SOME ANALYTICAL MODELS FOR BIOTECHNICAL METHODS OF PEST CONTROL

By

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ABSTRACT

A review of some simple analytical models for pest control is presented. The sterile insect release method is considered in detail, and models are also discussed for the release of sex pheromones to attract and kill insects. It is shown how these models apply to the control of fruit flies and new models appropriate to this control are suggested.

1. INTRODUCTION

The search for effective and acceptable means of insect pest control can be aided by mathematical models which explain and predict behaviour under certain assumptions. Such models supplement biological field and laboratory experiments, and can be used to guide experimentalists. This review focusses on simple, analytical, deterministic models which predict qualitative behaviour. Both discrete and continuous time variation are considered; the former probably being more appropriate to fruit flies with discrete non-overlapping generations.

Insecticides have not been a complete answer to the problem of insect pest control; although they are indeed useful as a component of integrated pest management (IPM). In particular, the sterile insect technique (SIT) has been used practically in many fruit fly control programs, for example for suppression and eradication of the Mediterranean fruit fly, Ceratitis capitata and the melon fly, Dacus cucurbitae. Theoretical models for this technique are reviewed in section 2. Pheromone traps are frequently used to survey and monitor pest populations, and their use in IPM has been suggested, (Silverstein, 1981). Models in which sex pheromones are released to attract and trap insects are reviewed in section 3. Both these methods are included under biotechnical methods of insect pest control (Boller, 1983), and may play an important role in IPM (Batra, 1982).

2. STERILE INSECT TECHNIQUE (SIT)

Knipling was the first to suggest and model this technique in which artificially sterilized insects are introduced into the pest population (Knipling, 1955) and the SIT has since been used successfully against several fruit fly species. Knipling's model assumes the insect has discrete non-overlapping generations and density independent geometric population growth. A 1:1 sex ratio is assumed, and a constant number n of sterile males are introduced which are assumed to be equally competitive with wild males. The difference equation governing the population growth is therefore

$$f_{t+1} = \lambda\ f_t\left(\frac{f_t}{f_t+n}\right) \tag{2.1}$$

where f_t = number of fertile females (= males) at time t and λ (with $\lambda > 1$) is the reproductive potential. This model predicts a critical number of introduced steriles $n_c \equiv (\lambda-1)f_0$ for control. When $n < n_c$ the population increases and escapes control, but when $n > n_c$ the population goes extinct. The overflooding ratio defined as n/f_0 must therefore be greater than $(\lambda-1)$ for control to be effective.

In discussions at this workshop it was agreed that as the irradiation dose used to sterilize fruit flies is increased, so their competitiveness greatly decreases. To examine these interrelating factors, let k (with $0 \le k \le 1$) be the residual fertility of males, that is the proportion of males which have been artificially sterilized but remain fertile, and let c (with $0 \le c \le 1$) be the competitiveness of sterile males compared to that of the wild males (for which the competitiveness is taken as unity). The difference equation governing the number of fertile females then becomes

$$f_{t+1} = \lambda \, f_t \left(\frac{f_t + kcn}{f_t + cn} \right), \tag{2.2}$$

giving

$$n_c = \frac{(\lambda - 1) f_0}{(1 - \lambda k) c} \, . \tag{2.3}$$

Thus the product of reproductive potential and residual fertility must be less than one for the SIT to be effective, and the number of steriles introduced must be large when their competitiveness is small. In a computer simulation (Klassen and Creech, 1971) incorporating these factors, it appears that, if the reproductive potential is large, then it is better to aim for a high level of sterility even if competitiveness decreases rather than a lower level of sterility without this decrease. The model above supports this qualitative result, but more detailed models are required to guide managers on this important practical question.

When density dependence is introduced into Knipling's model, the population is governed by the equation (Prout, 1978, Yamamura et al., 1978)

$$f_{t+1} = \lambda \, f_t \left(\frac{f_t}{f_t + n} \right) \Bigg/ \left[\frac{\lambda - 1}{K} \, f_t \left(\frac{f_t}{f_t + n} \right) + 1 \right], \tag{2.4}$$

where K is the carrying capacity which is the equilibrium population density when no steriles are present. This model has $n_c = (\lambda - 1)K/4$, with the population going extinct for $n > n_c$ and tending to a locally stable equilibrium in the interval $(K/2, K)$ for $n < n_c$. So, with a knowledge of the biological parameters λ and K, the number of steriles needed to cause extinction can be estimated. Note, that in contrast to the density independent model, this number is independent of the initial population.

In any practical SIT program there is the possibility of females which have already mated entering the region. This can be incorporated by considering the model (Prout, 1978)

$$f_{t+1} = \lambda\left(\frac{f_t^2}{f_t+n} + w\right) \Bigg/ \left[\frac{\lambda-1}{K}\left(\frac{f_t^2}{f_t+n} + w\right) + 1\right], \qquad (2.5)$$

where w is the number of immigrant fertilized females. For any $w > 0$ the model predicts that extinction is impossible, and for large w the effect of the SIT program is destroyed as steriles cannot substantially reduce the wild population.

