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MODELING AND SIMULATION IN AGRICULTURAL PEST MANAGEMENT*

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Abstract. This paper introduces some of the mathematical problems associated with the control of agricultural insect pests. The view advocated here is that since agricultural crops are managed biological systems, much of the applied mathematics developed for biological systems may be used in pest control. The problem is broken into three components: (1) strategy selection, (2) tactics selection, and (3) state estimation. The concept of strategy selection is illustrated through a discussion of the Sterile Insect Technique (SIT) as a means of population suppression. Tactics selection is illustrated by a discussion of the scheduling of pesticide applications. The concept of state estimation is illustrated through two examples. The first example is a discussion of sequential sampling for pests to determine if the pest density has crossed an economic threshold. The second example is a discussion of information provided by trapping for pests when trying to determine the extent of an infestation.

Key words. pest management, agriculture

AMS(MOS) subject classification. 92.02

1. Introduction. One of the most productive applications of mathematics in the biological sciences has been the modeling of populations. There is a rich and elaborate theory for single population dynamics (e.g. May (1981)), for predator–prey interactions (e.g. Hassell (1978)), for microevolution (e.g. Roughgarden (1979)), and even for ecosystem dynamics (e.g. Ulanowicz (1984)). Agricultural crop stands are basically managed ecosystems, and one of their principal management problems is the control of populations of pests that consume the crop. In devising strategies for the control of pest populations, pest management specialists have attempted to make use of the mathematical theories of population dynamics to aid them in their task. In this article we review applications of mathematics in insect pest management.

We do not intend to give a complete review of the literature; indeed, we are quite selective. Several reviews exist already. Ruesink (1976), Shoemaker (1982a), and Getz and Gutierrez (1982) provide an excellent access to the literature. A monograph edited by Huffaker (1980) describes in detail many recent applications of mathematical ideas in pest management. May (1974), (1981) and Hassell (1978) provide a detailed discussion of and access to the literature on analytical models in population dynamics and pest management. Our goals are to acquaint applied mathematicians with some of the problems of insect pest management, to show the wide variety of mathematical tools that are used in attacking these problems, and to express our views about the appropriate roles for mathematical models in the solution process.

Our opinion is shared by Logan (1982) who expresses it quite well in a recent review of the modeling of interactions of mite populations. (Logan's paper is in a volume that is, to say the least, off the beaten path of most mathematicians. The

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paper is an excellent one, though, and well worth the trouble that might be necessary to obtain it.) We feel that mathematical models may be called upon to play two roles, a descriptive one and a predictive one. Traditionally, analytical models have been used for the former role and simulation models for the latter. To be truly effective in an applied context such as agricultural pest control, modeling must be done at both levels, possibly linked by what Logan (1982) refers to as "composite" models. Analytical models by themselves do not provide solutions upon which detailed predictions may be based. Simulation models by themselves do not provide the insight into the system that is necessary to have confidence in the validity of the predictions.

Insects are commonly pests to agriculture, silviculture, or public health. In this article we concentrate on the agricultural case. The other cases are mathematically similar, but not identical. MacDonald (1965) provides an example of the application of mathematical modeling to medical pest management (actually it involves worms rather than insects); Ludwig et al. (1978) do the same for forest pest management. The agricultural ecosystem may be described schematically as shown in Fig. 1. The arrows indicate the primary directions of interaction between components. The pests, including insect pests, consume or damage the crop and are in turn attacked by natural enemies such as predators, parasites, and disease. The grower may intervene in this system at the level of the crop or the pest. The most common and well-known means of intervention is the application of pesticides. The grower's intervention frequently extends, in an unexpected and often disastrous manner, to the natural enemies as well. Finally, the environment, by which we mean primarily the weather, imposes itself in an often stochastic way on the whole system.

