A Model of Sterile Insect Release for Eradication of the Melon Fly, *Dacus cucurbitae* Coquillet

Yosiaki Itô

Okinawa Prefectural Agricultural Experiment Station, Naha 903, Japan

(Received July 14, 1977)

Based on a logistic model of population growth and Poisson-binomial model for frequency distribution of matings between sterile and normal insects, a simple model was presented to simulate population processes under mass-releases of sterile melon flies. Constants used in the model were determined according to the results of population studies made in Kume Is., Okinawa. It was suggested that, under the conditions assumed here, a 2:1 ratio of mature sterile males and normal males in an isolated target area was enough to result in eradication of the melon fly within one year.

INTRODUCTION

Many models have been presented to simulate the processes of the sterile insect release method (SIRM) (e.g. Knipling, 1955, 1964; Berryman, 1967; Lawson, 1967; Bogyo, Berryman and Sweeney, 1971; Berryman, Bogyo and Dickmann, 1973; Monro, 1973), but most of them deal with purely theoretical aspects; few can be used to predict the real processes of an SIRM project. Difficulty in supplying reliable population data to the programmer is a barrier to the construction of realistic models (Monro, 1973).

During the course of a project to eradicate the melon fly, *Dacus cucurbitae* Coquillet, from Kume Is., Okinawa, we constructed a simple model to mimic the SIRM processes, based on estimated density changes of the target species. Density-dependent reduction in the rate of population increase, multiple matings and random encounter of wild females with sterile and normal males were all included in the model. Notwithstanding its simplicity, the model is considered to represent some major features of the SIRM process, because modifications of our release program which had been made in accordance with the results of the simulation model, led to remarkable progress in suppressing the fertility of wild females and the ratio of infested to uninfested fruits. The structure of the model and an example of its application are described in this paper.

STRUCTURE OF MODEL

Fluctuations in the population density of the melon fly on Kume Is. (58.5 km²) over a period of 5 years, were described by Iwahashi et al. (1975). These estimates were based on changes in the numbers of male flies caught by monitor traps baited with a male-attractant (cuc-lure) and naled and distributed over the island. Despite the limited period of observation covered by this study, it was clear that there are two peaks of fly density each year, one in spring and another in autumn. The autumn
peaks are generally higher than the spring peaks. The lowest density (about 1/20 of a typical autumn peak) was usually in February or March. Using the method of mark-recapture, Tró et al. (1974) estimated the number of male flies on Kume Is. during an autumn peak (November, 1972) at 2,500,000 individuals. If we suppose that there is no significant change in trapping efficiency in different seasons and at different population densities, the average minimum number of males on Kume Is. each year is about 125,000.

Our first aim is to mimic density fluctuations during an untreated period. To incorporate density-dependent reduction in the rate of population increase, a logistic model was adopted:

\[ N = \frac{K}{1 + e^{a-rt}} \]  
(1)

where \( N, K, r \) and \( a \) mean the population density, density at the carrying capacity of the environment, the intrinsic rate of natural increase and a constant, respectively. For convenience, \( N \) indicates the number of females alone. In the actual calculation procedure, however, we generate the numbers of individuals at monthly intervals (‘generation’ \( g=0,1,2,3,\ldots,\infty \)).

Morisita (1965) found that the rate of population change, \( R \), in the logistic model could be represented by the following equation:

\[ R_g = \frac{N_{g+1}}{N_g} = \frac{e^r}{1 + N_g B} \]  
(2)

where \( B = (e^r - 1)/K \) and \( N_g \) means the number of females in the \( g \)th generation. Thus we can use the following models to simulate population trends during the untreated period and the period under the SIRM.

(1) For untreated period: \( N_{f(g+1)} = N_{f(g)} S_0 F_0 P_\varphi = N_{f(g)} R_0 \).  
(3)  
(2) For SIRM period: \( N_{f(g+1)} = N_{f(g)} S_0 F_0 P_\varphi H_g = N_{f(g)} R_0 H_g \).  
(4)

Here \( N_{f(g)} = \) the number of normal females at the \( g \)th generation, \( S = \) survival rate of females from egg to sexual maturity, \( F = \) number of eggs laid per female, \( P_\varphi = \) sex ratio, \( H_g = \) ratio of fertile to non-fertile eggs at the \( g \)th generation in the SIRM period, and \( R_0 = S_0 F_0 P_\varphi = \) rate of change of density of adult females.

