial distribution.

Another approach has used probability distributions to describe the extent of aggregation (Barclay 1992a). There is a long history of using these distributions in ecology, summarized by Pielou (1969) and Patil and Stiteler (1974). The most common distribution to quantify aggregation is the Negative Binomial Distribution in which the parameter k measures clumping. If aggregation is extreme, then k is close to zero; as k goes off to infinity, the dispersion approaches a random pattern. Another approach uses $1/k$, which increases with the degree of clumping. Barclay (1992a) used the negative binomial distribution to derive required sterile insect release rates of an aggregated population as a function of the clumping parameter, k . For moderately aggregated populations ($k=0.25$), it was found that the required release rate was about four times that for a randomly dispersed population. Shiga (1986) analysed spatial distributions in the context of fruit fly eradication using male annihilation and the SIT.

Many aspects of aggregation involve behavioural components. Horng and Plant (1992) modelled the impact of lek mating on the SIT, using a Poisson binomial distribution. They found that the sterility effect, presence or absence of female mate-choice, and sterile male mating competitiveness were the most important factors in their model in determining the success of a programme releasing sterile insects.

2.14. *Predation, Parasitism, and Competition*

The effects of predation on the efficiency of the SIT were first modelled by Knipling (1979) using a simple numerical model. His model predicted a synergistic interaction between predation and sterile insect releases, such that the net effect would be considerably greater than either alone. Barclay and Mackauer (1980b) included sterile insect releases in the Lotka-Volterra predator-prey model, and demonstrated that, not only was the critical release rate lower with than without predators, the system was also greatly destabilized, and population collapse often occurred with release rates well below the critical value. This model was subsequently shown by Harrison et al. (1982) to have a very complicated dynamic behaviour, and this is presumably related to the inherent instability. This model was then extended, and an even greater array of dynamical behaviour was found (Barclay and van den Driessche 1990). In addition, the general features of the predator-prey system were found similar to the situation involving hosts and parasitoids (Barclay 1987a). Knipling (1998) analysed extensively the effects of augmentation of predators and parasites on the efficiency of the SIT.

If the pest species is in competition for resources with another species, then this is of some value to the release programme, as it reduces the initial pest population size, but apart from that there seems to be little effect of the competing species on the release programme (Barclay 1981b).

2.15. *Stochastic Models*

Stochastic models involve the specification of certain variables as being random. If the processes involved are well known and the extent of variation is known, then stochastic models can give additional information on the expected variability of the resulting control, as well as deviations of mean values from those predicted by deterministic models. This is especially true in areas like genetics in which the mechanisms of variation, e.g. meiosis, are clear. However this information is often not well-known in animal ecology, and therefore stochastic models may be of limited use. In fact, if the wrong features are allowed to vary (e.g. birth rate is variable in the model, whereas in reality it is mortality that varies), then stochastic models can give misleading results. In addition, unless they are solved numerically, stochastic models are usually much more difficult to analyse than deterministic models, and for these reasons the history of stochastic population modelling has been rather disappointing.

Stochastic models of sterile insect releases were developed by Kojima (1971), Bogyo (1975), Costello and Taylor (1975), Taylor (1976) and Kimanani and Odhiambo (1993), and they confirmed the results of Knipling (1955) and others that used deterministic models. They also derived a threshold release rate that leads to local extinction, and showed that much greater release rates above this threshold will not result in a greatly reduced time to extinction, although Lawson (1967) and Itô and Kawamoto (1979) offered evidence to the contrary using both a deterministic model and a probabilistic model.

2.16. *Stability under Various Conditions*

Stability is a very important aspect of populations, and is of special interest to pest managers. If, for any reason, the population is likely to collapse, this is important. Barclay (1982b) examined four systems or cases for their relative stability under sterile insect releases. These were all differential-equation models and represented: (1) a simple one-species model with only one identifiable life stage (adult), (2) a one-species model with two life stages (larval and adult), (3) a model of two competing species, one of which is the pest, and (4) a predator-prey model in which the prey is the pest. There are many possible definitions of stability in ecology, and they involve various dynamic characteristics of the system. None has yet emerged as definitive, although an extensive analysis of the topic is now available (Mueller and Joshi 2000). Barclay (1982b) examined five criteria of stability for each system, and ranked the systems. These stability criteria involved characteristics such as extinctions, time to extinction, amplitude of fluctuations, and time until return to equilibrium. The most stable was the single species – single stage model, followed by the competing species model, then the two-stage model, and by far the least stable was the predator-prey system above (section 2.14.). The existence of obligate predators (or parasitoids) both lowers the critical release rate of sterile insects and also destabilizes the system, so that it is likely to collapse even when the sterile release rate is lower than the critical rate. Unfortunately there appears to be no experimental evidence to test these ideas.