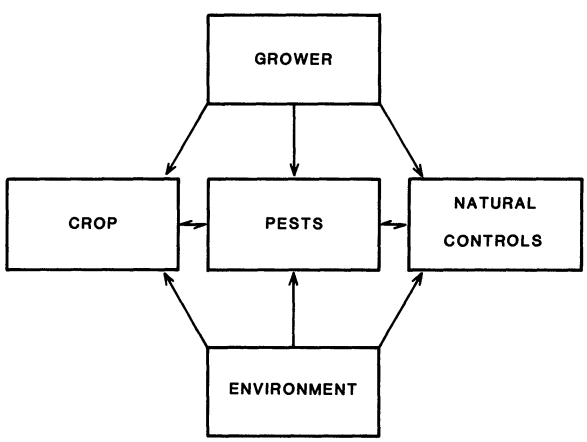

FIG. 1

The methods of intervention (i.e., of pest management) available to the grower are generally divided into three broad categories: chemical, biological and cultural. The most common form of chemical control is the general purpose pesticide, such as DDT or malathion. Other means of chemical control include specialized pesticides, which are toxic only to certain insect species; pheromones, which disrupt or confuse the insects' hormonal systems; and oviposition inhibitors, which impede the ability of female insects to lay eggs on host crops. The most common forms of biological control include sterile insect release, the breeding of resistant crops, and the release of predators, parasites, or disease agents. The most common cultural controls include

proper timing of the harvest, crop rotation, and the physical destruction of pests (e.g., of cocoons). An excellent introduction to the methods of pest management is given by Metcalf and Luckmann (1975).

The advent of inexpensive and efficient chemical pesticides after World War II led to the abandonment of many of the other methods of pest management. Repeated application of pesticides, however, soon resulted in the development of resistant strains of the target pest species. In addition, the chemical pesticides frequently destroyed nontarget pests that acted as natural controls of pest species. In many cases this resulted in massive resurgences of the target species as well as outbreaks of pest species that had previously had no economic importance. Finally, the buildup of pesticide residues in the environment has caused concern for the health of higher animals, including humans (Metcalf (1980)). All this has resulted in a renewed interest in nonchemical means of pest management. Starting in the late 1950s, this interest has focused on the concept of integrated pest management, or IPM (Stern et al. (1959)), in which chemical, biological, and cultural means are combined in a manner specific to the particular agroecosystem to create an efficient means of keeping pest damage at an economically acceptable level. Developers of IPM strategies generally assign a major role to mathematics in aiding in strategy selection. Perkins (1982) provides an excellent introduction to the history and philosophy of IPM.

The role of mathematics in pest management is to aid in decision making (Norton (1976)). Decision making in agricultural pest management is complicated by the highly stochastic and uncertain nature of the problem. Stochasticity has two primary effects (Bertsekas (1976)). The first is that decisions to withhold pesticide treatment may involve high gains and high short-term risks. For example, consider the simple situation shown in Table 1.1. The grower's expected profit is maximized if he does not apply the pesticide, but most growers faced with this situation would act in a risk averse manner and apply the pesticide.

TABLE 1.1

Decision	Apply pesticide	Do not apply
Outcome (probability)	\$70/acre profit (1)	\$200/acre profit (.5) \$ 20/acre loss (.5)
Expected Profit	\$70/acre	\$90/acre

The second primary effect of stochasticity is that frequently a decision must be made before significant information is available regarding the outcome. For example, many pest species are capable of persisting at low levels in the crop for an extended period and then suddenly growing rapidly in numbers. By the time an outbreak is detected, considerable damage to the crop may have already occurred. In such situations, growers frequently apply the pesticide prophylactically.

The agricultural pest management problem may be divided into three primary subproblems: strategy selection, tactics selection, and state estimation. Strategy selection involves determining, in a general way, the appropriate mix of chemical, biological, and cultural practices to be used in controlling the pest. Tactics selection follows strategy selection and consists of the determination of the specific way in which pest control will be applied in response to a particular state of pest infestation. State estimation involves the attempt by the grower or his agents to determine whether the pest infestation has reached a level where active pest control is appropriate. This level is called the economic threshold (Stern et al. (1959), Headly (1972)); the

economic threshold concept is the keystone of IPM. A few workers have attempted to incorporate more than one of these particular aspects into a theoretical study of a given problem (e.g. Shoemaker (1982b), Stefanou (1983)). Most effort has been devoted, however, to one or another aspect of the problem.

