

Robert McKelvey

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Information and Area-Wide Control in Agricultural Ecology

Marc Mangel

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Introduction and Motivations

Agricultural ecology is a topic which could take the entire period of time available for the Course in Mathematical Ecology offered at the ICTP. For that reason, one must carefully select topics in the lectures. The topics chosen for these lectures are motivated by questions concerning agricultural productivity in developing countries. Productivity is often hampered by pest insects, which may cause enormous crop losses during outbreaks. There is considerable need for predicting where and when outbreaks are likely to be severe and to be able to implement management strategies that are effective but not excessively costly. These sentiments are echoed in the United Nations Africa Relief Program, as reported in the *New York Times* on 2 June 1986. The UN General Assembly adopted an agreement on African recovery that included the following points concerned with agricultural development:

The immediate objective will be to cope with future emergencies and catastrophes through the following measures:

—To create and sustain national emergency preparedness;

from **Applied Mathematical Ecology**
(S.A. Levin, T.G. Hallam, and L.J. Gross,
editors). Springer-Verlag, Berlin 1989

still used. Thus, we should think of operations research as the scientific method applied to operational problems.

As part of their work, Morse and his colleagues developed what they came to call "hemibel thinking". A hemibel is the logarithm of 3 and the general objective of hemibel thinking is to look for big improvements through the introduction of analysis into an operational problem. Morse and Kimball (1946, p. 38) describe hemibel thinking as follows:

It is well to emphasize that these constants which measure the operation are useful even though they are extremely approximate; it might almost be said that they are more valuable *because* they are very approximate. This is because the successful application of operations research usually results in improvements in factors of 3 or 10 or more. Many operations are ineffectively compared to their theoretical optimum because of a single faulty component... when the "bottleneck" has been discovered and removed, the improvements in effectiveness are measured in hundreds or even thousands of per cent. In our first study of any operation we are looking for these large factors of possible improvement. They can be discovered if the constants of the operation are given only to one significant figure, and any greater accuracy simply adds unessential detail... Having obtained the constants of the operation under study in units of hemibels (or to one significant figure), we take our next step by comparing these constants. We first compare the value of the constants obtained in actual operations with the optimum theoretical value, if this can be computed. If the actual value is within a hemibel (i.e., within a factor of 3) of the theoretical value, then it is extremely unlikely that any improvement in the details of the operation will result in significant improvement. In the usual case, however, there is a wide gap between the actual and theoretical results. In these cases a hint as to the possible means of improvement can usually be obtained by a crude sorting of the operational data... In many cases a theoretical study of the optimum values of the constants will indicate possibilities of improvement.

Rephrased for the agricultural pest control problem, this quotation takes the following form. We are not particularly interested in describing the crop-pest interaction in excruciating detail. Instead, the objective is to identify the key processes and major strategies that will quickly improve yield. Rather than fine-tuning models, we are looking for large differences between theory and data, using the analysis to show how to increase the chance of success in the battle against agricultural pests.

The principles of hemibel thinking are as valid today as they were 40 years ago. Scientists who are aiding decision makers involved in problems of agricultural ecology should keep the hemibel principle in mind when developing models. It is worth noting, too, that hemibel thinking is at odds with much of the current philosophy concerning Integrated Pest Management (IPM). Models in the current IPM approaches are typically highly detailed computer models, in which insight concerning interactions can be obtained only after intensive computational expense. It is always helpful to try a simple model before developing such a complex model. In addition, the cost of such detailed models may be prohibitive in developing nations.

In the majority of pest problems, we gather information not for its own sake, but to decide if an action such as some kind of pest control should be taken. Determining the threshold for this action, particularly when there is uncertainty associated with the decision, is not an easy job. Plant (1986) gives a good discussion of uncertainty and the economic threshold for action in pest management problems. In general, in these lectures it will be assumed that the threshold for action has already been determined. The importance of proper government policy as a means

of avoiding disasters (see, e.g. the recent article on famine by Mellor and Gavian, 1987) can not be overstressed. Clark's lectures in this volume provide an example of how proper policy can be developed. Information transfer between the scientist and policy-maker is crucial, if scientific principles are going to be used in setting policy. It is essentially impossible to take too much care in insuring the effective transfer of scientific information.

Although it is very tempting to do so, one should not work on applied questions without a particular agricultural system and pest in mind. Most of the material presented in this chapter is concerned with methodology and the development of analytical tools, so that it will often appear that the problems are completely abstract ones. My own experience in problems of agricultural ecology comes from work on fruit flies of economic importance, such as the Mediterranean fruit fly or the apple maggot, and control of pests of cotton, particularly spider mites and lygus bug.

Modelling Pest Distributions

When considering a pest problem, the first thing that we need to know is the distribution and density of the damaging insect. To address these questions, consider a large region, of the order of perhaps hundreds of square kilometers, that is divided into cells and let A_i denote the area of the i th cell. The cells themselves might be of the order of square kilometers. For example, in California there are currently traps placed throughout the state for fruit flies of economic importance at a density of about one trap every 2.5 km². Let $N_i(t)$ denote the number of pests in cell i at the start of period t (if a discrete time formulation is used) or at time t (if a continuous time formulation is used). We are interested in the probability distribution of the vector $N(t) = \{N_i(t)\}$. This is defined by

$$p_i(n, t) = \text{Prob} \{N_i(t) = n\}. \quad (1)$$

Perhaps the simplest model is the Poisson distribution

$$p_i(n, t) = \exp(-\lambda(t)A_i)(\lambda(t)A_i)^n/n! \quad (2)$$

where $\lambda(t)$ is a parameter. The single parameter λ completely specifies the probability distribution, so that once it is known the entire distribution is known. The Poisson distribution has a very nice infinitesimal interpretation (which can also be used to derive Eq. (2)). Consider a small region $\Delta a \ll A$, where A denotes the area of a typical cell. Then Eq. (2) is equivalent to

$$\begin{aligned} \text{Prob} \{\text{no pest in } \Delta a\} &= 1 - \lambda(t)\Delta a + o(\Delta a) \\ \text{Prob} \{\text{one pest in } \Delta a\} &= \lambda(t)\Delta a + o(\Delta a) \\ \text{Prob} \{\text{more than one pest in } \Delta a\} &= o(\Delta a) \end{aligned} \quad (3)$$

where $o(z)$ represents terms such that $o(z)/z$ approaches 0 as z approaches 0. The parameter $\lambda(t)$ in the Poisson distribution can thus be interpreted as a proportionality constant relating the probability that a small region contains a pest and the size

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definition of conditional probability and Bayes's formula is required. Suppose that \mathcal{A} and \mathcal{B} are two possible outcomes of a probabilistic process. The conditional probability of \mathcal{A} given that \mathcal{B} has occurred is then defined by

$$\text{Prob}\{\mathcal{A}|\mathcal{B}\} = \text{Prob}\{\mathcal{A}, \mathcal{B}\} / \text{Prob}\{\mathcal{B}\}. \quad (6)$$

In this equation, $\text{Prob}\{\mathcal{A}, \mathcal{B}\}$ is the probability that both events occur and it is implicitly assumed that the probability that the event \mathcal{B} occurs is greater than 0. Rearranging Eq. (6) leads to

$$\text{Prob}\{\mathcal{A}, \mathcal{B}\} = \text{Prob}\{\mathcal{A}|\mathcal{B}\} \text{Prob}\{\mathcal{B}\} \quad (7)$$

and then noting that the roles of \mathcal{A} and \mathcal{B} can be interchanged in these equations leads to Bayes's theorem

$$\text{Prob}\{\mathcal{B}|\mathcal{A}\} = \text{Prob}\{\mathcal{A}|\mathcal{B}\} \text{Prob}\{\mathcal{B}\} / \text{Prob}\{\mathcal{A}\}. \quad (8)$$

Eq. (8) will turn out to be extremely important when we consider the analysis of information in pest control problems.

Suppose now that the parameter λ has a density function $f(\lambda)$ so that $f(\lambda)d\lambda$ is the probability that $\lambda \leq \lambda \leq \lambda + d\lambda$. The probability that $N_i(t)$ takes a particular value n is then found combining the conditional Poisson distribution with the density of λ so that

$$p_i(n, t) = \int [\exp(-\lambda(t)A_i)(\lambda(t)A_i)^n / n!] f(\lambda) d\lambda. \quad (9)$$

In order to easily implement Eq. (9), we want to choose a density $f(\lambda)$ that will easily integrate against the Poisson distribution. An appropriate density will be described momentarily. Before doing that it is worthwhile to briefly consider a sampling problem, in order to show how the framework developed thus far can be employed to obtain useful information about pest populations.

Suppose that an insect is distributed according to the Poisson distribution, but that the value of the Poisson parameter λ is unknown. In order to learn about the value of the parameter, we assume that cells are sampled and that the insect counts obtained through sampling are used to make inferences about the Poisson parameter. In particular, assume that in the i th cell λ has density $f(\lambda)$ and that when this cell is sampled, the number of insects discovered equals to n . (Assume for the time being that this sample information is perfect; it will be seen that this assumption is not crucial to the following argument.) We wish to compute the *posterior* (i.e., after sampling) density for λ , given the data that n pests were discovered in the sample. Let $f(\lambda|n)$ denote this density. Use of Bayes's theorem shows that

$$\begin{aligned} f(\lambda|n)d\lambda &= \text{Pr}\{\lambda \leq \lambda \leq \lambda + d\lambda | N_i(t) = n\} \\ &= \text{Pr}\{\lambda \leq \lambda \leq \lambda + d\lambda, N_i(t) = n\} / \text{Pr}\{N_i(t) = n\} \\ &= f(\lambda) [\exp(-\lambda A) (\lambda A)^n / n!] / \int f(\lambda) [\exp(-\lambda A) (\lambda A)^n / n!] d\lambda. \end{aligned} \quad (10)$$

Although it somewhat abuses notation, it is very helpful to adopt the convention that $\lambda \approx \lambda$ for the more exact relationship $\lambda \leq \lambda \leq \lambda + d\lambda$. This will be done

throughout the rest of the formulas, we should be able to do this easily. The density of the parameter. On v and α . This dens

$$f(\lambda; v, \alpha) = \exp(-\lambda)$$

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$$\Gamma(v) = \int_0^{\infty} \exp(-\lambda) \lambda^{v-1} d\lambda$$

From the definition (try it as an exercise)

$$\Gamma(v+1) = v\Gamma(v)$$

so that for integer v less than 1, Abramowitz (page 256, paragraph (13) and the formula worth owning!).

The information about doing what a density must integrate by the appropriate

$$\int \exp(-\alpha\lambda) \lambda^{v-1} d\lambda$$

The mean and variance equation gives

$$E\{\lambda\} = v/\alpha$$

$$E\{\lambda^2\} = (v/\alpha)$$

from which it follows that the CV of λ is $1/\sqrt{v}$. Also, note that the fact that one can hold v . Finally, note that the reader is encouraged to see the robustness of the gamma distribution

throughout the rest of the Chapter. From the viewpoint of implementation of these formulas, we should pick a density $f(\lambda)$ that will allow the integrals to be done easily. The density that is chosen is defined on $[0, \infty)$ for the range of values of the parameter. One choice for the density is the gamma density with parameters v and α . This density will be denoted by $f(\lambda; v, \alpha)$ and is

$$f(\lambda; v, \alpha) = \exp(-\alpha\lambda)\lambda^{v-1}\alpha^v/\Gamma(v) . \tag{11}$$

In this equation, $\Gamma(v)$ is the gamma function. For biologists who are not familiar with it, you can think of the gamma function in the same way that one thinks about the functions $\sin(x)$ or $\log(x)$. That is, the gamma function has one or more definitions, arises in particular situations, and has certain computational properties. The gamma function is defined by

$$\Gamma(v) = \int_0^{\infty} \exp(-t)t^{v-1} dt . \tag{12}$$

From the definition, we can show that the following recursion relationship holds (try it as an exercise!)

$$\Gamma(v + 1) = v\Gamma(v) \tag{13}$$

so that for integer values of its argument, $\Gamma(v + 1) = v!$. For values of the argument less than 1, Abramowitz and Stegun (1964) give an extremely accurate formula (page 256, paragraph 6.1.34). For values of the argument greater than 1, use Eq. (13) and the formula in Abramowitz and Stegun (which, by the way, is a book well worth owning!).