2.17. *Integration of Control Methods*

Since the SIT works best at low pest densities (section 2.11.), it is common practice to reduce the population with insecticide prior to the release of sterile insects. This brings the population down to a level at which the number of sterile insects (required to be produced by a rearing facility) is manageable. It might also be possible to combine contemporaneously the action of the SIT with other control methods to share the required mortality among two or more imposed sources, each one then having to impose only a modest level of mortality, and each one perhaps operating best under conditions not favourable to the others (Barclay 1992b; Mangan, this volume). On the other hand, certain combinations might interfere with each other and thus prove unsuitable (Barclay 1987c).

Knipling (1964, 1979) examined several combinations of various control methods with the SIT, using simple numerical intra-generational models. These include combinations of sterile releases with insecticides, sterilants, pheromones, parasitoids or predators. Barclay (1980b, 1987a, b) and Barclay and van den Driessche (1989) also examined some of these combinations using more general inter-generational algebraic models. They found that the results of the combined use of sterile insects and other control methods became less clear when other biotic interactions were included.

2.17.1. *SIT with Application of Insecticide*

It might be thought that insecticides and the SIT are incompatible since the insecticide would kill sterile, as well as fertile, insects. However, Knipling (1964, 1979) reasoned that insecticide application would kill both sterile and fertile insects in the same proportion, and thus maintain the overflooding ratio, rendering the two control methods compatible. By numerical examples he showed that these two methods could work well together, and thus reduce both total costs and the need for excessive insecticide application. If the sterile insects were also resistant to insecticide, then the combination would be even more effective.

Barclay (1980a, b) found that, when the pest species was considered in isolation, the application of insecticide coupled with the release of sterile insects increased total mortality. However, the results of the combined use of insecticide and sterile insects became less clear when other biotic interactions were included. For species with two life stages, and when used together with sterile insects, a larvicide appears to be more useful than an adulticide, but if the pest is already under considerable predation, the combination of insecticide and sterile insects might be detrimental.

2.17.2. *SIT with Pheromone Traps for Male Annihilation*

Knipling (1979) found that the combined use of sterile releases and pheromone traps was less efficient than an equivalent effort put into either method alone. This was because of the interference caused by the killing of sterile males in the pheromone traps. As a variant of this combination, Knipling proposed that releasing pheromone-treated sterile insects could enhance mate-finding, thus increasing the competitive ability of sterile insects, especially at low densities. It might also act as a vehicle for confusion of the wild population. Knipling found that, for insects in which the males produce female-attracting pheromone, such as the boll weevil *Anthonomus grandis grandis* Boheman, the release of pheromone-treated males would substantially increase the effectiveness of the control program, assuming that the applied pheromone did not deteriorate badly. Knipling also considered the situation in which females produce male-attracting pheromone, and he modelled the release of pheromone-treated sterile females alone. These would probably be most effective if they were free-living rather than contained in traps. He again found that this method was much more effective than the use of untreated sterile females, and that control might be possible using pheromone-treated sterile females where the release of only non-treated sterile females would be hopelessly inadequate.

Hamada and Miyai (1985), using a continuous model, modelled the combination of the simultaneous release of sterile insects and pheromone trapping for male annihilation (Box 8). They found that the two methods in combination required less effort for each control method than when using either method alone. Their recommendation was to use male annihilation first and then sterile releases, although the model did not specifically explore that scenario.

Barclay and van den Driessche (1989) also modelled this combination, and found that the two methods combine synergistically, especially when the fecundity and daily survivorship are both high. When the fecundity and survivorship are low, the synergism disappears. For parameter values approximating those of tsetse flies *Glossina* spp., synergism is reduced.

Box 8. Combination of Sterile Releases and Pheromone Trapping

Miyai's model consisted of four differential equations: $dM/dt = F(a-bF) - cM - kM$; $dV/dt = F(a-bF) - cV - \alpha[\min(M+S, V)]$; $dF/dt = \alpha[\min(M+S, V)] M / (M+S) - cF$; $dS/dt = R - cS - kS$; where M , V , F and S are the numbers of males, virgin females, fertilized females, and sterile insects, respectively. The parameters are: a is a density-independent fecundity, b is a density-dependent fecundity, c is a death rate, k is the rate of trapping of males, α is the mating efficiency, and R is the sterile insect release rate.