In actual application, the triad of strategy selection, tactics selection, and state estimation would be related to the same problem. It so happens, however, that the primary research effort on individual components has focused on different applications. We therefore consider each component separately, focusing on an individual application unrelated to that of the other two. This may be somewhat disorienting, but in the last section we discuss a hypothetical case in which all the components are combined to form a single pest management strategy. In our discussion of the individual components, we begin with strategy selection. In §2 we discuss the application of mathematical modeling to a particular case of strategy selection, the selection of an appropriate combination of pesticide application and sterile insect release for the suppression or eradication of an insect population. In §3 we discuss tactics selection in the context of determining the appropriate schedule for the application of a pesticide. In §4 we give two examples of the state estimation problem. The first is the estimation of the population of a pest species in a particular field. The second is the rapid delimiting of the extent of infestation of an invasive pest. Section 5 contains a summary and discussion of the ideas that we have presented.

2. Strategy selection: The IPM concept. In the modern theory of pest control, strategy selection is generally done in the context of an integrated pest management (IPM) plan. The basic concepts of IPM were put forth by Stern et al. (1959). The primary ideas are first that chemical controls should be used to complement, not replace, biological and cultural controls, and that no control action should be taken until the level of insect pest infestation surpasses a level, called the economic threshold, at which the cost of treatment becomes economically justifiable. Barfield and O'Neil (1984) discuss in some detail the principles of IPM and their use (and misuse).

The role of mathematical modeling in strategy selection in the IPM context is to aid in determining the optimal strategy for a given situation. In this section we consider one example of how mathematical analysis has helped to identify the appropriate situations for the optimal use of the strategy of releasing of sterile insects (generally males when separation by sex is possible). In addition to helping to determine the circumstances in which this method is appropriate, mathematical analysis shows how chemical controls can best be used in conjunction.

In 1955, E. F. Knipling published a landmark paper on eradication or control using sterile male release (Knipling (1955)). The simplest model of the sterile insect technique (SIT) is the following. Assume that the pest population has nonoverlapping generations, and a 1:1 sex ratio. Let P_n denote the number of females in generation n. In the absence of sterile males, the population is assumed to grow exponentially so that

$$P_{n+1} = rP_n. \tag{2.1}$$

In this equation, r is the intrinsic growth rate. Assume now that a constant number, S, of sterile males are released in each generation. Then (2.1) is replaced by

$$P_{n+1} = rP_n\left[\frac{P_n}{P_n+S}\right]. \tag{2.2}$$

The term in brackets in (2.2) represents a dilution of fertile males; it effectively reduces the growth rate. Figure 2 shows results of applying the simple formula (2.2) with two different values of S, given that $P_0 = 10^6$.

Equation (2.2) has an unstable fixed point at $\bar{P} = S/(r-1)$. Treating S as a parameter, this implies the existence of a threshold release level S^*, where for a given initial population P_0, S^* is given by

$$S^* = P_0(r-1). \tag{2.3}$$

The behavior of (2.2) is characterized by

$$P_n \to \begin{cases} 0 & \text{if } S > S^*, \\ \infty & \text{if } S < S^*, \\ P_0 & \text{if } S = S^*. \end{cases} \tag{2.4}$$

The existence of a threshold level of release was observed in eradication efforts against the screw worm fly (Baumhover et al. (1955)).