\( H_g \) is a function of the ratio of the number of sterile males to that of fertile (normal) males, that is

\[ H_g = f(N_s(g)/N_{f(g)}) \]  
(5)

where \( N_s(g) \) is the number of sterile males in the \( g \)th generation. A small proportion (20 percent on average) of eggs did not hatch even in the untreated area but this factor was included in \( F_0 \). Thus \( H_g \) means the degree of reduction of fertile egg ratio due to the SIRM.

For the calculation, we insert the following values in the appropriate equations mentioned above.

\( N_0 = N \) in February \( (g=0)^2 = 125,000 \)

\(^1\) Sex ratio is constant and almost 0.5, not only in field populations but also in artificially reared ones. Thus in our model, \( N_{s(g)} \), the number of sterile males at the \( g \)th generation can be compared with \( N_{f(g)} \), the number of females directly.

\(^2\) February is the month when the population density is near the minimum and also the month when mass-releases of sterile flies were begun on Kume Is.
Model of Sterile Insect Release

\[ K = 2,700,000 \]
\[ r = 1.2 \]
\[ a = 3.971 \]

The values for \( N_0 \) and \( K \) were selected to approximate the minimum and maximum densities of the fly on Kume Is. and values for \( r \) and \( a \) were selected to mimic the actual rate of population increase in spring and autumn. Then,

\[ R_g = \frac{3.3201}{1 + (0.859 \times 10^{-6})N_g} \]

except following generations when density-independent decrease (due to climatic conditions) took place.

\[ R_4 \] and \( R_5 = 0.5 \)
\[ R_{10} = 0.2 \]
\[ R_{11} = 0.238. \]

Calculation of \( N_g \)'s for the untreated period gave a series of bimodal curves of which 125,000 and 2,621,568 were annual minima and maxima, respectively (Curve A in Fig. 2).

The function \( f \) in Eq. 5 is considered to consist of three processes; (i) the distribution of the number of matings per female, (ii) the probability of multiple matings with sterile and normal males (we call this 'combined matings' hereafter), and (iii) the ratio of fertile to sterile eggs from the combined matings.

For the first item, a Poisson model was adopted. This is considered to be a reasonable procedure because the density of flies in the field is not high and mating is probably random. Ikenaga (unpublished) found that in small rearing cages, sexually mature (1-week to 10-day-old) males of the melon fly could copulate each day in the presence of ample females, but the mean interval between matings for individual females was about one week. Circumstantial evidence indicates that about 20 percent of sexually mature females die before ovipositing. Thus we use the Poisson distribution for which \( M_0 \) (frequency of zero item) is 0.2 and the mean is 1.61 as a model of mating frequency. In this model, about 0.6 percent of sexually mature females mate 6 times or more. For this to occur, 0.6 percent of females must survive more than 40 days assuming weekly intervals between matings. This seems to be a reasonable estimate because about the same value is obtained if we assume a constant survival rate of 0.5 per 5 days, which is very close to our field estimates (Ito et al., 1974).

<table>
<thead>
<tr>
<th>No. matings</th>
<th>Poisson freq.</th>
<th>( M_i )</th>
<th>Sterile mating</th>
<th>Combined mating</th>
<th>Fertile mating</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.290</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>( P_f (= 1 - P_3) )</td>
</tr>
<tr>
<td>1</td>
<td>0.322</td>
<td>0.402</td>
<td>( P_3 )</td>
<td>( 2P_3P_f )</td>
<td>( P_3^2 )</td>
</tr>
<tr>
<td>2</td>
<td>0.299</td>
<td>0.324</td>
<td>( P_3^2 )</td>
<td>( 3P_3^2P_f + 3P_3P_f^2 )</td>
<td>( P_3^3 )</td>
</tr>
<tr>
<td>3</td>
<td>0.139</td>
<td>0.174</td>
<td>( P_3^3 )</td>
<td>( 4P_3^3P_f + 6P_3^2P_f^2 + 4P_3P_f^3 )</td>
<td>( P_3^4 )</td>
</tr>
<tr>
<td>4</td>
<td>0.056</td>
<td>0.070</td>
<td>( P_3^4 )</td>
<td>( 5P_3^4P_f + 10P_3^2P_f^2 + 10P_3P_f^3 + 5P_3P_f^4 )</td>
<td>( P_3^5 )</td>
</tr>
<tr>
<td>5</td>
<td>0.018</td>
<td>0.023</td>
<td>( P_3^5 )</td>
<td>—</td>
<td>( P_3^6 )</td>
</tr>
<tr>
<td>6+</td>
<td>0.006</td>
<td>0.007</td>
<td>( P_3^6 )</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