Knipling (1979) described the interaction of methyl eugenol for male annihilation used concurrently with the release of both sterile males and females, and found no interference and a high degree of synergism. Since the development of resistance to methyl eugenol has been demonstrated (Shelly 1997), it might also be possible to incorporate the use of sterile insects of the resistant strain, and thus increase effectiveness even more.

In the case where the attractant is non-sex-specific, such as with food baits, Barclay and van den Driessche (1989) showed that the two methods combine synergistically, especially when sterile insects are fed before release, and fecundity and survivorship are high. For parameter values approximating those of tsetse flies, there is still some synergism.

2.17.3. *SIT with Release of Parasitoids*

This combination has the advantage that parasitoids work well at high host densities, while the SIT works best at low pest densities. Knipling (1979, 1998) considered the release of both sterile males and females, and also *Trichogramma* sp., an egg parasitoid. His tables showed clearly that these two methods were synergistic. A recent field study found that the two methods in combination were more efficient than either method alone (Bloem et al. 1998). In addition, the release of sterile females provides an egg resource for egg parasitoids, further augmenting the parasitoid population. Many parasitoids attack the larvae, so that the release of sterile females would not directly assist these parasitoids. If both sterile insects and parasitoids are released inundatively (Carpenter et al., this volume), then each should become more efficient as the density declines, offering a powerful source of synergism.

Barclay (1987b) modelled the interaction of the inundative release of parasitoids and sterile insects using several variations on the usual host-parasitoid equations. This combination shows a high degree of synergism in all the models investigated, and appears to be close to ideal (Fig. 8). The main problems to be anticipated probably involve dispersal and phenology.

2.17.4. *SIT with Sanitary Measures and Oviposition Traps*

If sanitation destroys oviposition habitat and traps destroy oviposited eggs, then there should be a complementary effect between the two, albeit moderated by density-dependence. If sterile insects are also released, then the system has three sources of population reduction, none of which interferes with any other. Knipling

(1979) calculated that these three should result in a highly efficient combination for control.

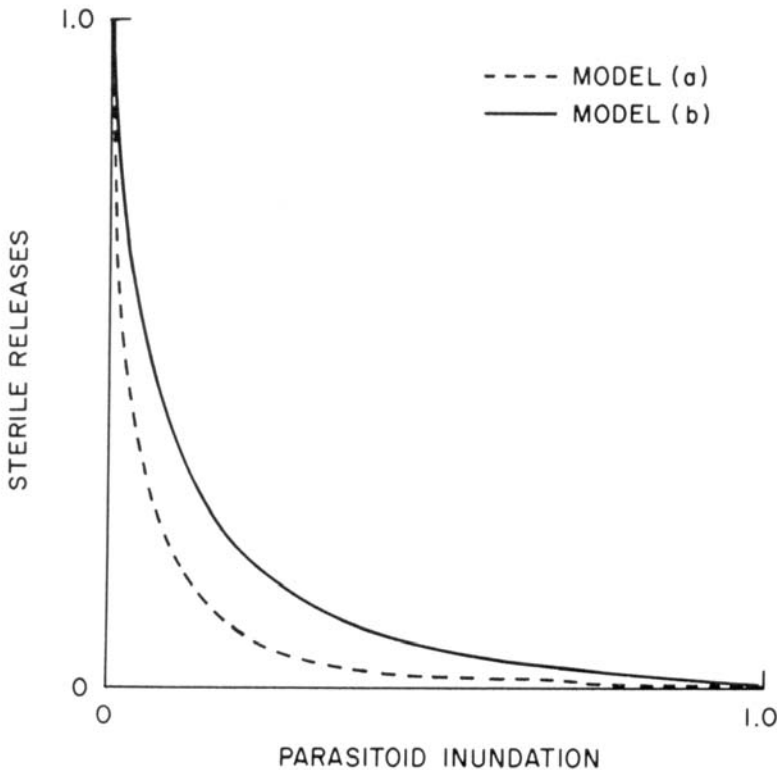


Figure 8. Critical release rates of sterile insects and parasitoids. All points on each curve are just sufficient to eradicate the pests. Density-dependence is in the hosts in model (a), and in the parasitoids in model (b). (Figure from Barclay 1987c, reproduced with permission.)