As indicated in Fig. 2, when sterile insects are applied in the same numbers over a period of several generations the natural population declines at a greater than geometric rate. This is known as the "Knipling effect" and makes the SIT potentially very useful for eradication campaigns. Sterile insect release may also be useful as a part of an integrated program to keep a pest population at a low level, particularly if the adult stage of the insect is not the stage that causes crop damage. The SIT is obviously not effective as a rapid population suppressant since it requires several generations to achieve its effect. In this review we focus on the SIT as an eradication tool.

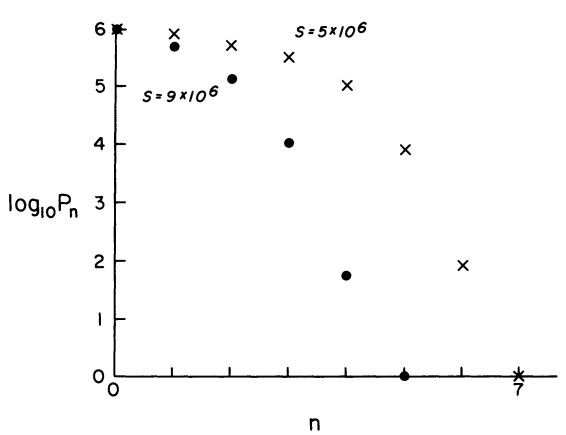

FIG. 2

The economic threshold concept discussed in §1 was not intended to apply directly to eradication programs. A similar concept does apply, however; the eradication effort should be conducted if its expected cost is less than the cost of managing the pest population (i.e., maintaining it below the true economic threshold) if it is not eradicated. Included in the cost of SIT applications must be the cost of developing sterilization techniques and plants. Bradbury and Loasby (1975) discuss the future commercialization of SIT. Spharim (1975) also considers the economics of developing the SIT procedure commercially.

Equation (2.3) shows that when the initial population is reduced, the threshold level of release is correspondingly reduced and the number of generations to eradication may also be cut. Pesticide application has been used to bring about this initial population reduction in eradicating the melon fly from an island in the Marianas (Steiner et al. (1965)). Cultural methods (primarily fruit stripping) were used for the same purpose to eradicate the Mediterranean fruit fly from Florida (Carey (1982)). These are examples of the application of the IPM concept, in which more than one control or eradication measure is applied.

In extending the work of Knipling, Prout (1978) studied a model that incorporates a carrying capacity. Prout's basic results, however, remain valid whether or not the model incorporates density dependence. His model is

$$P_{n+1} = P_n\left[\frac{rK}{K+(r-1)P_n}\right]. \tag{2.5}$$

Here K is the carrying capacity of the population, since (2.5) has a fixed point at $P_n = K$.

Prout considers two forms of release. In hard release, the number of sterile males released is held constant. If S is the (constant) number of sterile males released in each generation, then reasoning analogous to that leading to (2.2) shows that (2.5) should be replaced by

$$P_{n+1} = P_n\left\{\frac{P_n}{P_n+S}\right\}\left\{\frac{rK}{K+(r-1)P_n\{P_n/(P_n+S)\}}\right\}. \tag{2.6}$$

Simplifying (2.6) gives

$$P_{n+1} = \frac{rKP_n^2}{K(P_n+S)+(r-1)P_n^2}. \tag{2.7}$$

The equilibria of this model are the roots of the cubic equation

$$(r-1)X^3 - K(r-1)X^2 + KSX = 0. \tag{2.8}$$

Equation (2.8) always has $X = 0$ as a root. If $K(r-1) > 4S$ then there are also two positive roots. It is easy to show that the origin and the upper root are stable and that the middle root is unstable. If $K(r-1) < 4S$, then there are no other real roots of (2.8) and the population is driven to extinction. Figure 3 shows the results of calculations using this model. In this case, the critical value of S for eradication is $S = 10^6$. Figure 4 shows the number of generations until eradication for $P = 5 \times 10^6$.