The information that $f(\lambda; v, \alpha)$ is a probability density provides an easy guide to doing what appear to be complicated integrals. That is, since a probability density must integrate to 1, one can integrate Eq. (11) over $[0, \infty)$ and multiply by the appropriate constants to show that

$$\int \exp(-\alpha\lambda)\lambda^{v-1} d\lambda = \Gamma(v)/\alpha^v . \tag{14}$$

The mean and variance of λ can be found by directly applying Eq. (14). Using this equation gives

$$\begin{aligned} E\{\lambda\} &= v/\alpha \\ E\{\lambda^2\} &= (v/\alpha)^2 + (v/\alpha^2) \end{aligned} \tag{15}$$

from which it follows that the variance of λ is v/α^2 and the coefficient of variation is $CV\{\lambda\} = 1/\sqrt{v}$. Note that the coefficient of variation approaches 0 as v increases. Also, note that the mean of the distribution is constant when v/α is constant, so that one can hold the mean constant while varying the shape through changes in v . Finally, note that the density peaks at $\lambda^* = (v - 1)/\alpha$, a value less than the mean. The reader is encouraged to verify all of these statements by sketching the shape of the gamma density for a few values of the parameters. If that's done, one can see the robustness of the distribution in terms of different shapes.

Using the gamma density in Bayes's formula leads to

$$\begin{aligned} \Pr\{\lambda \approx \lambda | n \text{ pests present}\} &= \frac{[\exp(-\alpha\lambda)\lambda^{v-1}\alpha^v/\Gamma(v)][\exp(-\lambda A)(\lambda A)^n/n!]}{\int [\exp(-\alpha\lambda)\lambda^{v-1}\alpha^v/\Gamma(v)][\exp(-\lambda A)(\lambda A)^n/n!]d\lambda} \\ &= \exp(-(\alpha + A)\lambda)\lambda^{n+v-1}(\alpha + A)^{n+v}/\Gamma(n + v) \\ &= f(\lambda | v + n, \alpha + A). \end{aligned} \tag{16}$$

This equation is an example of an *updating rule*: we begin with a prior idea about the distribution of the parameter, obtain information, and update the idea about the distribution of the parameter to obtain a posterior distribution. In this case, the prior idea is that λ follows a gamma distribution with parameters v and α , the information is that n pests were in area A , and the posterior distribution of the parameter is a gamma distribution with parameters $v + n$ and $\alpha + A$. Note that as long as some "positive" information is obtained, in the sense that $n > 0$, there is a reduction in uncertainty since the coefficient of variation of the posterior distribution ($1/\sqrt{n+v}$) is less than the coefficient of variation of the prior distribution ($1/\sqrt{v}$).

The main justification for choosing a gamma prior is that it works: we start with a gamma prior, use Poisson sampling, and end with another gamma distribution. Thus, we only need to keep track of the parameters of the distribution, rather than the distribution itself. Statisticians call the gamma a *conjugate prior* for the Poisson distribution (see, e.g. Berger, 1980 or DeGroot 1970 for a fuller discussion of Bayesian decision theory). There is a small "biological" story for the choice of a gamma prior: Suppose that the parameter of the Poisson distribution is proportional to the number $B(t)$ of pests and that the number satisfies a stochastic differential equation (SDE) of the form

$$dB = B[r(1 - B/K)dt + \sigma dW]$$

where r, K and σ are parameters and dW is the increment in Brownian motion (see the Chapter by Riccardi, in vol. 17 of this series). Then the equilibrium distribution, defined as the $\lim_{t \rightarrow \infty} B(t)$, is often a gamma distribution. This kind of model would suggest that a gamma prior for the Poisson parameter is a reasonable choice.

The denominator in Eq. (16) is the probability that n pests are present in the region with area A . Doing the integrals and a little bit of algebra leads to the result

$$\begin{aligned} \Pr\{n \text{ pests present in region of area } A\} &= p(n, A) \\ &= (\Gamma(v + n)/n! \Gamma(v))(A/(\alpha + A))^n (\alpha/(\alpha + A))^v. \end{aligned} \tag{17}$$

This is the negative binomial (NB) distribution. It is computed using an algorithm similar to the one given for the Poisson distribution. That is, first set

$$p(0, A) = (\alpha/(\alpha + A))^v$$

and then use the iteration formula obtained directly from the definition in Eq. (17)

$$p(n + 1, A) = ((v + n)/(n + 1))(A/(\alpha + A))p(n, A). \tag{18}$$

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If N has a NB distribution given by Eq. (17), then the mean and variance of N are

$$\begin{aligned} E\{N\} &= (v/\alpha)A = m \\ \text{Var}\{N\} &= (v/\alpha)A + v(A/\alpha)^2 \\ &= m + m^2/v \end{aligned} \tag{19}$$

The parameter v , which is often denoted by k in the ecological literature, can thus be interpreted as an "over-dispersion" parameter in the following sense: When v is large, the mean and variance of the NB distribution are approximately equal so that NB distribution is essentially a Poisson distribution. (The more mathematically inclined reader may wish to consider the behavior of the gamma density when $v \rightarrow \infty$ and v/α is held constant.) When v is small, on the other hand, the variance of the NB distribution can be much larger than the mean. Because ecological data often involve variances that far exceed means, the NB distribution has enjoyed immense popularity in ecology. It is not without its problems, however, and some of these are discussed below.

From Eq. (19), the coefficient of N is given by

$$CV\{N\} = ((1/m) + (1/v))^{0.5} \tag{20}$$

This equation should be compared to Eq. (5). Since the mean of the NB distribution is proportional to the area A , as the sampled area increases, the mean m approaches ∞ and the coefficient of variation approaches a limit $v^{-0.5}$ which is non-zero and may be large when v is small. Thus, whereas for the Poisson distribution there was no limit on the relative accuracy of the sampling, for the NB distribution there is an inherent limit, determined by the over-dispersion parameter.

If Eq. (18) is rewritten in terms of m and k , a little bit of algebra shows that

$$\begin{aligned} p(n, A) &= p(n; m, k) \\ &= [\Gamma(k+n)/n! \Gamma(k)] (m/(k+m))^n (k/(k+m))^k \end{aligned} \tag{21}$$

The $p(n; m, k)$ form will be used in the rest of this chapter. A remarkable feature of the NB distribution is the preponderance of zeroes when k is small. From Eq. (21),

$$\begin{aligned} p(0; m, k) &= \Pr\{N = 0 \text{ when } m \text{ and } k \text{ are the parameters of the distribution}\} \\ &= (k/(k+m))^k \end{aligned} \tag{22}$$

and this probability may be considerable, even if m is immense, if k is sufficiently small. For example, if $k = .09$ we obtain the following results:

$\log(m)$	$\Pr\{N = 0\}$
0	0.799
1	0.734
2	0.672
3	0.614
4	0.562
5	0.513

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The interpretation of these numbers is the following: If N has a NB distribution with parameters $m = e^5$ and $k = 0.09$ then the probability that a particular region may have 0 pests is slightly larger than 1/2, even though the mean of the distribution is about 150! This kind of behavior is highly desirable when modelling pest insects, because pests are often totally absent from most regions (thus giving many zeroes) yet are abundant "on the average" because of a few highly intense, localized outbreaks.

Estimation of the parameters m and k is important in any applied problem. It is easy to show that if we have collected a data set and \bar{m} and s^2 are the sample mean and variance, then \bar{m} is the maximum likelihood estimate (MLE) for the mean of the NB distribution. Estimation of k is a little bit trickier. Kendall and Stuart (1979, page 78) show how MLE estimates for k can be determined. Two simple methods, which may be sufficient in many applied problems, are the following. We can simply use the moments of the empirical distribution and match them to the moments of the NB distribution. Thus, set $m = \bar{m}$ and, in light of Eq. (19), set

$$k = m^2 / (s^2 - m) \tag{23}$$

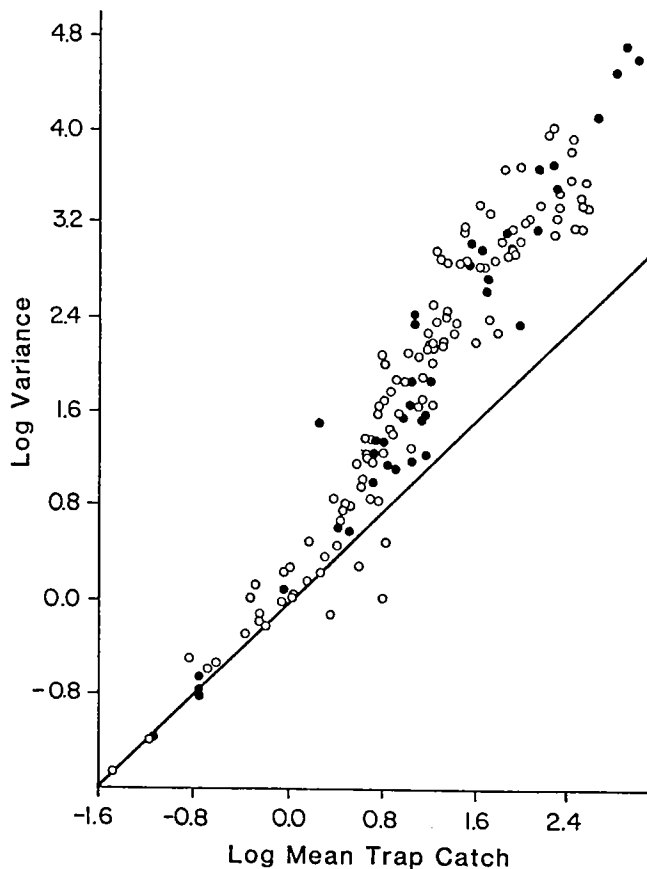
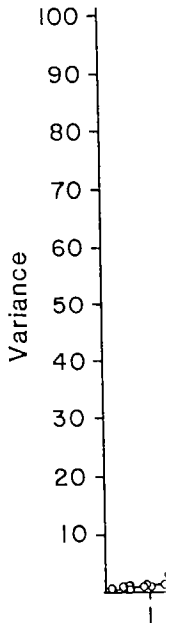


Fig. 1. P. Baker's data on medfly (*Ceratitis capitata* Wied) trapping. Open circles are Jackson traps, closed circles are delta traps



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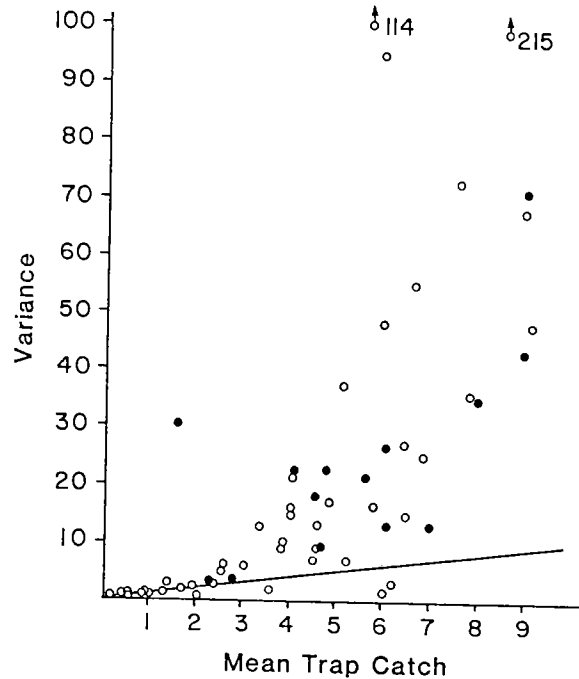


Fig. 2. P. Baker's data for small values of mean trap catch. Everything else is the same as in Fig. 1

as long as this equation makes sense (negative values of k , for example, are not allowed but may occur). Another approach is to rewrite the variance of N as

$$\log [\text{Var} \{N\}] = \log [(m^2/k)(1 + (k/m))] \tag{24}$$

so that for values of $k/m \ll 1$ one obtains

$$\begin{aligned} \log [\text{Var} \{N\}] &= \log (m^2/k) + \log (1 + (k/m)) \\ &= 2 \log (m) - \log (k) + o(k/m) \end{aligned} \tag{25}$$

where $o(z)$ represents a term such that $o(z)/z$ goes to 0 as z goes to 0. A plot of the logarithm of the variance against the logarithm of the mean of the distribution will lead to an estimate of k from Eq. (25).

An example of how actual pest count data appear, and how the NB distribution might be used is shown in Figures 1 and 2, using data collected by Peter Baker (1985) who was trapping fruit flies in Mexico. These figures show the variance of the trap catch as a function of the mean. We clearly see an increase in the variance as the mean increases; use of a simple NB model gives a value of $k \approx 2$.