2.18. Optimization of Programme Releasing Sterile Insects

Optimization inevitably involves economics. Although that is somewhat outside the scope of this chapter, a beginning has been made on this topic. Geier (1969) used demographic models incorporating density-dependence to analyse the efficiency of programmes that release sterile insects, and to derive optimal strategies for control. Barclay and Li (1991) used a general treatment of combinations of pest control to determine optimal proportions of each control method. Atzeni et al. (1992) examined the situation for the Old World screwworm fly *Chrysomya bezzania* (Villeneuve), and included buffer width, male competitiveness, and population

aggregation in their analysis. Anaman et al. (1994) performed a cost/benefit analysis with *C. bezzania*, and incorporated beef losses into the equation.

2.19. *Development of Resistance*

There has been a marked tendency for insects to develop resistance to insecticides or other control methods. It is conceivable that a wild pest population could develop resistance to the use of sterile releases as a means of control (Lance and McInnis, this volume; Whitten and Mahon, this volume). This resistance might involve behavioural mechanisms that would preclude the sterile-fertile matings (Barclay 1990). Selection for resistance to several pest control methods operating together has been modelled by Barclay (1996), and it appears that selection for resistance to a particular control method is a linear function of the amount of mortality being inflicted by that control method. Itô and Yamamura (this volume) develop further the subject of resistance.

2.20. *Educational and Instructional Modelling*

There have been a number of computer simulations of the SIT, for the purpose of instruction, in both the technique and in insect population dynamics generally. At least two have been documented and are available to the public. Both represent various elaborations on the original model of Knipling.

Sawyer et al. (1987) described a simulation that includes spatial heterogeneity, aggregation, immigration, random effects, and reduced sterile male competitiveness. This model was adapted and named "Curaçao" by Arneson (1996) to run on Microsoft Windows (3x or 95), and is available for downloading on the website. Instructions for running the programme are included on the website. The user can specify the various options, and then compare runs to draw conclusions.

Weidhaas (2001) constructed a similar model written in Visual Basic called "Sterility", which runs on a personal computer with DOS capabilities. It allows incomplete sterility in males, reduced sterile-male competitiveness, different sex ratios, and determination of the growth rate of the population, and runs for 12 generations to assess the results. It also has the capability to compute costs of the control programme.

3. PARAMETER ESTIMATION FOR THE MODELS

Knowledge of several parameters is crucial to the success of any programme that releases sterile insects. With reference to the models outlined above, the basic parameters that will always be of interest are: F , the population size; λ , the potential rate of population increase each generation; q_m and q_f , the proportions of the released males and females that remain fertile; and c , the competitive ability of sterile males relative to the wild fertile male population. Some of the estimations can be done using standard population biology methods. The population size can be crudely estimated from trap catches. Hargrove (1990) used mark-recapture techniques to

estimate the size of tsetse fly populations (Weidhaas 1973). The rate of increase, λ , would normally be determined using oviposition rates. The residual fertilities, q_m and q_f , could be determined by caging sterile males with fertile females, and fertile males with sterile females, either in groups or pairs, and noting the resulting fertile egg production. Competitive ability of sterile males, c , could then be determined from laboratory, field cage or small-scale field experiments, where immigration could be assumed to be negligible, using the equation involving competitive ability, and then solving for c . The information on λ , q_m and q_f must be determined first, or the equation becomes confounded. Alternatively, Meats (1998) used release and recapture techniques to estimate the quality of released sterile insects. Immigration into the control area could then be determined using either mark-recapture or the equation involving immigration and solving for v . Plant and Cunningham (1991) detailed procedures for estimating the dispersal of Mediterranean fruit flies *Ceratitis capitata* (Wiedemann), and estimates of immigration could be obtained from considerations of dispersal.

The determination of density-dependence is problematic, because there are many models and none of them is particularly mechanistic. Thus rates of oviposition and subsequent survivorship would have to be monitored at various densities to derive a function to describe the depressing effects at various levels. In many wild populations, even just detecting the existence of density-dependence is difficult, much less the quantification of depressing effects. However, in view of the potential assistance to the SIT, an estimation of the effects of density-dependence is worthwhile. Itô and Yamamura (this volume) develop further the subject of parameter estimation.

4. ASSESSMENT OF SIT MODELLING

4.1. *Uses of Models*

Models can be used to predict and explain the behaviour of a population. This information guides research, generates hypotheses, and aids teaching. Most models of the SIT have so far have been aimed mainly at predicting the behaviour of pest populations under various constraints, such as incomplete sterility, lack of competitive ability of sterile males, the immigration of wild insects into a control area, etc. One of the best uses of models is to generate ideas or hypotheses that are capable of experimental testing. Thus, ideally, modelling should go hand-in-hand with field and laboratory experiments to verify or falsify a model's predictions.