\( M_i \) means the proportion of individuals which mate \( i \) times.
The Poisson series gave the frequency distribution of matings shown in the 2nd column of Table 1, but, because we did not incorporate in Eq. 3 the ratio of females which did not mate (this factor was included in \( P \)), frequencies of matings were converted to those shown in the 3rd column, to make the sum of the frequencies of matings (once or more than once) equal to unity.

For the probability of matings with sterile and normal males and the probability of combined matings, we adopted the binomial distribution (Table 1, Cols. 4, 5 and 6). Mating frequencies in excess of 5 are all included in item \( M_0 \). Then the actual probability of mating, e.g. for individuals mated 4 times, is given by:

\[
0.070P_s^3 + 0.070(4P_s^2P_f + 6P_s^2 + 4P_sP_f^2) + 0.070P_f^4
\]

where \( P_s \) means the proportion of sterile males and \( P_f \) that of fertile males \((P_s + P_f = 1)\).

If the ratio of the numbers of sterile to normal males is 2 \((P_s = 0.667)\) in the above case and the index of sexual competitiveness, \( c \), (Fried, 1971) is unity,\(^4\) the actual probabilities are:

1) Normal female \( \times \) sterile male = 0.4816
2) Normal female \( \times \) normal male = 0.1777
3) Normal female \( \times \) both sterile and normal males (i.e. combined mating) = 0.3407.

The rate of egg hatch in matings with sterile males and normal ones are assumed to be 0 and 1, respectively. In the combined matings we assume that the overall rate is 0.5, regardless of the actual numbers of sterile and fertile matings by an individual.

---

\(^4\) In our model the index of sexual competitiveness was not incorporated into the equations, but used to modify the number of sterile males released. Thus 1,000,000 insects with sexual competitiveness \( c = 0.7 \), are equivalent to 700,000 fully efficient insects.
female. This assumption agrees reasonably well with the frequency distribution of hatchability of eggs laid by individual females collected on Kume Is. (IWASHI et al., 1976). Thus the proportion of females which can lay hatchable eggs in the above example is $0.1777 + 0.3407/2 = 0.3481$. The results of computation are shown in Fig. 1. This figure can be used to estimate the proportion of fertile eggs, $H_p$, using data on the ratio of marked (sterile) to unmarked (normal) males caught by monitor traps. The curve again suggests that our assumption is not far from the actual situation: in a pilot SIRM experiment on Kudaka Is., a small islet near the island of Okinawa (IWASHI, 1976), it was shown that when the ratio of the number of marked to unmarked males reached $8:1$ after 9 releases (if FRIED'S $c$ is 0.7—TERUYA and ZUKAYAMA, unpublished—the effective ratio might have been $5.6:1$), the rate of egg-hatch decreased to about 0.1, which is only slightly lower than the value derived from the curve. Fig. 1 also shows a curve of the expected egg-hatch when the females mate only once. It is noted that the two curves in Fig. 1 were not very different when the assumed egg-hatch in combined matings was 0.5.

RESULTS OF SIMULATION

The population processes were simulated using Eq. 4, assuming monthly releases of constant numbers of sterile flies. $H_p$ was read from Fig. 1 using the ratio of sterile

![Graph showing fluctuations of the number of flies in the model population without SIRM (A) and populations under SIRM. The initial ratios of sterile to normal males are 0.5:1 ($N_s = 62,500$) in B, 1:1 ($N_s = 125,000$) in C, and 2:1 ($N_s = 250,000$) in D, respectively. C' is the trend when winter mortality was halved in the treatment C. Seasonal trends in the ratio $N_s/N_f$ are shown in the lower section of the figure.