Other Models for Aggregated Distributions

The NB is only one of a family of distributions that can be used to model aggregated populations. It is sometimes misused, perhaps because simple over-enthusiasm and the ease with which it can be applied. A number of authors (e.g. Taylor et al. 1979

Fig. 1. P. Baker's data on medfly (*Ceratitis capitata* Wied) trapping. Open circles are Jackson traps, closed circles are delta traps

or Perry and Taylor 1986) have chastened individuals who use the NB distribution too glibly. In particular, the value of k often depends upon the mean. Taylor et al. (1979) and Perry and Taylor (1986) suggest that k is a function $k(m)$ of the mean, given by

$$k(m) = m/[am^{b-1} - 1]$$

where a and b are parameters. Perry (1981) discusses parameter estimation for this relationship (The motivation for this choice of functional form, and the interpretation of the parameters will be discussed below.) Another problem with the NB distribution is that the value of k may depend upon the sampling scale and structure of the population, so that blind use of the NB (or any other distribution!) could lead to silly results. For example, the reader may wish to consider a problem with about 50–100 cells in which $N_i = i^\beta$ where β is a parameter (e.g. try $\beta = 0.5, 1, 1.5$). Simply computing the mean and variance leads to a picture of considerable overdispersion, but it is not random overdispersion at all. Rather, there is a clear pattern to the data. Further discussion of this point is given by Debouzie and Thioulouse (1986). The essential point, however, is to use the NB distribution thoughtfully and to be aware that there are a number of other models that can be used with equal facility as the NB, especially with the accessibility and easy use of modern, desktop computers.

Some of these alternate models will now be discussed. They are all computationally more complicated than the NB distribution. None of them, however, is so complex that it can not be used with a small, desktop microcomputer. Rapid advances in computer technology are likely to make it even easier to use these distributions.

The Neyman Type- A distribution is obtained by compounding one Poisson distribution with another. If N follows a Neyman type A with parameters λ and θ then

$$\Pr\{N = n\} = \sum_{j=1}^{\infty} [\exp(-\lambda)\lambda^j/j!][\exp(-j\theta)(j\theta)^n/n!]. \tag{26}$$

The probability of a 0 in this model is

$$\Pr\{N = 0\} = \exp[-\lambda(1 - e^{-\theta})] \tag{27}$$

and the mean and variance of N are

$$\begin{aligned} E\{N\} &= \lambda\theta \\ \text{Var}\{N\} &= \lambda\theta(1 + \theta) \end{aligned} \tag{28}$$

so that it is clear that we can, by appropriate choice of the parameters, make the variance greatly exceed the mean.

A second class of contagious models are *urn models*. For pest control problems, they can be phrased as models involving an “occupancy approach”. The typical urn problem would be phrased as follows. We start with a mixture of “white” balls and “black” balls. Let $W(t)$ and $B(t)$ denote the number of white and black balls after t “drawings” or “samplings”. The sampling rules are the following:

1. A single ball is removed. This is the sample.
2. One adds $\alpha + 1$ balls of the same color and β balls of the opposite color.

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Although this is apparently a simple problem, its analysis is actually quite difficult. Feller (1968) provides a good introduction to urn problems. The paper by Bernard Friedman (Friedman 1948) is a gem of applied mathematics and still well worth reading. Two properties of urn models of special note are:

1. For the simple urn model just formulated, initial fluctuations drive the final outcome. That is, if one considers the proportion of white balls $p(t) = W(t)/(W(t) + B(t))$ as t increases, the distribution of $p(t)$ approaches a uniform distribution on $[0, 1]$. The behavior of a particular sample path is virtually completely determined by the first 10 or 20 samplings (subject to the values of α and β , of course). There is thus no "equilibrium" in the sense that all points in the (W, B) phase space are ultimately attracted to the same point.
2. A special case of the general urn problem is the Polya urn, in which $\beta = 0$. Under appropriate conditions, the Polya urn has a NB limiting distribution. This limit applies to the situation in which

$$\begin{aligned} W(0)/(W(0) + B(0)) &\rightarrow 0 \\ (\alpha + 1)/(W(0) + B(0)) &\rightarrow 0 \end{aligned}$$

and the number of samples $T \rightarrow \infty$ in such a way that

$$\begin{aligned} TW(0)/(W(0) + B(0)) &\rightarrow \theta \neq 0 \\ T(\alpha + 1)/(W(0) + B(0)) &\rightarrow \rho \neq 0. \end{aligned}$$

Under these conditions, the limiting distribution of the Polya urn is negative binomial (see Johnson and Kotz 1969 for further discussion).

The limiting distribution actually has a nice biological interpretation for the development of aggregation. As an example, consider how an aggregated distribution of insect eggs might arise. Suppose that as insects encounter possible habitats for their eggs they follow the rule of sampling a small volume of the habitat and, if they discover other eggs, adding some of their own eggs to those already present. (The basic idea here is that if other eggs are present, a previous female has decided that this is an acceptable habitat.) With the exception of having to add a description of the first insect that lays its eggs in the habitat, the description just given follows the spirit of a Polya urn model.

A third, and quite general model, for aggregation is known as *Taylor's power law*. It arises out of the statistical analysis of the relationship between the mean and variance of pest sampling data. If m and s^2 denote the sample mean and variance, we fit a relationship of the form (see Taylor et al. 1979 for more details)

$$s^2 = am^b \tag{29}$$

where a and b are parameters. These parameters are then used with a particular probability distribution. For example, if the pest distribution follows a NB model, then the mean and variance are related by the formula $\text{Variance} = m + (m^2/k)$. Using equation (29) gives a method for finding a functional form for the overdispersion parameter k as a function of the mean. This is the equation given previously.

Pest Growth and Movement

The picture established thus far is a large region, divided into cells with $N_i(t)$ denoting the number of pests in cell i at the start of period t . In the absence of any control actions, the values of $\{N_i(t+1)\}$ will be determined by growth and movement of the pest populations. These are both complicated processes and each has been modelled in several different ways (see, e.g. Hargrove 1981, Minogue and Fry 1983, Rogers 1979, Sawyer and Haynes 1985, 1986 or Taylor 1986). The purpose of this section is simply to state the assumptions that will be used in the next two or three sections on trapping and control.

In most applied problems, we want to be able to detect and control the pests at a relatively low population level, so that density dependent effects can be ignored. This leads to mathematically simple relationships (which are thus somewhat uninteresting to mathematicians!), simplifies much of the further analysis, and makes parameter estimation easier. Thus, in the absence of any movement, we might assume that

$$N_i(t+1) = r_i(t)N_i(t) \quad (30)$$

where $r_i(t)$ is the growth rate for the pest population in cell i during period t . We could easily incorporate more complicated growth models, with density dependence, if there is evidence for their need.

Movement is a little bit trickier to characterize. Small scale or local movements of the pest can often be effectively described by some kind of random walk or diffusion model (see, e.g. Broadbent and Kendall 1953, Gillis 1956 for "classic" work or Kareiva and Shigesada 1983, Root and Kareiva 1984 or Sawyer and Haynes 1985, 1986 for more recent work). Sometimes large scale motion can also be modelled using diffusion models. Although random walk models provide nice qualitative pictures for insect movements, there are even some difficulties with these models as descriptions of short scale movement. For example, Kareiva and Shigesada (1983) show that the actual movement of butterflies is wider ranging than the movement predicted by a random walk model. That is, the actual movement is more diffuse than the random walk.

In agricultural pest control problems, we are more likely to be interested in large scale movements of pests. Large scale movements are often driven by factors such as wind or the movements of animals and people that carry the pest (intentionally or not). In this case, wind patterns and roadway maps may provide the best information about the movement of pests. There is a paucity of data on the large scale movements of pests of interest in agricultural problems. Taylor (1986) provides one of the best descriptions of large scale movement. In general, however, we must tailor the movement model to the problem of interest.

Trapping and Information

In this section, a variety of trapping models are developed for the analysis of trapping for information, rather than control. (Also see Janesen and Metz, 1979;

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Mangel, 1985, 1986; Mangel et al., 1984; McClendon et al., 1976; Metz et al., 1983, and Plant and Wilson, 1985).

As a motivation for the development of mathematical models, it is worthwhile to consider the experiments of Cunningham and Couey (1986) in which large numbers of marked Mediterranean fruit flies were released at differing distances from a single trap in an orchard. The proportion of flies released r feet from the trap and captured by the trap was measured. Cunningham and Couey found an almost perfect fit of their data to the formula

$$q(r, t) = A(t) \exp(-B(t)r) \tag{31}$$

where $q(r, t)$ is the proportion of flies released r feet from the trap and captured by time t , and $A(t)$ and $B(t)$ are parameters. Cunningham and Couey found that $A(24 \text{ hrs}) = 0.6527$, $B(24 \text{ hrs}) = 8.637 \times 10^{-3}$ and that $A(\infty) = 0.6970$, $B(\infty) = 6.723 \times 10^{-3}$ where " ∞ " is understood to mean the total trapping period, which ended when no more flies were captured. Note that $A(t) < 1$ means that flies released at the trap were not necessarily captured. There is even anecdotal evidence that fruit flies may enter certain kinds of traps, fly around inside them and then exit! An interesting open question is what kind of movement models lead to functional forms such as Eq. (31)? I will briefly discuss a model for these experiments at the end of the next section.

The "Classical" Trapping Problem and Its Extensions

As a first model of a trapping consider an approach based on partial differential equations or difference equations (Jansen and Metz, 1979; Mangel, 1986). Although this method usually turns out to be computationally impracticable, it is a good starting point. The experimental region is represented by a square of length L and the trap is located at the center of the square. Associated with the trap is a "trap radius" r_t with the property that if distance between the pest and the center of the square is less than r_t , then the pest is trapped. We can define a probability density for an untrapped pest as follows:

$$f(x, y, t) dx dy = \Pr \{ \text{at time } t \text{ the pest is in the small area } dx dy \text{ around the point } (x, y) \text{ and is not trapped} \} \tag{32}$$

The equation that $f(x, y, t)$ satisfies is determined by the movement model. Two models are the diffusion model and the large deviation model of motion. The biological assumption behind the diffusion model is that in a small interval of time the pests are likely to move, but only a short distance. The distribution of displacement in a short interval of time Δt is assumed to be Gaussian with mean displacement $0 + o(\Delta t)$ and variance $D\Delta t + o(\Delta t)$. In this case, the the equation that $f(x, y, t)$ satisfies is

$$\partial_t f = (D/2) \{ \partial_x^2 f + \partial_y^2 f \} \tag{33}$$

where $\partial_i f$ denotes the partial derivative of $f(x, y, t)$ with respect to the i th variable, $\partial_i^2 f$ denotes the second partial derivative and D is the diffusion coefficient.

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An alternative to the diffusion model (in which the movement is implicitly small scale) is a large deviation model. The assumption here is that it is possible for the pest to make a large movement in a short interval of time. We thus explicitly specify the size and the probability of a displacement. In this case, the appropriate equation for $f(x, y, t)$ is (e.g. Knessl et al., 1984)

$$f(x, y, t) = \sum \sum f(x - \epsilon_i, y - \epsilon_j, t - \Delta t) \rho(\epsilon_i, \epsilon_j | x - \epsilon_i, y - \epsilon_j) \quad (34)$$

where $\rho(u, v | x, y)$ is the probability of taking a jump of size (u, v) from the point (x, y) , (ϵ_i, ϵ_j) is the size of the jump taken and the summation extends over all points in the region of interest. Although they may appear formidable, Eq. (33) and (34) are easily derived. Consider, for example, Eq. (34). We ask: what is the probability that a pest is around the point (x, y) at time t ? The answer is this: to get to (x, y) at time t , the pest could have been at some point (u, v) at time $t - \Delta t$ and taken a jump $(x - u, y - v)$ in the interval Δt . Summing over all possible u and v gives Eq. (34). Equation (33) can then be derived by a Taylor expansion of Eq. (34), assuming that only small jumps occur. The reader is encouraged to try such an expansion.

In order to solve Eqs. (33) or (34) initial and boundary conditions are needed. If the pest is uniformly distributed in the region when $t = 0$, the appropriate initial condition is $f(x, y, 0) = 1/(L^2 - \pi r_t^2)$. Since the pest is trapped upon entering the trap radius, one boundary condition is $f(x, y, t) = 0$ when $x^2 + y^2 = r_t^2$. The boundary condition at the edges of the square is more difficult. If there is a single trap, then the only other condition that can be reasonably applied is that $f(x, y, t)$ is bounded for $x, y \rightarrow \infty$. Alternately, we might assume that if the pest leaves the square under consideration, it enters another square of size L with a trap at the center. In such a case, a reflecting condition is appropriate; that is, the normal derivative of $f(x, y, t)$ vanishes on the boundary of the square.