The analogue of (2.4) for continuous population growth with density dependent deaths is (Barclay and Mackauer, 1980) the differential equation system:

$$\begin{aligned} \dot{f} &= a_1 f\left(\frac{f}{f+n}\right) - a_2 f - 2gf(f+n) \\ \dot{n} &= R - a_2 n - 2gn(f+n) \end{aligned} \qquad (2.6)$$

where $\cdot \equiv d/dt$, a_1, a_2 are density independent birth rate, death rate respectively, g is a crowding parameter $\propto 1/K$, R is the constant rate of release of sterile males ($\equiv$ sterile females), and the number of sterile females in the population is a variable. The biological assumptions of the model are discussed fully in the paper by Barclay and Mackauer and in a later paper by the first author (Barclay, 1984). This model predicts that, for small a_2/a_1, $R_c \simeq 2a_1^2/(27g)$. It shows that density dependence assists control in the SIT, and that the SIT is very effective for low population values, and thus can be an important part of an IPM program when the population has been reduced by other means, for example, insecticides. The inclusion of immigrant fertilized females in this model (with fixed n) can destroy the effect of steriles, as stated for the discrete case above. A generalization of this continuous model (Barclay, 1982) indicates again that male competitive ability is of primary importance in determining the outcome of the SIT with R_c being very large when this competitiveness is small.

For insects with several stages in their life cycle, the previous models must be extended. For a two-stage life cycle (Barclay, 1980) an extension of (2.6) shows that the SIT is favourable for species in which the larval stage is a problem, for example, fruit flies. Plant gives a theoretical study of the SIT to eradicate Ceratitis capitata taking age structure into account (Plant, 1986).

The sterile females of Ceratitis capitata also sting and damage fruit, and so it is vital to develop mechanisms for releasing sterile males only; genetic sexing is now feasible (Robinson, 1986). A continuous model for the release of sterile males only, which is a modification of (2.6), shows that the number of sterile males required to reach the critical level is about 20% higher than the number of males needed if both sexes are being released (Barclay and Mackauer, 1980). The release of sterile males only thus has great possibilities, and is a subject of current research.

Models discussed above have assumed no spatial variation, but in practical applications dispersion of insects may be important, for example, in the case of the olive fruit fly, Dacus oleae. As an attempt to incorporate spatial variation into the SIT model (Manoranjan and van den Driessche, 1985) consider a strip of territory surrounded by a hostile region. This is modelled by a reaction-diffusion equation and it is found that there is a critical strip width below which the population cannot sustain itself. Above this width the population is still unable to sustain itself unless the initial population is high enough. So the SIT can be evaluated as one component of an IPM program including, for example, crop cutting and insecticides.

3. PHEROMONES

For some insects, pheromones can be used to trap and kill one sex. For a species in which females emit pheromone which attracts males (for example, olive fruit fly, Dacus oleae) a model is constructed in which it is assumed that there are v_0 caged virgins (or pheromone equivalents) and that every male attracted to a cage is killed. This discrete, density independent model (Barclay and van den Driessche, 1983) is based on an earlier model (Knipling and McGuire, 1966). Assuming male polygamy and female monogamy, it has the form:

$$\begin{aligned} f_{t+1} &= \frac{sm_t v_t}{v_0 + v_t} + sf_t \\ v_{t+1} &= af_{t-T} + sv_t - \frac{sm_t v_t}{v_0 + v_t} \\ m_{t+1} &= af_{t-T} + \frac{sm_t v_t}{v_0 + v_t} \end{aligned} \qquad (3.1)$$

where f, v, m are the number of wild fertilized females, virgin females, males respectively, with $m \leq v_0 + v$, a is the birth rate, s the survivorship and T the developmental time from eggs to adults. This model predicts a critical value $v_{0c}(a,s)$ so that when $v_0 > v_{0c}$ extinction occurs, with the method being most effective against species with low a and s.

As with the SIT, control is found to be very difficult with the immigration of even a moderate number of fertilized females (Barclay, 1984). Density dependence can also be included in the model, and is found (Fisher et al., 1985) to confer considerable reduction in v_{0c}, especially for high a and s; in fact this is even more pronounced than in the SIT models.

For insects in which male-produced pheromone attracts only females, it is found (Barclay, 1983) that the dynamics of pest control by releasing this pheromone and so killing females are similar to those of model (3.1) except when females remate regularly. At this workshop (Howse, 1986) there was a report of a new male pheromone for *Ceratitis capitata* which attracts both male and virgin females. This has the potential for use as a pest control method for killing both sexes, and a theoretical model for the use of this pheromone in traps is needed.

4. CONCLUSIONS

The two biotechnical methods of pest control considered, namely the SIT and release of pheromones to trap insects, look promising, especially as components of an IPM program. Immigration causes difficulty in both techniques, and, in addition, male competitiveness and residual fertility are problems in the SIT. Pheromones are used extensively in trapping insects for monitoring, and the models in section 3 consider their use in mass trapping for insect pest control. At high density, pheromones disrupt mate-finding (Silverstein, 1981) and cause confusion, this feature needs to be incorporated in the mathematical models. It is vital that models are developed alongside experimental work, so that modellers can be provided with accurate details of and realistic data for a particular insect pest. The theoretical predictions should then be field tested, and the simple models extended for individual situations incorporating as many as possible of the important biological and environmental variables. In this way analytic models prove to be a useful tool to guide experimental scientists and managers.

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