---

5 The number of sterile flies released means, in this instance, the number of sexually mature flies. When we release sterile flies in the pupal stage (as in Kume Is.), there might be high mortalities among pupae and teneral adults.
to normal males \( \rho (=N_s/N_r) \).

On Kume Is. we are releasing sterile flies weekly. Eq. 4, however, does not include a term to allow for an input of adults, it simply estimates the actual number of adults present at a fixed time in every month. Based on estimated survival rates of adults (0.4 to 0.5 per 5 days on average), Iró et al. (1974) estimated that the number of flies which are recruited during a month must be at least 3 times the estimated number of adults, if the population density is to remain stable. A more precise calculation, however, has shown that the rates of recruitment per month are 5.1 times for a survival rate of 0.4 per 5 days and 3.9 times for a survival rate of 0.5 per 5 days. Thus monthly release might be more realistic than weekly release, if we like to compare directly the results of simulation with the actual processes on Kume Is.

From Fig. 2, it can be seen that if we begin with the release of sterile flies at a ratio of 2 sterile: 1 normal males (sexually matured) at the time of minimum density, the melon fly should be eradicated within 8 generations. If we start with releases at an initial ratio of 1 : 1, there should be two peaks in the density of wild flies in the 1st year, but eradication before the 18th generation. In a release program beginning with an initial ratio of 0.5 : 1, however, eradication should never be achieved for long years.

DISCUSSION

Although Knipling (1955) suggested that a ratio in the field of 9 sterile to 1 fertile insects should provide reasonable assurance of a downward trend in most populations, some workers have suggested (or have actually carried out) sterile releases at far higher ratios. For example, in a suppression experiment against Mediterranean fruit fly in Nicaragua (Rhode et al., 1971) the sterile : normal ratio in monitor traps reached 112 : 1 one month after the beginning of sterile insect releases; and in a project against the same species on the island of Procida (Cirio and Murtas, 1974), the ratio reached 316 : 1 after 1 months releases.

It is notable that, however, if we consider the ratio of sterile to fertile flies at the sexually mature stage (this ratio should correspond to the ratio of marked to unmarked flies in monitor traps bated with male lures because fruit flies generally became most attracted to these lures at ages near sexual maturity), even a 1 : 1 ratio of release at the starting point can lead to eradication within a short period. From the lower section of Fig. 2, it is clear that in a release project of 125,000 flies per month the ratio of sterile: wild flies decreases below 0.2 at the population peaks, but it is still possible to achieve eradication during a subsequent declining phase of the fluctuations.

In addition, it can be stated that wild populations respond in a very sensitive manner to changes in the numbers of sterile insects released. Even doubling the number of releases can considerably accelerate the eradication process. Of course the duration of the period of release is inversely correlated with \( r \), but our assumption of a 3-fold increase per month \((e^{1.2}=3.3)\) at low density levels is realistic for the melon fly, and probably not unreasonable for other insect pests.

The model described here was put to practical use in the SIRM project against melon fly on Kume Is., the input data being taken mainly from Iwashashi et al. (1976). In this project, releases were commenced in February, 1975, when the population density was estimated to be below 1/20 of that in November, 1972. Initially releases were constant at about 1,000,000 pupae (500,000 males) per week. Neither the rate
of egg-hatch nor the rate of infested fruits, however, decreased significantly for several months. The sterile : normal ratio was estimated to be 0.09 in July 1975, and the hatchability of eggs laid by females collected on the island reached 91 percent. In August it was decided to increase the releases to 2,000,000 pupae per week and to improve the pupal release buckets in order to reduce mortalities of pupae and adults just after eclosion. These changes were made during autumn, 1975. Thereafter the hatchability of eggs declined, and reached about 30 percent in March, 1976, when the sterile : normal ratio was about 3 : 1 (if $\epsilon$ was 0.7, the effective ratio would have been 2.1 : 1; see Fig. 1).