The geometry of this problem, a square region with a circular internal boundary, makes it extremely difficult to solve. As an approximation, one can replace the square by a circle of radius R . There are at least three good choices for R : one can inscribe the square of side L in a circle of radius R , circumscribe the square in a circle of radius R , or choose R so that areas are equal. Each of these has an operational interpretation which is left to the reader as an exercise.

If we choose to use an exterior boundary that is a circle, it is natural to switch to polar coordinates. Then, for example, $f(x, y, t) = f(r, t)$ (assuming radial symmetry) and the full problem associated with Eq. (33) is

$$\begin{aligned} \partial_t f &= D(1/r) \partial_r (r \partial_r f) \\ f(r_t, t) &= 0; \quad \partial_r f|_{r=R} = 0 \\ f(r, 0) &= \begin{cases} 1/(\pi(R^2 - r_t^2)) & \text{if } r > r_t \\ 0 & \text{otherwise} \end{cases} \end{aligned} \quad (35)$$

The solution of this problem, and numerous variants of it, can be looked up in Chapter 13 of Carslaw and Jaeger (1959).

As appealing as this approach may be, there are a number of difficulties with the classical trapping problem. Some of the most important ones are:

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- *Intercell movement* trapped by a trapping program becomes attracted from

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- *Imperfect trapping*: In most operational situations, it is likely that pests are not always trapped when they enter a trap, but the classical procedure assumes perfect trapping.
- *Nonconstant coefficients*: The classical model assumes that the diffusion coefficient (and drift coefficient, if there is one) are constant over space and time. This is likely not to be the case.
- *Intercell movement*: The classical model assumes that a pest in cell i can not be trapped by a trap in cell j . This assumption will often be violated in real trapping programs because pests can move freely across boundaries of cells and may be attracted from one cell to another by the presence of distant traps.

There are ways to incorporate these ideas into the classical trapping problem. For example, define

$$\Psi(x, y, z) dt = \Pr \{ \text{pest is trapped by one of } N \text{ traps during the interval } (t, t + dt) | \text{at time } t \text{ the pest is located at } (x, y) \text{ and the vector of trap locations is } \mathbf{z} \} . \quad (36)$$

The vector of trap locations is understood in the following way:

the vector $\mathbf{z} = (z_{x1}, z_{y1}; z_{x2}, z_{y2}; \dots z_{xN}, z_{yN})$ where (z_{xi}, z_{yi})

is the center of the i th trap. Two models for the trapping function are the following:

$$\Psi(x, y, z) = \sum \delta(x - z_{xi}) \delta(y - z_{yi}) a_i \quad (37a)$$

where $a_i \leq 1$ is a trapping coefficient (with equality corresponding to perfect trapping) and $\delta(u)$ is the Dirac delta function. That is, trapping occurs with probability a_i if the pest enters the trap centered at (z_{xi}, z_{yi}) . A model similar to this one has been analyzed by Szabo et al. (1984) for problems related to partial trapping of random walks in chemical physics.

Another model for the trapping function is

$$\Psi(x, y, z) = \sum a_i [q_i + (x - z_{xi})^2 + (y - z_{yi})^2]^{-v} \quad (37b)$$

where $a_i, q_i,$ and v are parameters. This model is chosen in analogy to certain detection formulas from search theory (Koopman, 1980) but has not been applied to problems in agricultural pest control.

With these trapping models, it can be shown (Mangel, 1981) that the probability density for the location of an untrapped pest now satisfies

$$\partial_t f = D(\partial_x^2 f + \partial_y^2 f) - \Psi(x, y, z) f \quad (38)$$

with the same initial condition. This equation can sometimes be solved by analytically, especially if we are willing to accept approximate techniques such as asymptotic methods (Mangel, 1981). Otherwise, numerical methods are needed.

Rosenstock (1980), in a paper on problems of trapping chemical physics, gives formulae for the mean time to trapping for a random distribution of traps on a lattice. In particular, suppose that the pests execute some kind of random walk to nearest neighbors on a lattice and assume that a fraction q_i of the lattice points are traps. Rosenstock shows that the mean time until trapping is well approximated

by the value $(1/\pi q_i)(-\log(\pi q_i) + 1 - C)$ where $C = 0.577216$ is Euler's constant (see Abramowitz and Stegun, 1965).

Any of these models might be employed to analyze trapping data, such as the data developed by Cunningham and Couey. There are two main questions. First, how do such data arise from particular motion models? Second, given such trapping data, what should be done with the data? My colleague Richard Plant is currently working on an extension of a diffusion model, as a means of modeling the Cunningham and Couey data from "first principles". The extension works as follows. A pest located at the point (x, y) at time t may do one of two things between t and $t + \Delta t$: i) It may make a displacement that is normally distributed with mean 0 and variance proportional to Δt . If it moves, there is a certain probability of being trapped. ii) It may settle at the point (x, y) and stop moving. Plant assigns a probability to each of the choices and then derives an extension of Eq. (33). This model leads to a trapping curve similar to the one found by Cunningham and Couey. The model, however, does not explain the origin of the "move/stay" decision. Determining the behavioral origin of this decision is an interface of behavioral ecology (Krebs and Davies (1984)) and applied ecology.

Next consider what is done with trapping data, once it is obtained. For example, suppose that the probability that a pest is ultimately trapped given that initially it is r units away from the trap is $q(r) = Ae^{-Br}$ and that the trap center-to-center distance is L miles, so that each trap is at the center of a square that is L miles

Table 1. Values of q_L for varying R_M

R_M (miles)	q_L for	
	One day	Entire trapping period
0.01	0.48	0.55
0.02	0.36	0.44
0.03	0.28	0.35
0.04	0.21	0.29
0.05	0.17	0.23
0.06	0.13	0.19
0.07	0.11	0.16
0.08	0.086	0.13
0.09	0.071	0.11
0.10	0.059	0.096
0.20	0.016	0.027
0.30	0.007	0.012
0.40	0.0037	0.0066
0.50	0.0024	0.0043
0.60	0.0017	0.0030
0.70	0.0012	0.0022
0.80	0.00096	0.0017
0.90	0.00076	0.0013
1.00	0.00062	0.0011

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on a side. The probability q_L that a pest located anywhere in this cell is trapped is given by the average of $q(r)$ over the cell, so that

$$q_L = \iint A \exp(-B(x^2 + y^2)^{1/2}) dx dy / L^2$$

where the region of integration is $-L \leq x \leq L$, $-L \leq y \leq L$ and the factor L^2 in the denominator comes from $dx dy / L^2$ being the probability that a pest is located in the small area $dx dy$. Although q_L can be found numerically, an exact formula can be computed by replacing the square by a circumscribed circle, and inscribed circle, or a circle of equivalent area. Let R_M denote the radius of the circle of interest. Switching to polar coordinates and integrating by parts once gives the result

$$q_L = (2A/R_M^2) [(1/B^2) \{1 - e^{-BR_M}\} - R_M e^{-BR_M}/B].$$

Table 1 shows values of q_L computed in this manner. This table gives an idea of the efficacy of different trap spacings. It is useful for the analysis of information in trapping.

Analysis of Information in Trapping

This section is concerned with how to best analyze trap catch data to obtain as much information as possible (also see Plant and Wilson, 1985; Wilson et al., 1985). Questions about the analysis of information naturally lead to a Bayesian framework in which two related questions can be asked:

i) What can be said about population levels if there is no trap catch?

ii) What can be said about population levels if there is a positive trap catch?

Although a minor modification of question ii) includes question i), it is operationally useful to separate the two. The answers to these questions give information about the level of the pest population. A third question relates the population level or trap catch and the damage caused by the pest (e.g. Prokopy et al., 1982), but that will not be treated here. My opinion is that the third question is still essentially an experimental one.

Once again, consider a large region divided into cells in which the pest population in the i th cell has a negative binomial distribution with parameters m and k . In the analysis that follows, it is assumed that the overdispersion parameter is known (for example by analogy with other trapping situations) and, for pedagogic ease and simplicity, constant but that the mean m of the negative binomial distribution is not known. The objective of the analysis is thus to use the trap data to make statements about the possible values of m . (The analysis given here can be used with minor modification for the case in which the overdispersion parameter $k = k(m)$ as well.) Assume that

$$q_i = \Pr \{ \text{trapping a pest in the } i\text{th cell during the period} \\ \text{of interest} \mid \text{a pest is present} \}. \quad (39)$$

The value of q_i depends upon the number of traps in the cell, the efficacy of a single trap, and the length of the trapping interval. In principle, the q_i can be

computed from formulas such as Eq. (31). If the mean of the NB distribution takes the value $\mathbf{m} = m$, the trap distribution itself is negative binomial with parameters $q_i m$ and k . That is, the overdispersion parameter is the same, but the mean of the trapping distribution is the mean of the pest distribution times the probability of trapping. (This result can be verified most easily by noting that the trap distribution is obtained by compounding a binomial distribution with parameters N, q_i with a negative binomial distribution with parameters m, k . Use of generating functions, or simply slogging through the resulting summations, leads to the stated result.)

The probability of no trap catch in the i th cell during the interval of interest is thus

$$\Pr\{\text{no catch in the } i\text{th cell}\} = \{k/(k + q_i m)\}^k. \quad (40)$$

If the region of interest is divided into a total of C cells and we treat the trap catches in different cells as independent random variables, the likelihood of no trap catch in any of the cells is

$$\mathcal{L}_C(m) = \prod_{i=1}^C \{k/(k + q_i m)\}^k. \quad (41)$$

If all cells have the same trapping probability $q_i = q$ for all i , the likelihood becomes

$$\mathcal{L}_C(m) = \{k/(k + qm)\}^{Ck}. \quad (42)$$

The objective of a Bayesian analysis of the trapping information is the computation of the posterior density $f_p(m|0)$ for the mean of the negative binomial distribution, given no trap catch. Using Bayes's theorem gives

$$\begin{aligned} f_p(m|0)dm &= \Pr\{m \leq \mathbf{m} \leq m + dm | \text{no catch}\} \\ &= \frac{\Pr\{m \leq \mathbf{m} \leq m + dm, \text{no catch}\}}{\Pr\{\text{no catch}\}} \\ &= f_0(m)dm \mathcal{L}_C(m) / \int f_0(m) \mathcal{L}_C(m) dm \end{aligned} \quad (43)$$

where $f_0(m)$ is the prior density for the value of \mathbf{m} . It is used to summarize prior information about the value of the mean. For a situation in which there is little prior information, two reasonable choices are the *uniform prior* in which

$$f_0(m) = 1 \text{ for all values of } 0$$

and the *noninformative prior* in which

$$f_0(m) = [m(k + m)]^{-1/2}.$$

The uniform prior attributes equal prior weight to all values of \mathbf{m} . The noninformative prior (DeGroot 1970, Martz and Waller 1982) gives more prior weight to small values of \mathbf{m} . The non-informative prior is chosen, roughly, so that the data change only the position but not the shape of the posterior distribution. Neither of these is integrable on the interval $(0, \infty]$ and are thus called improper prior densities. It will be seen, however, that the posterior density given by Eq. (43) will be integrable.

Often, the posterior density itself is not of interest. Instead the interesting quantity is the probability that the mean \mathbf{m} is less than a threshold for action m_T

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(which is, at this point, assumed to be given exogenously). The appropriate posterior probability is

$$\Pr\{m \leq m_T | \text{no trap catch}\} = \int_0^{m_T} f_0(m) \mathcal{L}_c(m) dm / \int_0^\infty f_0(m) \mathcal{L}_c(m) dm. \quad (44)$$

When the uniform prior is used, the integrals can be done exactly, giving

$$\Pr\{m \leq m_T | \text{no trap catch}\} = 1 - [k/(k + qm_T)]^{ck-1}. \quad (45)$$

When the non-informative prior is used, the resulting integrals can be easily done numerically; a trigonometric substitution to convert the denominator to a finite domain integral. Table 2 shows the results of computations using this approach, for the uniform prior. A table such as this one allows us to interpret the trap catch.

The Bayesian approach is especially well suited for sequential decision problems in which traps are periodically inspected. For such sequential problems, the posterior density from period t becomes the prior density in period $t + 1$.