Prout (1978) also considers "soft-release" in which the ratio of released to native males is held constant. If a is the ratio used, then P_{eq} is the new equilibrium level defined by

$$P_{eq} = \frac{r-1-a}{r-1}. \tag{2.9}$$

Clearly, the condition for eradication in this case is that

$$\frac{1+a}{r} > 1$$

or

$$a > r-1. \tag{2.10}$$

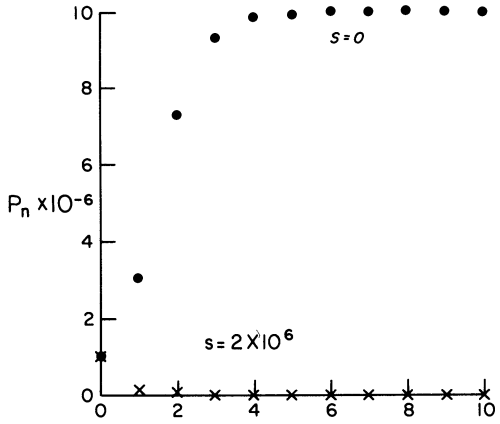

FIG. 3

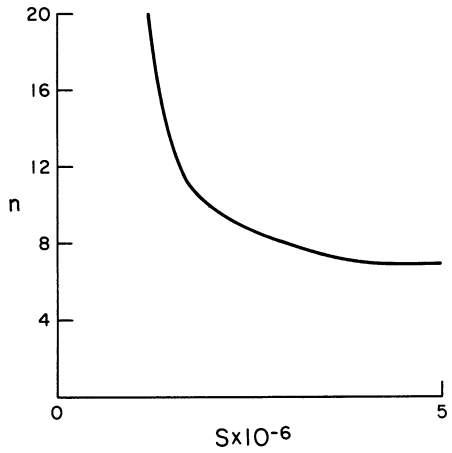

FIG. 4

In most pest infestations, there is immigration of pests into the release area. In the recent California Mediterranean fruit fly infestation, it was suggested that migration effects were a primary cause of the failure of the SIT to achieve eradication (Lindquist and Nadel (1982)). Prout considers hard and soft migration. In hard migration, the number of migrants M is constant. In soft migration, the ratio of immigrants to natives is constant. There are now four different population dynamics: hard/soft migration combined with hard/soft release. For example, if both migration and release are hard, then the population dynamics are given by

$$P_{n+1} = \frac{rK(P_n^2 + M(P_n + S))}{K(P_n + S) + (r-1)(P_n^2 + M(P_n + S))}. \tag{2.11}$$

The equilibria of this model are the roots of the equation

$$(r-1)X^3 + X^2(r-1)(M-K) + X(MS(r-1) + K(S-Mr)) = rKMS. \tag{2.12}$$

Unlike (2.8), $X = 0$ is not a solution of (2.12) if $M > 0$; this means that eradication is

not possible. To see the effect of migration on an eradication program, assume that

$$K(r-1)<4S, \tag{2.13}$$

which is the condition that leads to eradication in the event that there is no migration. To help simplify the analysis of (2.12), introduce scaled variables by

$$x=\frac{X}{K}, \quad m=\frac{M}{K}, \quad s=\frac{S}{K}. \tag{2.14}$$

Dividing (2.12) by K^3 gives

$$rms=(r-1)x^3+x^2(r-1)(m-1)+x(m(sr-s-r)+s). \tag{2.15}$$

Denote $f(x;\, m,\, s)$ by

$$f(x;m,s)=(r-1)x^3+x^2(r-1)(m-1)+x(m(sr-s-r)+s) \tag{2.16}$$

so that (2.15) becomes

$$f(x;m,s)=rms. \tag{2.17}$$

The objective is now to study the behavior of (2.17) as a function of m and s. Figure 5, which sketches the curves $f(x;\, m,\, s) - rms$ for various combinations of r, m, and s, schematically shows the behavior. First set $m = 0$; then (2.17) becomes

$$f(x;0,s)=0, \tag{2.18}$$

which is the same as (2.8). The critical value of s for eradication is $s^* = (r-1)/4$. Panels (a) and (b) in Fig. 5 illustrate the solution of (2.20). When m is slightly larger than zero, with $s > s^*$, as in Fig. 5(c), the possibility of eradication disappears. The equilibrium at $x = 0$ moves to $x > 0$ and thus the population becomes endemic. For