The overall rate of emergence of released pupae in the buckets was 60 percent and the survival rate during the 10 days after emergence was, if we adopt estimates by Itô et al. (1974), 0.16 to 0.25. Thus the number of released males which survived until sexual maturity from the releases of 1,000,000 pupae per week, was probably only 48,000 to 75,000. It is not surprising, therefore, that 5 months after the beginning of the programme, the ratio of sterile to normal males declined to about 0.1, and there was no significant decrease in the hatchability of eggs.

Acting on the results of preliminary simulation experiments using the models presented here, we increased the number of sterile flies released to 4,000,000 pupae per week from May, 1976, to accelerate the eradication process. The result is notably good, the hatchability and the fruit infestation declined rapidly and no infestation was recorded during October, 1976 to the present time (October, 1977). We concluded that the melon fly was eradicated from the Kume Is. (IWAHASHI, 1977).

ACKNOWLEDGEMENTS

I wish to thank Dr. M. A. BATeman, Division of Entomology, C. S. I. R. O. for critical reading of the manuscript. Review of the manuscript by Mr. T. NAKANO, Laboratory of Mathematical Biology, Kyushu University, from the mathematical viewpoint is also appreciated.

REFERENCES


IWAHASHI, O., R. TERUYA, T. TERUYA and Y. ITÔ (1975) Changes in abundance of the melon fly, Daucus carotaetiae COQUILLET, before and after the suppression with cue-lure baits and protein-hydrolysate.
APPENDIX

A Sterile: Normal Ratio Required for Maintaining A Wild Population at Certain Levels

Ryoichi Hamada

Okinawa Branch, Tropical Agriculture Research Center, Ishigaki 907-01, Japan

Both the mating competitiveness of sterile males and the competitiveness of sterile sperm are assumed to be unity in the model presented by Ito. Accordingly, the proportion of fertile eggs at the $g$th generation, $H_g$, can be written as follows:

$$H_g = \sum_{i=1}^{5} M_i \left[ P_f^i + \frac{1}{2} \left( 1 - (P_s^i + P_f^i) \right) \right] = \frac{1}{2} \sum_{i=1}^{5} M_i (1 + P_f^i - P_s^i). \quad (1)$$

The ratio of sterile to fertile males, $\rho$, is

$$\rho = P_s/P_f. \quad (2)$$

Since $P_f + P_s = 1$, $P_f$ and $P_s$ are represented by using $\rho$ as follows.

$$P_f = 1/(1 + \rho), \quad P_s = \rho/(1 + \rho). \quad (3)$$

![Graph showing values of $\rho$ which are necessary to maintain the numbers of a wild population at certain levels under given values of $N_f(g)$](image)

Fig. 3. Graph showing values of $\rho$ which are necessary to maintain the numbers of a wild population at certain levels under given values of $N_f(g)$. 
From equations (1), (3), and (4), $H_{g}$ is expressed by

$$H_{g} = \frac{1}{2} \sum_{i=1}^{s} M_{i} \left[ 1 + \left( \frac{1}{1 + \rho} \right)^{i} \right] - \frac{1}{2} \sum_{i=1}^{s} M_{i} \left[ 1 + \frac{1 - \rho^{i}}{(1 + \rho)^{i}} \right].$$  \hspace{1cm} (5)

The value of $(1 - \rho^{i})/(1 + \rho)^{i}$ in equation (5) when $i=1$ is equal to that when $i=2$. The $H_{g}$ can be written as follows,

$$H_{g} = \frac{1}{2} \left( M_{1} + M_{2} \right) \left[ 1 + \frac{1 - \rho}{1 + \rho} \right] - \frac{1}{2} \sum_{i=3}^{s} M_{i} \left[ 1 + \frac{1 - \rho^{i}}{(1 + \rho)^{i}} \right]$$

$$= \frac{M_{1} + M_{2}}{1 + \rho} + \frac{1}{2} \sum_{i=3}^{s} M_{i} \left[ 1 + \frac{1 - \rho^{i}}{(1 + \rho)^{i}} \right].$$  \hspace{1cm} (6)

Since the numerical value of $H_{g}$ is determined predominantly by the first term on the right-hand side of equation (6) and this ratio is not greatly influenced by the value of $\rho$, the value of $H_{g}$ can be approximated by assuming the female flies to mate only once. Fig. 1 shows that there are only slight differences in the $H_{g}$'s resulting from multiple and single matings. The procedure outlined above, therefore, will be used in the discussions which follow.