An alternative approach is based on likelihood arguments (Edwards 1972). In the absence of trap catch, the likelihood $\mathcal{L}_c(m)$ takes its maximum value when $m = 0$ and is a monotonically decreasing function of m . Although the maximum likelihood value of m is 0, we can construct confidence intervals directly from the likelihood function. Hudson (1971) provides an approximate method for doing this. The method consists of considering an interval of the form

Table 2. Probability that $m < 1$ for the uniform prior with $k = 2$ and no trap catch

Number of traps	Prob $\{m < 1\}$ for a trap spacing of		
	1 mile	0.5 mile	0.3 mile
10	0.010	0.040	0.107
20	0.023	0.080	0.208
30	0.032	0.119	0.297
40	0.043	0.156	0.377
50	0.053	0.192	0.447
60	0.063	0.226	0.510
70	0.074	0.258	0.545
80	0.084	0.289	0.614
90	0.094	0.319	0.657
100	0.104	0.348	0.696
200	0.197	0.576	0.908
300	0.281	0.724	0.972
400	0.356	0.820	0.992
500	0.423	0.883	0.997
600	0.483	0.924	0.999
700	0.537	0.950	~1*
800	0.585	0.968	~1
900	0.628	0.979	~1
1000	0.667	0.986	~1

*Here ~1 denotes values that exceed 0.9995

Table 3. Likelihood $\mathcal{L}_C(1)$ for different values of C (number of cells)

Trap Spacing (miles)	$\mathcal{L}_C(1)$ for		
	$C = 10$	$C = 100$	$C = 1000$
1	0.995	0.946	0.577
0.5	0.979	0.807	0.117
0.1	0.626	0.009	~0

$\{m: \mathcal{L}_C(m) \geq e^{-\beta} \mathcal{L}_C(\hat{m})\}$ where \hat{m} is the MLE and β is a parameter. Under relatively general conditions, Hudson shows that the choice $\beta = 2$ leads to likelihood intervals that are approximate 95% confidence intervals. For the situation of no trap catch, the MLE is $\hat{m} = 0$ with likelihood 1 so that the confidence interval is simply $\{m: \mathcal{L}_C(m) \geq e^{-\beta}\}$ and Hudson's method is easily applied. Table 3 shows likelihoods for various values of C and trap spacing.

Analysis of Information When There Is Trap Catch

Next consider the situation in which there is trap catch. The trap data can take two forms:

i) *Presence-absence data.* The trap information in this case is that C_p of the traps had pests (positive counts) and $C_n = C - C_p$ of the traps had no pests (negative counts). Kuno (1969) and Plant and Wilson (1985) discuss methods for presence-absence sampling that differ from the ones discussed here.

ii) *Actual counts.* In this case, the data consist of the actual trap counts, denoted by X_i which is the number of pests trapped in the i th cell.

The kinds of questions that we want to answer concern the information provided by the trapping (e.g., what can be said about the value of the mean m of the NB distribution) and what kind of action should be taken, given the information provided by the trapping.

The answers to these questions can be built up in a manner analogous to the methods used in the previous section. For simplicity of presentation, the case in which all $q_i = q$ will be the only one considered here. Extensions to differing q_i are relatively straightforward, but also are problem dependent.

For the case of presence-absence sampling, the likelihood function depends upon the value of q , m , C_p and C_n . It is given by

$$\mathcal{L}(m, C_p, C_n) = [k/(k + qm)]^{C_n k} [1 - (k/(k + qm))^k]^{C_p} . \quad (46)$$

The maximum likelihood estimate (MLE) for m is found by differentiating Eq. (46) with respect to m , setting the derivative equal to 0 and solving. This gives the MLE

$$\hat{m} = (k/q) [(1 + (C_p/C_n))^{(q/k)} - 1] . \quad (47)$$

Although appealing for its simplicity, the MLE given in Eq. (47) can be highly biased, in the sense that $E(\hat{m})$ may deviate considerably from the true value of the

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m that generates the data. Mangel and Smith (1989) describe ways of eliminating the bias in the MLE \hat{m} .

A second approach is to consider the likelihood ratio $\mathcal{R}(m_T, \hat{m})$ defined as the ratio of the likelihood of the threshold value of m to the MLE value of m . This ratio is easily computed. It suffers the same drawback as the MLE procedure itself in that using the MLE \hat{m} may be very misleading.

A third approach is to use a Bayesian procedure and derive a posterior distribution analogous to Eq. (43) using the likelihood function (46). This approach does not suffer from the biased nature of the MLE and also provides a very natural way for incorporating additional information.

For the situation in which actual trap counts are used, consider the question of estimating the population mean in a single cell. This is justified if the cells are assumed to be relatively large and thus trap counts in cells may be viewed as independent variables. The objective is then to estimate m_i (i.e., the value of the NB mean in the i th cell) and from this mean compute the distribution of the population vector $\{N_i\}$. Again for pedagogic ease, only one cell is considered, so that the subscripts can be dropped. Then the datum is that X pests were trapped in the cell, and we want to find the mean of the NB distribution that generates the trap catch in the cell. The NB distribution (21) can be reinterpreted as the likelihood $\mathcal{L}(m|x, q)$ that the mean m takes the value m , conditioned on the data that x pests were trapped when the trapping probability for a single pest is q .

Table 4. Likelihood of values of m relative to the MLE value when 6 flies are trapped with trap spacing 1 mile

m	Relative likelihood
500	5.56×10^{-3}
1500	0.230
2500	0.600
3500	0.853
4500	0.972
5500	0.999
6500	0.978
7500	0.931
8500	0.872
9500	0.811
10500	0.752
11500	0.694
12500	0.642
13500	0.593
14500	0.549
15500	0.510
16500	0.473
17500	0.440
18500	0.410
19500	0.383

Ignoring all of the terms in (21) that are independent of the value of m gives

$$\mathcal{L}(m|x, q) \propto (k + qm)^{-k} [qm/(k + qm)]^x. \quad (48)$$

The MLE for m is $\hat{m} = x/q$, a very natural result. Since the data X have a NB distribution, the MLE \hat{m} will also have a NB distribution. Bayesian methods using the likelihood (48) or general likelihood argument can now be applied to find the distribution of \hat{m} .

The likelihood function (48) is nearly flat for operational values of the parameters. For example, if $q = 0.0011$ (corresponding roughly the 1 trap/2.6 km² from the Cunningham and Couey curve), $k = 2$, and $x = 6$ flies trapped, then the MLE for m is $\hat{m} = 5455$, but values of m in the range [2000, 16,000] are roughly half as likely as the MLE value (Table 4 shows the likelihood ratio over a wide range of values of m .) This suggests that we should be wary about reporting point estimates to decision makers without confidence that the point estimate is very accurate. It is almost always better to report reasonable ranges for the values of the parameters of interest and let the decision makers determine how to use the information. To do otherwise is often recipe for double disaster. First, the decision maker may end up with a tremendous error because he or she did not consider the range of eventualities that could arise from the decision. (For example, the point estimate may indicate that the pest population is low and the decision is made accordingly when in fact the population is high—only a few pests were detected—with obvious consequences.) Second, the analyst loses credibility with the decision maker; this is often an irreplaceable loss.

Mangel et al. (1984) bring all of these ideas together in a study of the delimiting of pest infestations, with particular application to the medfly problem in California in the early 1980s.

Area Effects in Resistance Management and Sterile Insect Methods

In this section, two problems associated with area wide control of pests are considered. The first problem is the simultaneous management of resistance to pesticide and optimization of crop yield. In this case, the question is whether to treat only the region containing the crop with pesticide, or the entire region. The second problem concerns the effects of either incorrectly assessing the extent of a pest infestation or of external sources of pests when trying to control through the sterile insect method.

Managing Pesticide Resistance

The general difficulty in the management of pesticide resistance is the mixture of a renewable and non-renewable resource system. The crops are a renewable resource, however, susceptibility to pesticide is fundamentally an exhaustible

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resource since each time a crop is sprayed and insects are killed, some genetic selection for resistance occurs and thus some of the susceptibility to the pesticide is lost. The literature associated with management of pesticide resistance is considerable (e.g., Comins, 1977; Feder, 1979; Feder and Regev, 1975; Hall and Norgaard, 1973; Heuth and Regev, 1974; Kable and Jeffrey, 1980; Knipling, 1984; Lewis, 1981; May and Dobson, 1986; Moffitt and Farnsworth, 1981; Omer et al., 1980; Plapp et al., 1979 and Sawicki et al., 1978, 1980) and will not be reviewed here. Instead the basic scientific information needed for formulation of a simple model will be discussed and then the model developed.

In order to deal with the management of pesticide resistance, we must be consider some aspects of population genetics. In many cases we can use single locus, two allele models to describe resistance (e.g. Omer et al., 1980). The two alleles are the resistance allele (R) and the susceptible allele (r); three types of pests are homozygous resistant (RR) individuals, heterozygous (Rr) individuals, and homozygous susceptible (rr) individuals. Often, individuals with the susceptibility allele will be more fit in the absence of spraying. For example, growth rates and fecundity of Rr or rr individuals may be higher than those of RR individuals. On the other hand, the RR individuals will have a higher fitness when pesticide is applied, in the sense that for the same dose of pesticide fewer RR individuals are killed than Rr or rr individuals. If $k_i(d)$ denotes the fraction of type i individuals killed at pesticide level d (usually measured in parts per million, ppm, of pesticide) then $k_{RR}(d) < k_{Rr}(d) < k_{rr}(d)$ for virtually all doses. In general, for i fixed the $k_i(d)$ curves are sigmoidal functions of d , rising from 0% towards 100% as d increases. The percent kill is usually measured in a scale called *probits* in which 5 probits are 50% kill and $5 \pm x$ probits is $50\% \pm x$ -standard deviations of a normal (0, 1) random variable. For example, 6 probits is about 85% kill and 7 probits is about 97.5% kill.

In a population that is well mixed and at equilibrium, the evolution of the frequency of the alleles can be described by the Hardy-Weinberg formula (e.g. Emlen, 1984 or Roughgarden, 1979) which states that $RR:Rr:rr = p^2:2p(1-p):(1-p)^2$ where p is the frequency of the R allele. If $p(n)$ is the frequency of the R allele in generation n , then $p(n)$ satisfies the difference equation (Comins, 1977)

$$p(n+1) = [S_{RR}p(n)^2 + S_{Rr}p(n)(1-p(n))]/\mathcal{S} \quad (49)$$

where

$$\mathcal{S} = S_{RR}p(n)^2 + 2S_{Rr}p(n)(1-p(n)) + S_{rr}(1-p(n))^2 \quad (50)$$

and S_{ij} is the survivorship probability of an individual of genotype ij in generation n . Perhaps the most important aspect of the dynamics in Eq. (49) is that if $p(n)$ is small, then

$$p(n+1) \approx (S_{Rr}/S_{rr})p(n) + o(p(n)) \quad (51)$$

so that there is exponential growth or decay of resistance for small levels of resistance and the rate of growth or decay just depends upon relative survivorships. Omer et al. (1980) give firm evidence that the growth of resistance to a pesticide is a phenomenon that can be very well described by the simple dynamics just

described. May and Dobson (1986) analyze the rate of evolution of pesticide resistance and use an equation analogous to (51) to explain the relative constancy of the number of generations taken for a significant development of resistance.

The specific question of interest here is the role of refugia. That is, suppose that there are two regions. One of them (called the field) has crops in it and the other (called the pool) has natural vegetation that supports the pest. Suppose that the pest immigrates from the pool to the field. The question is: Do we treat both regions (area wide control) or just the region containing the crop. The answer must be determined by the pay-off in terms of crop yield:

Approach	Crop yield	Resistance
Area wide	Increase	Presumably increases
Crop only	May decrease	?

The role of analysis is to help develop methods that can be used to assess this trade-off. The following model is a variant of work done by Mangel and Plant (1983), Plant et al. (1985) and Stefanou et al. (1985). Imagine that the season is broken into discrete time periods, with $t = 1$ denoting the start of the season and $t = T$ denoting the end of the season. The crop dynamics are assumed to be

$$\begin{aligned} C(t+1, j) &= C(t, j)r_c(1 - \Delta(t)) \\ C(1, j) &= C_0 \end{aligned} \quad (52)$$

where C_0 is the initial crop biomass, $C(t, j)$ is the biomass of the crop at the start of period t in year j , r_c is the intrinsic growth rate of the crop and $\Delta(t)$ is the damage to the crop in period t caused by the pest. A simple model of this damage function might be

$$\Delta(t) = 1 - \exp(-\gamma(t)[X_{RR}(t) + X_{Rr}(t) + X_{rr}(t)]) \quad (53)$$

where $\gamma(t)$ is a measure of the damage that the individual pest can cause during period t and $X_{ij}(t)$ is the number of pests of genotype ij at the start of period t .