4.2. *Advantages and Limitations of Modelling*

The models of the SIT constructed thus far fall generally into three groups: (1) models that investigate processes that determine the proportion of eggs laid that are sterile, (2) models involving population dynamics and other population level phenomena, and (3) models that investigate the interactions of the SIT with other control methods, although it might be argued that the last two really belong together.

The first category, including residual sterility, reduced sterile competitive ability, mating patterns, and immigration, is of crucial importance in planning and executing a programme that releases sterile insects. Unless one can accurately predict the level of sterility in eggs produced by the wild females, the programme is liable to fail. In addition, it is here that models are most likely to give realistic answers, as these processes rely mostly on determinable proportions or coefficients, rather than somewhat nebulous population processes.

Models of more general aspects of population dynamics involve many hidden factors, such as the strength of density-dependence, the functional responses of predators, synchrony of pest and predator phenologies, the degree of pest population aggregation, the extent to which sterile insects assume the same spatial patterns as the wild insects, etc. These are not easy to determine, and the models in the second and third categories must be taken as heuristic, rather than quantitatively predictive. They provide insights into the kinds of responses to expect, but quantitative accuracy must await species-specific simulations based on accurate and detailed biological and ecological information regarding the whole system.

4.3. Transient versus Equilibrium Models

Many analytic models of the SIT are solved for equilibrium, and the results of the parameters on the equilibrium are noted. In real life, populations are almost always changing. Analysis of the equilibrium behaviour certainly has much to say about the effects of the parameters on the transient behaviour as well as on the equilibrium, but a proper analysis should include the effects of the parameters on the dynamics of transient behaviour. The problem is that there is an infinite number of trajectories that any population can follow, and to encapsulate the behaviour of these in digestible form is no small task. One criterion that can be used is that of stability of the system, in its various forms. Stability characteristics can be related to parameter ranges, and certain characteristics of the resulting transient behaviour can be inferred from them.

4.4. Future Directions and Information Needs

The models reviewed in this chapter cover most of the relevant topics in the dynamics of the SIT. However, it is only a good beginning, and there is much left to do. Models that have a more realistic ecological basis will be required to suggest new hypotheses and to give more accurate predictions of behaviour. One area still largely untapped is metapopulation models — models including patches with migration among patches, local extinctions and re-establishments. A start has been made with the models including immigration, heterogeneity, and diffusion. The next step is to tie these together into a meaningful whole.

Another area, which will yield useful information, is the construction of species-specific models for the SIT, including all relevant factors. Many species-specific models have been constructed, but many appear to have inadequate detailed ecological information. In addition, the area of behavioural ecology will probably emerge as being especially relevant.

Testing models, experimentally and in the field, is in its infancy. Information is needed on the effects of pest density-dependent regulation on the efficiency of the SIT, the effects of predators and parasites on the dynamics of the SIT, and the effects of ecosystem resilience. The simultaneous use of other control methods with the SIT is still largely hypothetical, and this potentially useful area needs considerable investigation.