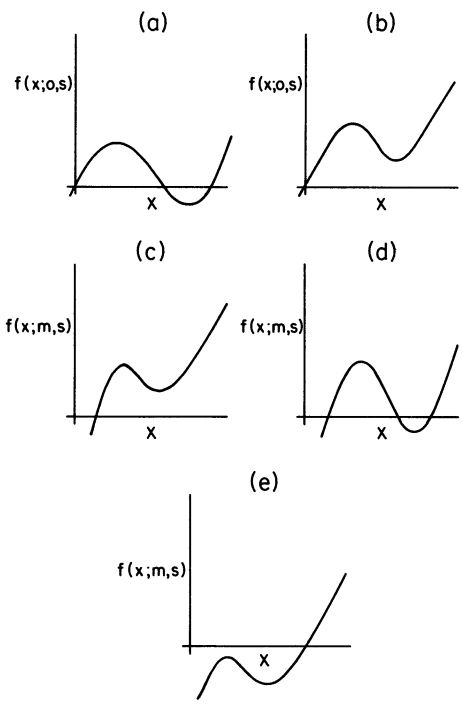

FIG. 5

larger values of m (Fig. 5(d)) a region of multiple equilibria may exist, depending upon the values of r and s. For even larger m, the multiple equilibria disappear and only a high level of population remains (Fig. 5(e)).

The region of multiple equilibria can be computed as follows. The critical points of $f(x; m, s)$ are solutions of $f'(x; m, s) = 0$. Denote them by $x_2(m, s)$ and $x_1(m, s)$ with $x_2(m, s) \geqq x_1(m, s)$. The first value of m at which multiple equilibria may exist is given by

$$f(x_2(m,s); m, s) = rms. \tag{2.19}$$

The largest possible value of m for which multiple equilibria exist is given by

$$f(x_1(m,s); m, s) = rms. \tag{2.20}$$

Equations (2.19), (2.20) can be used to construct a bifurcation picture in the (m, s) plane characterizing the region of multiple equilibria. The algebra is somewhat tedious, but we encourage the reader to try it. Prout considers the other combinations of release and migration. Conclusions are drawn in an analogous fashion and the methods are similar.

The papers of Knipling and Prout are deterministic. Deterministic models may be unsatisfactory for a number of reasons. First, populations are discrete and often mate randomly; the deterministic models usually do not take that into account. Second, environmental "shocks," essentially random phenomena, are probably very important in pest management. For example, a severely cold or very wet winter may more effectively control a population than any human action. Deterministic models do not account for such random shocks. Third, extinction is inherently a random phenomenon.

Costello and Taylor (1975) introduce a general stochastic model for the analysis of SIT problems. Let $P(t)$ denote the population at time t. They replace the Knipling model (2.2) by the continuous time, discrete state space model

$$\Pr\{P(t+\Delta t) = n+1 \mid P(t) = n\} = \begin{cases} \dfrac{n^2 b}{n+S}\Delta t + o(t), & n < K, \\ 0, & n \geqq K, \end{cases} \tag{2.21}$$

$$\Pr\{P(t+\Delta t) = n-1 \mid P(t) = n\} = dn\Delta t + o(\Delta t),$$

$$\Pr\{P(t+\Delta t) = n \mid P(t) = n\} = \left(1 - \frac{n^2 b}{n+S}\Delta t - dn\Delta t\right) + o(\Delta t), \tag{2.22}$$

$$\Pr\{\text{any other transitions} \mid P(t) = n\} = 0.$$

In these equations, b and d are birth and death parameters and S is the number of sterile insects. Let $\lambda_n = bn^2/(n+S)$ and $\mu_n = dn$. In the stochastic case, one must deal with the moments of the time to extinction, instead of the time itself. Of most interest is the first moment. Let T be the time to extinction and set