The astute reader will recognize that a number of implicit assumptions have been made in Eqs. (51)–(53). For example:

- *No density dependence for the crop:* In the absence of pests, the crop is assumed to grow exponentially throughout the season. This assumption is easily modified.
- *All pests do the same damage.* The damage function in Eq. (53) ignores all age structure (pests of different ages might have different levels of damage) and other complications of the pest population dynamics.

In a model of a particular pest-crop system, these assumptions would need careful study and validation. For a qualitative understanding of the problem, however, another assumption is helpful. Assume that there are only two types of pests: resistant (R) and susceptibles (S) (Mangel and Plant, 1983). Let $R_f(t, j)$ and $S_f(t, j)$ denote the population level of resistant and susceptible pests in the field at the start of period t in year j and let $R_p(t, j)$ and $S_p(t, j)$ denote the population levels in the pool. Assume that, as long as there is no spraying, the field provides a better

habitat for growth of the pest so that pests migrate from the pool to the field. Let $\mu(j)$ denote the fraction of resistant pests in the pool at the start of year j and let $I(t)$ denote the immigration to the field during period t . Assuming that the migration of the pests is independent of their resistance type, the number of pests moving from pool to field during period t is $I(t) = i(t)(R_p(t, j) + S_p(t, j))$ where $i(t)$ is the fraction of pests moving in period t . The dynamics within a year, in the absence of spraying thus become

$$\begin{aligned} R_f(t+1, j) &= \lambda_R R_f(t, j) + \mu(j)I(t) \\ S_f(t+1, j) &= \lambda_S S_f(t, j) + (1 - \mu(j))I(t) \\ R_p(t+1, j) &= \max [\gamma \lambda_R R_p(t, j) - \mu(j)I(t), 0] \\ S_p(t+1, j) &= \max [\gamma \lambda_S S_p(t, j) - (1 - \mu(j))I(t), 0] . \end{aligned} \tag{54}$$

In these equations, it is understood that $\lambda_R < \lambda_S$ so that in the absence of spraying susceptible pests grow faster than resistant pests and that $\gamma < 1$, so that the field is a superior habitat for the pests. The initial condition when solving Eq. (54) connects one year to the next. Assume that at the end of the growing season (period T) the crop is harvested and the pests in the field and pool mix. Let $R(T, j) = R_f(T, j) + R_p(T, j)$ denote the total population of resistant pests in period T in year j and let $S(T, j)$ denote the total population of susceptible pests in period T in year j . Assuming that the pests can only overwinter and breed in the pool, the initial conditions for Eq. (54) become

$$\begin{aligned} R_f(1, j) &= S_f(1, j) = 0 \\ R_p(1, j) &= r_0(R(T, j-1)) \\ S_p(1, j) &= s_0(S(T, j-1)) \end{aligned} \tag{55}$$

where $r_0(z)$ and $s_0(z)$ are fecundity functions. The other connection between years is through the fraction of resistant pests, $\mu(j)$. That is

$$\mu(j+1) = r_0(R_p(T, j)) / [r_0(R_p(T, j)) + s_0(S_p(T, j))] . \tag{56}$$

A spray schedule corresponds, in this model, to a sequence $U(j) = \{U_1, U_2, \dots, U_{T-1}; j\}$ where U_i is the spray level applied in period i in year j . From it, we compute the fraction of resistant and susceptible pests killed in period i . Thus, for example, if $S_f(t)$ were the susceptible population at the start of period t in the absence of spraying, after spray is applied the population level will be $S_f(t)k_S(U_i)$. The crop dynamics are still given by Eq. (52) and the damage function can still be modelled by Eq. (53), with an appropriate modification. All of these equations can now be combined to study the efficacy of different spraying strategies over years. To do this, define a crop-value function

$$V = \sum_{j=1}^H \delta^{j-1} C(T, j) \tag{57}$$

where H is the time horizon over which planning is done and $\delta \leq 1$ is a "discounting" factor that weights future crop yields. Note that if $\delta = 1$, then the crop yield in year H is as important as the yield in year 1.

The value function V depends upon many parameters in the model and upon

the control strategy U . A good way to view it, however, is that the underlying state variable in the model is $\mu(j)$. That is, the relatively complicated dynamics in Eqs. (54) and following are used to relate $\mu(j)$ and $\mu(j+1)$. Holding all parameters constant, including the spray strategy U , allows us to formally write $\mu(j+1) = F(\mu(j))$, where $F(\cdot)$ is determined through the dynamics of the pest. The appropriate initial condition is now that $\mu(1) = \mu_0$, assumed to be given. The value function can be determined in an iterative fashion (this is essentially the method of deterministic dynamic programming, without the optimization step). Let $V(x, y; U)$ denote the crop value function from year y to year H , given that $\mu(y) = x$ and that spraying strategy U is applied. First note that $V(x, y; U)$ satisfies the end condition that

$$V(x, H; U) = \delta^{H-1} C(T, H). \quad (58)$$

Second, note that for values of $y < H$, we can determine $V(x, y; U)$ iteratively. That is,

$$V(x, y; U) = \delta^{y-1} C(T, y) + V(F(x), y+1; U). \quad (59)$$

By iterating these equations backwards, we can study the value associated with a given spraying strategy.

The final step, which will not be taken here, would be to optimize over the spraying strategies (e.g. Plant, Mangel and Flynn, 1985). It is often better, however, to report the results of a broad range of strategies, than to simply report the "optimal" strategy. This is particularly true in a problem such as the one just described, since so many assumptions are used in the model. The importance of reporting ranges of options, and not just single "best" strategies, is as important here as it is in the estimation of pest populations.

Area-Wide Effects in the Sterile Insect Method

The basic idea of the sterile insect method (SIM) can be traced to a paper by E.F. Knipling (1955). In this section, area-wide effects associated with the SIM will be discussed; there are many other interesting topics that will not be discussed (e.g. Barclay (1980, 1982, 1987a, b), Barclay and MacKauer (1980), Berryman (1967), International Atomic Energy Agency (1984), Ito (1977), Ito and Kawamoto (1979), Ito and Koyama (1982), and Plant (1986)).

The basic idea of the SIM is to "dilute" the reproductive potential of a population by adding sterile insects, typically males, to the population. The method is most effective for insects which mate only once in their lives; if a sufficient number of sterile males is used, many females will mate with steriles and thus produce no offspring. If the population has a 1:1 sex ratio, then it is sufficient to track females only. Let $F(n)$ denote the number of females in generation n . If the population has non-overlapping generations and grows exponentially, in the absence of sterile males the dynamics of $F(n)$ are

$$F(n+1) = rF(n) \quad (60)$$

where r is the intrinsic growth rate of the population. The idea is to add sterile males to the population, until $r < 1$. In particular, if $S(n)$ denotes the number of sterile males released in generation n , the dynamics in Eq. (60) are replaced by

$$F(n+1) = r[F(n)/(F(n) + S(n))]F(n) \quad (61)$$

where the first two terms on the right hand side now represent the effective growth rate in the presence of sterile insects. Plant (1986) discusses more realistic models for the pest dynamics and SIM; the models used here, such as Eq. (61) are chosen mainly for pedagogic purposes.

The dynamical properties of Eq. (61) can be studied through its fixed points. Consider the case in which a constant number of sterile insects, $S(n) = S$, is released in each generation. The fixed point F of Eq. (61) satisfies

$$F = rF^2/(F + S) \quad (62)$$

so that there is a fixed point at $F = 0$ (not very surprising) and another fixed point at

$$F_u = S/(r - 1). \quad (63)$$

It is easy to demonstrate that the fixed point F_u is unstable in the sense that if the initial population $F(0) < F_u$ then $F(n)$ decreases towards 0 whereas if the initial population $F(0) > F_u$, the population grows without bound. (Recall the original dynamics are exponential growth and that a constant number of sterile insects are being released in each generation.) We now flip Eq. (63) around, to determine the minimum number of steriles that must be released S_t to have the population decrease from one generation to the next. This is called the threshold release level and is given by

$$S_t = F(n)(r - 1) \quad (64)$$

with the property that

$$\begin{aligned} < F(n) & \text{ if } S(n) > S_t, \\ F(n+1) = F(n) & \text{ if } S(n) = S_t, \\ > F(n) & \text{ if } S(n) < S_t. \end{aligned} \quad (65)$$

Another way of interpreting Eq. (65) is that $F(n) \rightarrow 0$ if $S(n)$ exceeds the threshold S_t in each generation, $F(n)$ stays constant if $S(n)$ equals the threshold S_t , and $F(n)$ grows if $S(n)$ is less than the threshold. Typical dynamics for the case of a constant, sufficiently large number of releases are that $F(n)$ decreases very slowly at first, but then the decrease in $F(n)$ accelerates with n (see Plant and Mangel 1987 for more details).

The value of $F(n)$ is thus extremely important in actual implementation of the SIM. In general, $F(n)$ will be determined by trapping, so that the first section of this chapter and this section are tied together through the operations of detection and control.

If the SIM is applied in a large region, it may again be worthwhile to divide the region into cells. Then let $F_i(n)$ denote the number of females in the i th cell at the start of generation n . Assume that the areas are sufficiently large to be treated independently and that the insects reproduce and then disperse. Let $G_i(n)$ denote

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the population level in the i th cell after reproduction but before dispersal. If $S_i(n)$ steriles are placed in the i th cell during generation n , then

$$G_i(n) = rF_i(n)^2/[F_i(n) + S_i(n)]. \quad (66)$$

The population in the i th cell at the start of generation $n + 1$ is then

$$F_i(n+1) = \mathcal{F}(G(n)) \quad (67)$$

where $G(n)$ is the vector $(G_1(n), G_2(n), \dots, G_C(n))$ and $\mathcal{F}(z)$ is the model for movement. The total population at the start of generation n is then $F_T(n) = \sum F_i(n)$, with the summation extending over all cells. In most SIM control programs, the total number of sterile insects available for use is limited. This adds one additional constraint that $\sum S_i(n) \leq S_T(n)$, where $S_T(n)$ is the total number of sterile insects available in generation n . A relatively complex stochastic optimization problem arises in a natural fashion: Minimize $E\{F_T(H)\}$ through choices of $\{S_i(n)\}$ where H is the time horizon. The problem is stochastic because of imperfect information obtained through trapping. In the real application of SIM, producing sterile insects may also be a major difficulty (see, e.g. Plant, 1986) especially for pests with low individual fecundity such as the tsetse fly.

Prout (1978) developed a number of elaborations of the SIM. Two of the most important are i) the SIM in populations with a carrying capacity and ii) the SIM when there is migration into the region being treated (that is, non-area wide treatment). In Prout's model with a carrying capacity, Eq. (60) is replaced by

$$F(n+1) = F(n)\{rK/(K + (r-1)F(n))\}. \quad (68)$$

The carrying capacity in this model is $F(n) = K$. If a fixed number of steriles S are released in each generation (Prout calls this "hard" release), then the dynamics are replaced by

$$\begin{aligned} F(n+1) &= F(n)\{F(n)/(F(n) + S)\}[rK/\{K + (r-1)F(n)(F(n)/(F(n) + S))\}] \\ &= rKF(n)^2/[K(F(n) + S) + (r-1)F(n)^2]. \end{aligned} \quad (69)$$

The fixed points F of this equation now satisfy the cubic equation

$$(r-1)F^3 - K(r-1)F^2 + KSF = 0. \quad (70)$$

Note that $F=0$ is always a solution of this equation. It is the only real solution as long as $K(r-1) < 4S$. If $K(r-1) > 4S$, there are two additional, real solutions of Eq. (70), with the middle root unstable.

Next, consider the effect of migration on the population with a carrying capacity. That is, assume that pests move into the region being treated with the SIM. Let M denote the number of migrants into the region in each generation. The dynamics for $F(n)$ then become

$$\begin{aligned} F(n+1) &= rK[F(n)^2 + M(F(n) + S)]/[K(F(n) + S) \\ &\quad + (r-1)(F(n)^2 + M(F(n) + S))] \end{aligned} \quad (71)$$

and the fixed points of this equation satisfy

$$(r-1)F^3 + (r-1)(M-K)F^2 + \{MS(r-1) + K(S-Mr)\}F = rKMS. \quad (72)$$

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Note that $F=0$ is no longer a fixed point of the system. The operational interpretation of this result is that when migration occurs, eradication can not be achieved solely through use of the sterile insect method.