When $M_{1}$ equals unity and $M_{2}$ to $M_{s}$ are zero, $H_{g}$ is given by:

$$H_{g} = 1/(1 + \rho).$$  \hspace{1cm} (7)

Let us, then, examine the maximum density of normal females which can be successfully eradicated with a given value of $N_{r}$. $N_{f_{(g+1)}}$ is given by the following equation in this model.

$$N_{f_{(g+1)}} = N_{f_{(g)}} R_{g} H_{g}. \hspace{1cm} (8)$$

Assuming that the population density does not change, that is, $N_{f_{(g+1)}} = N_{f_{(g)}}$, then

$$R_{g} H_{g} = 1. \hspace{1cm} (9)$$

From equations (7) and (9), $R_{g}$ is

$$R_{g} = 1/H_{g} = 1 + \rho. \hspace{1cm} (10)$$

Consequently $\rho$ satisfies the following relationship if the population density does not change from generation (month) to generation.

$$\rho = R_{g} - 1. \hspace{1cm} (11)$$

$R_{g}$ is given by

$$R_{g} = e^{rac{1 + \rho}{1 + N_{f_{(g)}} B}}. \hspace{1cm} (12)$$

Then

$$\rho = \frac{e^{rac{1 + \rho}{1 + N_{f_{(g)}} B}} - 1}{1 + N_{f_{(g)}} B}. \hspace{1cm} (13)$$

From equation (13), $\rho$ can be calculated for given values of $N_{f_{(g)}}$ (Fig. 3). As the sex ratio is assumed to be 0.5, $\rho$ can be written as

$$N_{r}/N_{f_{(g)}}. \hspace{1cm} (14)$$

If we assume that $N_{r}$ is a fixed number during the course of an SIRM project, we can calculate $N_{f_{(g)}}$ at a constant density from equations (13) and (14). Lines expected from equation (14) are also plotted in Fig. 3 for different values of $N_{s}$. $N_{s}$ is the number of sterile males when the line of equation (14) is tangent to the curve of equation (13). The calculated value of $N_{s}$ was 786,821 (Fig. 3). It is apparent from Fig. 3 that there are two different values of $N_{f_{(g)}}$ which satisfy both the equations (13) and (14) simultaneously if $N_{r} < N_{s}$. Denoting these values by $N_{f_{1}}$ and $N_{f_{h}}$, the following population trends emerge:

- $N_{f_{1}}<N_{f_{h}}$ population decrease,
- $N_{f_{1}}<N_{f_{h}}<N_{f_{1}}$ increase,
- $N_{f_{h}}<N_{f_{1}}$ decrease.

Accordingly $N_{f_{1}}$ is a stable equilibrium and $N_{f_{h}}$ is an unstable equilibrium. Then the $N_{r}$ should be less than a critical point, $N_{f_{1}}$, for successful eradication. The calculated values of $N_{f_{1}}$ for $N_{s}$=62,500, 125,000 and 250,000 are 27,870, 57,787 and 125,133, respectively. Consequently, eradication should be attainable when $N_{f_{(g)}}$ is less than $N_{f_{1}}$ for each $N_{r}$, or $N_{f_{(g)}}$ becomes less than $N_{f_{1}}$ during the period in which density-independent decrease takes place. On the other hand, the stable equilibrium no longer exists if $N_{r}$ is greater than or equal to $N_{s}$. It is notable that $N_{s}$ is not particularly large; in our model it is only about 30 percent of $K$. Under these conditions, eradication can be attained even if the population is not reduced by density-independent factors.
It is of interest that these results are similar to those obtained by Miller and Weidhaas (1974) in the following aspects: (1) stable and unstable equilibria exist in the given $N_0$ and (2) a stable equilibrium does not exist if $N_t$ becomes greater than specified level. As the value of $H_e$ given by equation (7) is approximated and is slightly overestimated, the estimated $N_{f1}$ and $N_{se}$ tend to be slightly greater than the correct values. This may be the reason why the population initially increases when $N_t=250,000$ (see Fig. 2) even though $N_{f1(0)}$ is less than $N_{f1}$.

REFERENCE