$$W_n = E\{T \mid P(0) = n\} \tag{2.23}$$

where $E\{\cdot\}$ denotes the expectation. It is easy to show that W_n satisfies the following equation

$$W_n = \frac{1}{\lambda_n + \mu_n} + \frac{\lambda_n}{\lambda_n + \mu_n} W_{n+1} + \frac{\mu_n}{\lambda_n + \mu_n} W_{n-1}. \tag{2.24}$$

The terms on the right-hand side of (2.24) are, respectively, the mean exit time from the state $P(0) = n$, the probability of a jump to population level $n + 1$ times the mean time to extinction from that state, and the probability of a jump to population level $n - 1$ times the mean time to extinction from that state. Equation (2.24) is best solved numerically. Table 2.1 shows some of the numerical results. The * in the table indicates that extinction does not occur within a time span they could compute. The numerical results suggest that, regardless of the number of sterile insects, the lower limit for the first moment of the extinction time is 1.5 generations.

TABLE 2.1
Expected number of lifespans to extinction.

Initial population	Number of sterile males			
	300	600	1000	>2000
100	*	1000	7	5
50	*	10	5	4
2	*	1.5	1.5	1.5

The following conclusions can be drawn from the analysis in this section. Determining the threshold of the number of sterile males to be released is an important operational question. Missing this threshold makes the procedure ineffective. In the presence of immigration, eradication is impossible and the best that one can hope for is reduction of the population to an endemic state. The sterile insect release method is therefore most effective in a geographically isolated setting such as an island, or when used to eradicate an insect population that is not widely distributed, for example, one that has been recently introduced. In conjunction with a sterile insect release program, chemical or cultural methods are most effective in reducing the initial population of the insect pest.

3. Tactics selection: The scheduling of pesticide application. Having selected a particular strategy for dealing with an insect pest, the grower must next determine the tactics to be used in implementing this strategy. In this section we give a specific example of the application of mathematical modeling to tactics selection. We assume that the grower has selected the strategy of complete reliance on a single pesticide, and that he plans to apply that pesticide prophylactically, without monitoring the pest population. The problem is then to determine the best time or times to apply the pesticide. We assume that the grower wishes to maximize his net profit, subject to discounting, over a fixed time horizon.

It may happen that a tiny fraction of the pest population has a genetically conferred resistance to the pesticide. Resistance may be due to any number of factors (Georghiou (1972)), for example, to enzymes that break down the pesticide, or to a thickened cuticle. Since resistant individuals are more likely to survive a pesticide application, the succeeding generation has a higher portion of their descendents, and consequently a higher portion of resistant individuals. Repeated applications of the pesticide results in still higher portions of resistant individuals, and eventually the portion will be so high that the pesticide will no longer be effective. This transition to ineffectiveness may take place with remarkable speed, frequently occurring in just a few years. Georghiou (1972) provides a good explanation of the reasons for this.

Since resistance is a genetic phenomenon occurring in a population, it should be amenable to study by the theory of population genetics. Although some work (e.g. Plapp et al. (1979)) has been done using multilocus models, in general the simplicity of the single locus model, and the reasonableness of the results obtained by using it, make this the model of choice. In the model, resistance is conferred by a single genetic locus with two alleles, R (resistant) and S (susceptible). Homozygous resistant (RR) individuals are more resistant to the pesticide than homozygous susceptibles (SS), and heterozygotes (RS) are somewhere in between, depending on the degree of dominance of the resistance gene.