In order to analyze Eq. (72), it helps to introduce scaled variables, in which the carrying capacity is used to nondimensionalize population levels. Set

$$\begin{aligned} x &= F/K \\ m &= M/K \\ s &= S/K \end{aligned} \tag{73}$$

so that Eq. (72) becomes

$$f(x; m, s) = (r-1)x^3 + (r-1)(m-1)x^2 + \{m(sr-s-r) + s\}x - rms. \tag{74}$$

The equilibria of the pest dynamics can now be determined by study of the bifurcations of the cubic equation (74). The following properties are determined (see Plant and Mangel, 1987, for more details):

i) When $m=0$ and $s < s_c = (r-1)/4$, the equation $f(x; 0, s) = 0$ has three solutions. One of them is the origin.

ii) When $m=0$ and $s > s_c$, the only solution of $f(x; 0, s) = 0$ is $x=0$ so that eradication is possible.

iii) If $s > s_c$ and m is slightly positive, the solution of $f(x; m, s) = 0$ shifts from the origin to a value of $x > 0$, so that eradication is not possible. As m increases, two additional real roots of the equation appear, so that there is a region of multiple steady states of the population. As m increases further, the only root of $f(x; m, s) = 0$ is a large one. The reader is encouraged to work out the details and to see how the bifurcations provide information about the population structure.

Conclusions

Hopefully, the reader has seen the wealth of interesting and challenging problems that arise in agricultural pest control. In recent years, a number of books on the subject of pest management have appeared (e.g., Huffaker and Rabb, 1984; Kogan, 1986; Conway, 1985; Curry and Feldman, 1987). The book of Curry and Feldman is closest to this paper in spirit and approach; it provides a natural departure point for continuing with the material presented here.

Different agricultural problems will require different, and often new, types of mathematics. Even so, it is possible to provide a few general guidelines which will help make the analysis and modelling as good as possible:

- Don't be tied down by what's been done before; think broadly and widely about the problem.
- Be prepared for the unexpected (see Holling, 1987), since a model is always a caricature of reality. It is easy to miss—especially on the first attempt—crucial driving factors.
- Get as close to the problem as possible by spending considerable amounts of

- time with the biologists who know the pest and crop and the decision maker who has the responsibility of choosing the action. Understand the biology of pest and crop and the sociology of policy making and try to integrate these in the analysis, as much as is possible. (Barrett, 1984).
- Build confidence. Often this is most easily done by listening and asking good questions, rather than acting as if you've got all the answers. Another way is to solve a "trivial" problem that is of interest to the people you're working with.
 - Be problem, not technique, oriented (Barrett, 1985). The objective of bringing analysis to agricultural problems is to be able to solve agricultural problems, not to find problems which fit a particular mathematical technique. Trying to force a problem into the form so that a favorite technique can be used is often recipe for disaster.

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Bibliography

Note: Not all of the references listed in this bibliography were cited in the text. They are included with the idea that they might be helpful to individuals who are trying to develop libraries associated with pest management

- Abramowitz, M., Stegun, I. (1964) Handbook of Mathematical Functions. Dover, New York
- Ackoff, R.L. (1979) The future of operational research is past. *Journal of the Operational Research Society* 30, 93
- Ackoff, R.L. (1979) Resurrecting the future of operational research. *Journal of the Operational Research Society* 30, 189
- Aluja, M., Liedo, P.F. (1986) Perspectives on future integrated management of fruit flies in Mexico. In: Mangel, M. (eds.) *Pest Control: Operations and Systems Analysis in Fruit Fly Management*. Springer, New York, pp. 9-42
- Anderson, J.R., Dillon, J.L., Hardaker, B. (1977) *Agricultural Decision Analysis*. Iowa State University Press, Ames, Iowa
- Ascher, W. (1977) *An Appraisal for Policy Makers and Planners*. Johns Hopkins University Press, Baltimore, Maryland
- Austin, J.E. (1981) *Agroindustrial Project Analysis*. Johns Hopkins University Press, Baltimore, Maryland
- Baker, P. (1985) *Medfly dispersal, attraction and trapping*. Final Report MOSCAMED Program, Tapachula, Mexico
- Barclay, H. (1980) Models for the sterile insect release method with concurrent release of pesticides. *Ecological Modelling* 11, 167
- Barclay, H. (1982) Pest population stability under sterile releases. *Research Population Ecology* 24, 405
- Barclay, H. (1987a) Models for pest control: complementary effects of period releases of steriles pests and parasitoids. *Theoretical Population Biology* (to appear)
- Barclay, H. (1987b) Combining methods of pest control: complementarity of methods and a guiding principles. *Natural Resources Modelling* (to appear)
- Barclay, H., Mackauer, M. (1980) The sterile insect release methods for pest control: a density dependent model. *Ecological Entomology* 9, 81

- Barfield, C.S., O'Neil, R.J. (1984) Is an ecological understanding a prerequisite for pest management? *Florida Entomologist* 67, 42
- Barrett, G.W. (1984) Applied ecology: An integrative paradigm for the 1980s. *Environmental Conservation* 11, 319-322
- Barrett, G.W. (1985) A problem-solving approach to resource management. *Bioscience* 35, 423-427
- Beddington, J.R., Free, C.A., Lawton, J.H. (1978) Characteristics of successful natural enemies in models of biological control of insect pests. *Nature* 273, 513
- Berger, J.O. (1983) *Statistical Decision Theory*. Springer, Berlin Heidelberg New York
- Berryman, A. (1967) Mathematical description of the sterile male principle. *Canadian Entomologist* 99, 859
- Broadbent, S.R., Kendall, D.G. (1953) The random walk of *Tricho-trongylus Retortaeformis*. *Biometrics*, December, pp. 460-467
- Carlson, G.A. (1970) A decision-theoretic approach to crop disease prediction and control. *American Journal of Agricultural Economics* 52, 216
- Carlson, G.A. (1977) Long-run productivity of insecticides. *American Journal of Agricultural Economics* 59, 543
- Carslaw, H.S., Jaeger, J.C. (1959) *Conduction of Heat in Solids*. Oxford University Press, Oxford, England
- Cavalloro, R. (ed.) (1983) *Fruit Flies of Economic Importance*. Balkema, Rotterdam, The Netherlands
- Cavalloro, R. (ed.) (1984) *Statistical and Mathematical Methods in Population Dynamics and Pest Control*. Balkema, Rotterdam, The Netherlands
- Cavalloro, R., Crovetto, A. (eds.) (1985) *Integrated Pest Control in Olive Groves*. Balkema, Rotterdam, The Netherlands
- Comins, H. (1977) The management of pesticide resistance. *Journal of Theoretical Biology* 65, 399
- Cunningham, R., Couey, H.M. (1985) Mediterranean fruit fly (Diptera: Tephritidae): Distance response curves to trimedure to measure trapping efficiency. *Environmental Entomology* 15, 71-74
- Curry, G.L., Feldman, R.M. (1987) *Mathematical Foundations of Population Dynamics*. Texas A&M University Press, College Station, Texas
- Day, R.H. (1965) Probability distributions of field crop yields. *Journal of Farm Economics* 47, 713
- Debouzie, D., Thioulouse, J. (1986) Statistics to find spatial and temporal structures in populations. In: Mangel, M. et al. (eds.) *Pest Control: Operations and Systems Analysis in Fruit Fly Management*. Springer, Berlin Heidelberg New York, pp. 263-282
- DeGroot, M.H. (1970) *Optimal Statistical Decisions*. Mc-Graw Hill, New York
- Dowell, R.V., Wange, L.K. (1986) Process analysis and failure avoidance in fruit fly programs. In: Mangel, M. et al. (eds.) *Pest Control Operations and Systems Analysis in Fruit Fly Management*. Springer, Berlin Heidelberg New York, pp. 43-65
- Edwards, A.W.F. (1972) *Likelihood*. Cambridge University Press, Cambridge, England
- Feder, G. (1979) Pesticides, information and pest management under uncertainty. *American Journal of Agricultural Economics* 61, 97
- Feder, G., Regev, U. (1975) Biological interactions and environmental effects in the economics of pest control. *Journal of Environment Economics and Management* 2, 75
- Feller, W. (1968) *An Introduction of Probability Theory and Its Applications*, vol. 1. Wiley, New York
- Feller, W. (1971) *An Introduction to Probability Theory and Its Applications*, vol. 2. Wiley, New York
- Friedman, B. (1948) A simple urn model. *Communications in Pure and Applied Mathematics* 2, 59
- Georghiou, G.P., Lagunes, A., Baker, J.D. (1983) Effect of insecticide rotations on the evolution of resistance. In: *Proceedings of the International Congress on Pesticide Chemicals*, Kyoto, Japan. Pergamon Press, London
- Georghiou, G.P., Taylor, C.E. (1977) Operational influences in the evolution of insecticide resistance. *Journal of Economic Entomology* 70, 653
- Gillis, J. (1956) Centrally biased discrete random walk. *Quarterly Journal of Mathematics (Oxford)* 2, 144-152
- Hall, D.C., Norgaard, R.B. (1973) On the timing and application of pesticides. *American Journal of Agricultural Economics* 55, 198
- Hargrove (1981) Tsetse dispersal reconsidered. *Journal of Animal Ecology* 50, 351

- Hassell, M.P. (1978) *The Dynamics of Arthropod Predator Prey Systems*. Princeton University Press, Princeton, New Jersey
- Hassell, M.P. (1980) Foraging strategies, population models and biological control: a case study. *Journal of Animal Ecology* 49, 603
- Hawkes, C. (1972) The estimation of the dispersal rate of the adult cabbage root fly (*Erioschia Brassicae* (Bouche)) in the presence of brassica crop. *Journal of Applied Ecology* 9, 617
- Holling, C.S. (1986) The resilience of terrestrial ecosystems: local surprise and global change. Chapter 10 in: Clark, W.C., Munn, R.E. (eds.) *Sustainable Development of the Biosphere*. Cambridge University Press, Cambridge, England, pp. 292-317
- Hudson, D.J. (1971) Interval estimation from the likelihood function. *Journal of the Royal Statistical Society* 33, 256-262
- Hueth, D., Regev, U. (1974) Optimal agricultural pest management with increasing pesticide resistance. *American Journal of Agricultural Economics* 56, 543
- Huffaker, C., Rabb (1984) *Ecological Entomology*
- International Atomic Energy Agency (Wagrammerstrasse 5, POB 100, A-1400, Vienna, Austria) (1984) *The Sterile Insect Technique for Tsetse Control or Eradication in Developing Countries in Africa*.
- International Institute for Applied Systems Analysis (Laxenburg Austria). (1980) *Expect the Unexpected: An Adaptive Approach to Environmental Management*.
- Ito, Y. (1977) A model of sterile insect release for eradication of the melon fly. *Dacus cucurbitae* Coquillett. *Appl. Ent. Zool.* 12, 303
- Ito, Y., Kawamoto, J. (1979) Number of generations necessary to attain eradication of an insect pest with sterile insect release method: a model study. *Researches in Population Ecology* 20, 216
- Ito, Y., Koyama, J. (1982) Eradication of the melon fly: role of population ecology in the successful implementation of the sterile insect method. *Protection Ecology* 4, 1
- Jansen, M.J.W., Metz, J.A.J. (1979) How many victims will a pitfall trap make? *Acta Biotheoretica* 28, 98
- Johnson, N.L., Kotz, S. (1969) *Discrete Distributions*. Wiley Interscience, New York
- Kable, P.F., Jeffrey, H. (1980) Selection for tolerance in organisms exposed to sprays of biocide mixtures: a theoretical model. *Phytopathology* 70, 8
- Kendall, M., Stuart, A. (1973) *The Advanced Theory of Statistics*, vol. 2. Griffin and Company, London, England
- Knessl, C., Mangel, M., Matkowsky, B.J., Schuss, Z., Tier, C. (1984) Asymptotic solution of the Kramers-Moyal equation and first passage times for Markov jump processes *Physical Review* A29, 3359
- Knipling, E.F. (1955) Possibilities of insect control or eradication through the use of sexually sterile males. *Journal of Economic Entomology* 45, 459
- Knipling, E.F. (1984) Influence of insecticide use patterns on the development of resistance to insecticides: a theoretical study. *Southwestern Entomologist* 9, 351
- Kogan, M. (1986) *Ecological Theory and IPM*.
- Koopman, B.O. (1980) *Search and Screening*. Pergamon Press, New York
- Krebs, J.R., Davies, N.B. (1984) *Behavioural Ecology*. Blackwell Scientific Press, Oxford
- Kuno, E. (1969) A new method of sequential sampling to obtain the population estimates with a fixed level of precision. *Researches in Population Ecology* 11, 127
- Levins, R., Wilson, M. (1980) *Ecological theory and pest management*. *Annual Review of Entomology* 25, 287
- Lewis, T. (1981) Pest monitoring to aid insecticide use. *Philosophical Transactions of the Royal Society of London* B295, 153
- Luttrell, C.B., Gilbert, R.A. (1976) Crop yields: random, cyclical or bunched? *American Journal of Agricultural Economics* 58, 522
- Mangel, M. (1981) Search for a randomly moving object. *SIAM Journal on Applied Mathematics* 40, 327
- Mangel, M. (1982) Applied mathematicians and naval operators. *SIAM Review* 24, 289
- Mangel, M. (1985) *Decision and Control in Uncertain Resource Systems*. Academic Press, New York
- Mangel, M. (1986) Trapping and fruit fly management. In: Mangel, M. et al. (eds.) *Pest Control: Operations and Systems Analysis in Fruit Fly Management*. Springer, Berlin Heidelberg New York
- Mangel, M., Clark, C.W. (1983) Uncertainty, search and information in fisheries. *Journal of the International Council for the Exploration of the Seas* 41, 93