5. REFERENCES

- Ailam, G., and R. Galun. 1967.** Optimal sex ratio for the control of insects by the sterility method. *Annals of the Entomological Society of America* 60: 41–43.
- Anaman, K. A., M. G. Atzeni, D. G. Mayer, and M. A. Stuart. 1994.** Benefit-cost analysis of the use of sterile insect technique to eradicate screwworm fly in the event of an invasion from Australia. *Preventive Veterinary Medicine* 20: 79–98.
- Arneson, P. A. 1996.** Curaçao. The sterile insect release method — a simulation exercise. In Radcliff's IPM world textbook. University of Minnesota. <http://www.ipmworld.umn.edu/chapters/SirSimul.htm>
- Atzeni, M. G., D. G. Mayer, and D. G. Butler. 1992.** Sterile insect release method — optimal strategies for eradication of screwworm fly. *Mathematics and Computers in Simulation* 33: 445–450.
- Barclay, H. J. 1980a.** The sterile insect release method for species with two-stage life cycles. *Researches on Population Ecology* 21: 165–180.
- Barclay, H. J. 1980b.** Models for the sterile insect release method with the concurrent release of pesticides. *Ecological Modelling* 11: 167–178.
- Barclay, H. J. 1981a.** Population models on the release of chemosterilants for pest control. *Journal of Applied Ecology* 18: 679–695.
- Barclay, H. J. 1981b.** The sterile insect release method for a pest species in competition with another species. *Researches on Population Ecology* 23: 145–155.
- Barclay, H. J. 1982a.** The sterile release method with unequal male competitive ability. *Ecological Modelling* 15: 251–263.
- Barclay, H. J. 1982b.** Population stability under sterile releases. *Researches on Population Ecology* 24: 405–416.
- Barclay, H. J. 1984.** Demographic consequences of monogamy and polygamy for a sterile release programme. *Protection Ecology* 6: 209–217.
- Barclay, H. J. 1987a.** Models of sterile insect releases for populations under attack by parasitoids. *Ecological Modelling* 36: 155–169.
- Barclay, H. J. 1987b.** Models for pest control: complementary effects of periodic releases of sterile pests and parasitoids. *Theoretical Population Biology* 32: 76–89.
- Barclay, H. J. 1987c.** Combining methods of pest control: complementarity of methods and a guiding principle. *Natural Resource Modeling* 2: 299–323.
- Barclay, H. J. 1990.** Uncertainties associated with release agents for autocidal control, pp. 185–193. In J. Marois and R. Plant (eds.), *Risk assessment in agricultural biotechnology*. University of California, Davis, California, USA.
- Barclay, H. J. 1992a.** Modelling the effects of aggregation on the efficiency of insect pest control. *Researches on Population Ecology* 34: 131–141.
- Barclay, H. J. 1992b.** Combining methods of insect pest control: partitioning mortality and predicting complementarity. *Researches on Population Ecology* 34: 91–107.
- Barclay, H. J. 1996.** Combining methods of insect pest control: modelling selection for resistance to control methods in combination. *Researches on Population Ecology* 38: 75–85.
- Barclay, H. J. 2001.** Modeling incomplete sterility in a sterile release program: interactions with other factors. *Researches on Population Ecology* 43: 197–206.
- Barclay, H., and C. Li. 1991.** Combining methods of pest control: minimizing cost during the control programme. *Theoretical Population Biology* 40: 105–123.
- Barclay, H., and M. Mackauer. 1980a.** The sterile insect release method for pest control: a density-dependent model. *Environmental Entomology* 9: 810–817.
- Barclay, H., and M. Mackauer. 1980b.** The sterile insect release method for species under predation or parasitism. *Researches on Population Ecology* 22: 136–146.