- Princeton University Press,
 Control: a case study. *Journal of Applied Ecology* 9, 617
- of global change. Chapter 10 in *The Biosphere*. Cambridge University Press, Cambridge
- Journal of the Royal Statistical Society B 47, 101-114
- Increasing pesticide resistance. *Journal of Applied Ecology* 20, 216
- 1000, Vienna, Austria) (1984) *Developing Countries in Africa*. Oxford University Press, Oxford
- (1980) *Expect the Unexpected: The Case of the Curculionid*. Dacus cucurbitae. *Journal of Applied Ecology* 17, 216
- Evolution of an insect pest. *Journal of Applied Ecology* 20, 216
- Evolutionary ecology in the successful invasion of a new host. *Acta Biotheoretica* 28, 98
- New York University Press, New York
- Sprays of biocide mixtures. *Journal of Applied Ecology* 17, 216
- Chapman and Company, London, 1971
- Asymptotic solution of the Lotka-Volterra equations. *Physical Review A* 29, 1303-1306
- On the use of sexually sterile individuals. *Journal of Applied Ecology* 17, 216
- Evolution of resistance to insecticides. *Journal of Applied Ecology* 17, 216
- Krebs, J.R., Davies, N.B. (1981) *Ecology: A Population Biology Approach*. Prentice-Hall, Englewood Cliffs, New Jersey
- Population estimates with a fixed effort. *Journal of Applied Ecology* 17, 216
- Annual Review of Entomology 27, 1-22
- Transactions of the Royal Society of London B 285, 1-10
- Why? *American Journal of Applied Mathematics* 40, 327-330
- Journal of Applied Ecology 24, 289
- Academic Press, New York
- et al. (eds.) *Pest Control: Operations and Systems Analysis in Fruit Fly Management*. Springer Berlin Heidelberg New York
- Journal of the Royal Statistical Society B 47, 101-114
- Mangel, M., Carey, J.R., Plant, R.E. (1986) *Pest Control: Operations and Systems Analysis in Fruit Fly Management*. Springer, Berlin Heidelberg New York
- Mangel, M., Plant, R.E. (1983) Multiseasonal management of an agricultural pest. I: Development of the theory. *Ecological Modelling* 20, 1
- Mangel, M., Plant, R.E., Carey (1984) Rapid delimiting of pest infestations: a case study of the mediterranean fruit fly. *Journal of Applied Ecology* 21, 563
- Mangel, M., Smith, P.E. (1989) Presence-absence plankton sampling in fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* (to appear)
- Mangel, M., Stefanou, S., Wilen, J.E. (1985) Modelling *Lygus hesperus* injury to cotton yields. *Journal of Economic Entomology* 78, 1009
- Martiz, H.F., Waller, R.A. (1982) *Bayesian Reliability Analysis*. Wiley Interscience, New York
- May, R.M., Dobson, A.P. (1986) Population dynamics and the rate of evolution of pesticide resistance. In: *Pesticide Resistance: Strategies and Tactics to Management*. National Academy Press, Washington, DC, pp. 170-193
- McClendon, R.W., Mitchell, E.B., Jones, J.W., McKinion, J.M., Hardee, D.D. (1976) Computer simulation of pheromone trapping systems as applied to boll weevil population suppression: a theoretical example. *Environmental Entomology* 5, 799
- McPhee, W.J., Nestmann, E.R. (1983) Predicting potential fungicide resistance in fungal populations using continuous culturing technique. *Phytopathology* 73, 1230
- Mellor, J.W., Gavian, S. (1987) Famine: Causes, prevention, and relief. *Science* 235, 539-545
- Metz, J.A.J., Wedel, M., Anguio, A.F. (1985) Discovering an epidemic before it has reached a certain level of prevalence. *Biometrika* 39, 765
- Minogue, K.P., Fry, W.E. (1983a) Models for the spread of disease: model description. *Phytopathology* 73, 1168
- Minogue, K.P., Fry, W.E. (1983b) Models for the spread of disease: some experimental results. *Phytopathology* 73, 1173
- Moffitt, L.J., Farnsworth, R.L. (1981) Bioeconomic analysis of pesticide demand. *Agricultural Economics Research* 33, 12
- Morse, P.M. (1977) *In at the Beginnings: A Physicist's Life*. MIT Press, Cambridge, Mass
- Murdoch, W.W., Chesson, J., Chesson, P.L. (1985) Biological control in theory and practice. *American Naturalist* 125, 344
- Omer, S.M., Georghiou, G.P., Irving, S.N. (1980) DDT/pyrethroid resistance inter-relations in *Anopheles stephensi*. *Mosquito News* 40, 200
- Perkins, J.H. (1982) *Insects, Experts, and the Insecticide Crisis*. Plenum Press, New York
- Perry, J.N. (1981) Taylor's power law for dependence of variance on mean in animal populations. *Applied Statistics* 30, 254-263
- Perry, J.N., Taylor, L.R. (1986) Stability of real interacting populations in space and time: implications, alternatives and the negative binomial k_r . *Journal of Animal Ecology* 55, 1053-1068
- Plant, R.E. (1986) The sterile insect technique: a theoretical perspective. In: Mangel, M. et al. (eds.) *Pest Control: Operation and Systems Analysis in Fruit Fly Management*. Springer Berlin Heidelberg New York, pp. 361-386
- Plant, R.E. (1986) Uncertainty and the economic threshold. *Journal of Economic Entomology* 79, 1-6
- Plant, R.E., Wilson, L.T. (1985) A Bayesian method for sequential sampling and forecasting in agricultural pest management. *Biometrics* 41, 203
- Plant, R.E., Wilson (1986) A computer based pest management aid for San Joaquin valley cotton. In: *1986 Beltwide Cotton Production Research Conference Proceedings*
- Plant, R.E., Mangel, M. (1987) Modeling and simulation in agricultural pest management. *SIAM Review* 29, 235-262
- Plant, R.E., Mangel, M., Flynn, L. (1985) Multiseasonal management of an agricultural pest. II: The economic optimization problem. *Journal of Environmental Economics and Management* 12, 45
- Plapp, F.W., Browning, C.R., Sharpe, P.J. (1979) Analysis of rate of development of insecticide resistance based on simulation of a genetic model. *Environmental Entomology* 8, 494
- Pouliquen, L.Y. (1970) *Risk Analysis in Project Appraisal*. Johns Hopkins University Press, Baltimore, Maryland

- Prokopy, R., Hubbell, G.L., Adams, R.G., Hauschild, K.I. (1982) Visual monitoring trap for tarnished plant bugs on apple. *Environmental Entomology* 11, 200
- Prout, T. (1978) The joint effects of the release of sterile males and the immigration of fertilized females on a density regulated population. *Theoretical Population Biology* 13, 40
- Reutlinger, S. (1970) *Techniques for Project Appraisal Under Uncertainty*. Johns Hopkins University Press, Baltimore, Maryland
- Rodgers, D. (1972) Random search and insect population models. *Journal of Animal Ecology* 41, 369
- Rodgers, D. (1979) Tsetse population dynamics and distribution: a new analytical approach. *Journal of Animal Ecology* 48, 825
- Rosenstock, H.B. (1980) Absorption time by a random trap distribution. *Journal of Mathematical Physics* 21, 1643
- Roughgarden, J. (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. MacMillan Press, New York
- Sage, A. (1977) *Systems Engineering: Methodology and Applications*. IEEE Press, New York
- Sawicki, R.M., Devonshire, A.L., Rice, A.D., Moores, G.D., Petzing, S.M., Cameron, A. (1978) The detection and distribution of organophosphorous and carbamate insecticide resistant *Myzus persicae* (Sulx.) in Britain in 1976. *Pesticide Science* 9, 189
- Sawicki, R.M., Devonshire, A.L., Payne, R.W., Petzing, S.M. (1980) Stability of resistance in the peachpotato aphid *Myzus persicae* (Sulxer). *Pesticide Science* 11, 33
- Sawyer, A.J., Haynes, D.L. (1985) Simulating the spatiotemporal dynamics of the cereal leaf beetle in a regional crop system. *Ecological Modelling* 30, 83
- Sawyer, A.J., Haynes, D.L. (1986) Cereal leaf beetle spatial dynamics: simulation with a random diffusion model. *Ecological Modelling* 33, 89
- Shoemaker, C.A. (1981) Applications of dynamic programming and other optimization methods in pest management. *IEEE Transactions on Automatic Control* AC 26, 1125
- Stenseth, N.C. (1981) How to control pest species: application of models from the theory of island biogeography in formulating pest control strategies. *Journal of Applied Ecology* 18, 773
- Stern, V.M., Smith, R.F., van den Bosch, R., Hagen, K.S. (1959) The integrated control concept. *Hilgardia* 29, 81
- Stokey, E., Zeckhauser, R. (1978) *A Primer for Policy Analysis*. Norton, New York
- Squire, L., van der Tak, H.G. (1975) *Economic Analysis of Projects*. Johns Hopkins University Press, Baltimore, Maryland
- Szabo, A., Lamm, G., Weiss, G.H. (1984) Localized partial traps in diffusion processes and random walks. *Journal of Statistical Physics* 34, 225-238
- Taylor, L.R. (1971) Aggregation as a species characteristic. In Patil, G.P. et al. (eds.) *Statistical Ecology*. Pennsylvania State University Press, State College, Pennsylvania, pp. 357-377
- Taylor, L.R. (1986) Synoptic dynamics: migration and the Rothamsted insect survey. *Journal of Animal Ecology* 55, 1
- Taylor, L.R., Woiwod, I.P., Perry, J.N. (1979) The negative binomial model as a dynamic ecological model for aggregation, and the density dependence of k . *Journal of Animal Ecology* 48, 289
- Watson, T.F., Moore, L., Ware, G.W. (1975) *Practical Insect Pest Management*. Freeman, W.H., San Francisco, Calif
- Wellington, W.G. (1977) Returning the insect to insect ecology: some consequences for pest management. *Environmental Entomology* 6, 1
- Wickwire, K. (1977) Mathematical models for the control of pests and disease: a survey. *Theoretical Population Biology* 11, 182
- Wilson, L.T., Gonzalez, D., Plant, R. (1985) Predicting sampling frequency and economic status of spider mites on cotton. In: 1985 Beltwide Cotton Production Research Conference Proceedings
- Wolf, W.W., Kishaba, A.N., Toba, H.H. (1971) Proposed method for determining density of traps required to reduce an insect population. *Journal of Economic Entomology* 64, 872
- Wood, R. (1986) Control strategies designed to reduce the chance of resistance with special reference to tephritid fruit flies. In: Mangel, M. et al. (eds.) *Pest Control: Operations and Systems Analysis in Fruit Fly Management*. Springer, Berlin Heidelberg New York, pp. 399-438
- Yekutieli, P. (1981) Lessons from the big eradication campaigns. *World Health Forum* 2, 465