- Barclay, H. J. and P. van den Driessche. 1989.** Pest control models of combinations of sterile releases and trapping. *Insect Science and its Application* 10: 107–116.
- Barclay, H. J. and P. van den Driessche. 1990.** A sterile release model for control of a pest with two life stages under predation. *Rocky Mountain Journal of Mathematics* 20: 847–855.
- Berryman, A. 1967.** Mathematical description of the sterile male principle. *The Canadian Entomologist* 99: 858–865.
- Berryman, A. A., T. P. Bogyo, and L. C. Dickmann. 1973.** Computer simulation of population reduction by release of sterile insects: II. The effects of dynamic survival and multiple mating, pp. 31–43. *In* Proceedings, Panel: Computer Models and Application of the Sterile-Male Technique. Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture, 13–17 December 1971, Vienna, Austria. STI/PUB/340. IAEA, Vienna, Austria.
- Bloem, S., K. A. Bloem, and A. L. Knight. 1998.** Oviposition by sterile codling moths, *Cydia pomonella* (Lepidoptera: Tortricidae) and control of wild populations with combined releases of sterile moths and egg parasitoids. *Journal of the Entomological Society of British Columbia* 95: 99–109.
- Bogyo, T. P. 1975.** Mathematical models and computer simulation of insect control, pp. 161–168. *In* Proceedings, Symposium: Sterility Principle for Insect Control 1974. International Atomic Energy Agency and Food and Agriculture Organization of the United Nations, 22–26 July 1974, Innsbruck, Austria. STI/PUB/377. IAEA, Vienna, Austria.
- Bogyo, T. P., A. A. Berryman, and T. A. Sweeney. 1971.** Computer simulation of population reduction by release of sterile insects. I. A study of the relative importance of the parameters of a mathematical model, pp. 19–25. *In* Proceedings, Panel: Application of Induced Sterility for Control of Lepidopterous Populations. Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture, 1–5 June 1970, Vienna, Austria. STI/PUB/281. IAEA, Vienna, Austria.
- Costello, W. G., and H. M. Taylor. 1975.** Mathematical models of the sterile male technique of insect control, pp. 318–359. *In* A. Charnes and W. R. Lynn (eds.), *Mathematical analysis of decision problems in ecology*. Lecture Notes in Biomathematics, Volume 5. Springer-Verlag, Berlin, Germany.
- Dietz, K. 1976.** The effect of immigration on genetic control. *Theoretical Population Biology* 9: 58–67.
- Geier, P. W. 1969.** Demographic models of population response to sterile-release procedures for pest control, pp. 33–41. *In* Proceedings, Panel: Insect Ecology and the Sterile-Male Technique. Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture, 7–11 August 1967, Vienna, Austria. STI/PUB/223. IAEA, Vienna, Austria.
- Hamada, R., and S. Miyai. 1985.** Theory of eradication, pp. 79–97. *In* S. Ishi, K. Kiritani and T. Kocha (eds.), *Eradication of fruit flies: theory and practice*. (In Japanese). Japan Agriculture Aviation Association, Tokyo, Japan.
- Hargrove, J. W. 1990.** Population estimation from mark-recapture data. Equations for a pooled mark system and for pooled data, with applications to a study on island populations of tsetse flies in Zimbabwe, pp. 79–114. *In* Proceedings, Panel: Sterile Insect Technique for Tsetse Control and Eradication. Final Research Co-ordination Meeting, Joint FAO/IAEA Division of Nuclear Techniques in Food and Agriculture, 6–10 June 1988, Vom, Plateau State, Nigeria. STI/PUB/830. IAEA, Vienna, Austria.
- Harrison, G. W., H. J. Barclay, and P. van den Driessche. 1982.** Analysis of an insect release model with predation. *Journal of Mathematical Biology* 16: 33–47.
- Hassell, M. P. 1978.** The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey, USA.
- Hawkes, C., and T. H. Coaker. 1977.** A model for chemosterilization experiments with special reference to the cabbage root fly (*Erioischia brassicae* (Bouche)). *Journal of Applied Ecology* 14: 43–53.
- Horng, S. B., and R. E. Plant. 1992.** Impact of lek mating on the sterile insect technique: a modeling study. *Researches on Population Ecology* 34: 57–76.
- Itô, Y. 1977.** A model of sterile insect release for eradication of the melon fly, *Dacus cucurbitae* Coquillett. *Applied Entomology and Zoology* 12: 303–312.
- Itô, Y., and H. Kawamoto. 1979.** Number of generations necessary to attain eradication of an insect pest with the sterile insect release method: a model study. *Researches on Population Ecology* 20: 216–226.
- Iwahashi, O. 1977.** Eradication of the melon fly, *Dacus cucurbitae*, from Kume Is., Okinawa with the sterile insect release method. *Researches on Population Ecology* 19: 87–98.

- Kimanani, E. K., and J. W. Odhiambo. 1993.** A stochastic model for the sterile male technique. *Biometrics* 49: 577–585.
- Klassen, W., and J. F. Creech. 1971.** Suppression of pest population with sterile male insects. Miscellaneous Publication, Number 1182. USDA/ARS, Washington, DC, USA.
- Klassen, W., J. V. Adams, and M. B. Twohey. 2004.** Modeling the suppression of sea lamprey populations by the release of sterile males or sterile females. *Journal of Great Lakes Research* 30: 463–473.
- Knipling, E. F. 1955.** Possibilities of insect control or eradication through the use of sexually sterile males. *Journal of Economic Entomology* 48: 459–462.
- Knipling, E. F. 1959.** Sterile male method of population control. *Science* 130: 902–904.
- Knipling, E. F. 1960.** Use of insects for their own destruction. *Journal of Economic Entomology* 53: 415–420.
- 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 (Series) 33–98.
- Knipling, E. F. 1979.** The basic principles of insect population suppression and management. Agriculture Handbook Number 512. USDA/SEA, Washington, DC, USA.
- Knipling, E. F. 1998.** Role of parasitoid augmentation and sterile insect techniques in areawide management of agricultural insect pests. *Journal of Agricultural Entomology* 15: 273–301.
- Kojima, K. I. 1971.** Stochastic models for efficient control of insect populations by sterile-insect release methods, pp. 477–487. *In* Proceedings, Symposium: Sterility Principle for Insect Control or Eradication. International Atomic Energy Agency and Food and Agriculture Organization of the United Nations, 14–18 September 1970, Athens, Greece. STI/PUB/265. IAEA, Vienna, Austria.
- Lawson, F. R. 1967.** Theory of control of insect populations by sexually sterile males. *Annals of the Entomological Society of America* 60: 713–722.
- Lewis, M. A., and P. van den Driessche. 1993.** Waves of extinction from sterile insect release. *Mathematical Biosciences* 116: 221–247.
- Manoranjan, V. S., and P. van den Driessche. 1986.** On a diffusion model for sterile release. *Mathematical Biosciences* 79: 199–208.
- Marsula, R., and C. Wissel. 1994.** Insect pest control by a spatial barrier. *Ecological Modelling* 75: 203–211.
- Meats, A. 1998.** Predicting or interpreting trap catches resulting from natural propagules or releases of sterile fruit flies. An actuarial and dispersal model tested with data on *Bactrocera tryoni*. *General and Applied Entomology* 28: 29–38.
- Miller, D. R., and D. E. Weidhaas. 1974.** Equilibrium populations during a sterile-male release programme. *Environmental Entomology* 3: 211–216.
- Mueller, L. D., and A. Joshi. 2000.** Stability in model populations. Monographs in population biology 31. Princeton University Press, Princeton, New Jersey, USA.
- Patil, G. P., and W. M. Stiteler. 1974.** Concepts of aggregation and their quantification: a critical review with some new results and applications. *Researches on Population Ecology* 15: 238–254.
- Pielou, E. C. 1969.** An introduction to mathematical ecology. John Wiley, New York, USA.
- Plant, R. E., and R. T. Cunningham. 1991.** Analyses of the dispersal of sterile Mediterranean fruit flies (Diptera: Tephritidae) released from a point source. *Environmental Entomology* 20: 1493–1503.
- Prout, T. 1978.** The joint effects of the release of sterile males and immigration of fertilized females on a density regulated population. *Theoretical Population Biology* 13: 40–71.
- Sawyer, A. J., Z. Feng, C. W. Hoy, R. L. James, S. E. Naranjo, S. E. Webb, and C. Welty. 1987.** Instructional simulation: sterile insect release method with spatial and random effects. *Bulletin of the Entomological Society of America* 33: 182–190.
- Shelly, T. E. 1997.** Selection for non-responsiveness to methyl eugenol in male oriental fruit flies (Diptera: Tephritidae). *Florida Entomologist* 80: 248–253. <http://www.fcla.edu/FlaEnt/fe80p248.pdf>
- Shiga, M. 1986.** Analysis of spatial distribution in fruit fly eradication, pp. 387–398. *In* M. Mangel, J. R. Carey and R. E. Plant (eds.), *Proceedings: Pest Control: Operations and Systems Analysis in Fruit Fly Management*. NATO Advanced Workshop, 5–9 August 1985, Bad Windsheim, Germany. Springer-Verlag, Berlin, Germany.
- Staley, D. H., W. N. Cannon, Jr., and W. R. Holt. 1971.** A mathematical model of an insect population with overlapping generations where the females are polyandrous and the males are subject to auto-sterilization. *Annals of the Entomological Society of America* 64: 325–330.
- Taylor, C. R. 1976.** Determining optimal sterile male release strategies. *Environmental Entomology* 5: 87–95.

- Wall, R., and J. Howard. 1994.** Autosterilization for control of the housefly *Musca domestica*. *Journal of Theoretical Biology* 171: 431–437.
- Wehrhahn, C. F. 1973.** An approach to modelling spatially heterogeneous populations and the simulation of populations subject to sterile insect release programs, pp. 45–64. *In* Proceedings, Panel: Computer Models and Application of the Sterile-Male Technique. Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture, 13–17 December 1971, Vienna, Austria. STI/PUB/340. IAEA, Vienna, Austria.
- Weidhaas, D. E. 1973.** Principles of the sterile male technique with emphasis on ecology, pp. 17–22. *In* Proceedings, Panel: Computer Models and Application of the Sterile-Male Technique. Joint FAO/IAEA Division of Atomic Energy in Food and Agriculture, 13–17 December 1971, Vienna, Austria. STI/PUB/340. IAEA, Vienna, Austria.
- Weidhaas, D. E. 2001.** “Sterility” computer model, available on request; e-mail: afn12842@afn.org
- Zouros, E. 1969.** On the role of female monogamy in the sterile male technique of insect control. *Annales de l’Institut Phytopathologique Benaki* 9: 20–29.