Assume that the pest population exists in discrete, nonoverlapping generations. If there were no difference in the survivorship (i.e., fitness) between the phenotypes corresponding to the R and S genes, the natural assumptions to apply would be those leading to the Hardy–Weinberg law (Ewens (1969)). These are an oversimplification in that they ignore the sex of the individual and assume random mating, but experience has shown them to be sufficiently accurate for a model such as the present one. Under these assumptions, the Hardy–Weinberg theorem states that after one generation the genotypes of the population attain a stable distribution in the ratio

$$\text{RR}:\text{RS}:\text{SS}=p^2:2pq:q^2 \tag{3.1}$$

where the values of p and q are the gene frequencies in the original population.

For our problem the assumption of differential survivorships between the genotypes is essential. Assume that in the nth generation the RR, RS, and SS genotypes confer survivorships A_n, B_n, C_n, respectively. Then the frequency of the R gene in generation $n+1$ may be calculated from the formula (e.g. Ewens (1969))

$$p_{n+1}=\frac{A_n p_n^2+B_n p_n q_n}{A_n p_n^2+2B_n p_n q_n+C_n q_n^2}\triangleq F_n(p_n) \tag{3.2}$$

where p_n and q_n denote the frequencies of the R and S genes in generation n. Taylor and Headly (1975) derive fairly general equations for the dynamics of a population under these assumptions. They point out that these equations are difficult or impossible to analyze without some simplifying assumptions. The standard assumption of population genetics, that A_n, B_n, and C_n are approximately equal, does not hold in the case of pesticide spraying (Comins (1977b)). Indeed, the primary assumption is that $A_n \gg C_n$. Other simplifying assumptions are, however, possible in this case.

Comins (1977b) assumes that $p_n \ll 1$. He then expands $F_n(p_n)$, defined in (3.2), to obtain

$$F_n(p_n)=\frac{B_n}{C_n}p_n+o(p_n). \tag{3.3}$$

Several inferences may be drawn from (3.2) and (3.3). If, as is often the case, each generation of the population is treated with roughly the same level of pesticide, so that B_n and C_n may be considered fixed, then the frequency of the resistance gene grows geometrically during the early stages. Moreover, the intrinsic rate of increase depends on the degree of dominance of the resistance gene. If the gene is dominant, so that $B_n \gg C_n$, then the rate of increase is high; if the gene is recessive, so that $B_n \sim C_n$, the rate of increase is low.

Comins (1977b) continues the analysis by assuming that the pest has m generations per growing season. He further assumes that $B_n = C_n^{(1-\beta)}$ where β varies

between 0 for a dominant gene and 1 for a recessive gene. If we let

$$S = \prod_{n=1}^{m} \frac{B_n}{C_n} \tag{3.4}$$

(3.2), (3.3), and (3.4) imply the relation

$$\Delta \ln p_n = \beta |\ln S| \tag{3.5}$$

where $\Delta \ln p_n$ is the change in $\ln p_n$ from one season to the next. Comins identifies (3.5) as the measure of the decline in pesticide susceptibility from one year to the next, and concludes that the time for resistance to develop in a population is inversely related to ln S. By assuming that the total yearly cost of applying the pesticide is proportional to ln S, and that the perceived cost of resistance is a function of this same quantity, Comins derives a set of m coupled equations defining the optimal strategy for a single season's pesticide application schedule. An example of this strategy applied to the control of the sugarcane froghopper is given. The conclusion is that pesticide should be applied in such a way that the damage done to the crop is roughly the same for each pest generation. In a later paper, Comins (1979) refines and extends his theory.

An alternative simplifying hypothesis to that which led to (3.3) is that the pesticide kills all of the homozygous susceptible individuals. Mathematically this implies that $C_n = 0$ in (3.2). Note that in this case the function F in (3.2) is not analytic at zero, so that a Taylor expansion as in (3.3) is not possible. In a series of papers, Georghiou and Taylor (1977a, b) and Taylor and Georghiou (1979) explore the consequences of this second hypothesis. They assume that the population reproduces itself in a density dependent manner according to equations of the form

$$N_{n+1} = N_n \exp(r[K - N_n]/K). \tag{3.6}$$

In their model each genotype obeys an equation of this form, and the genotypes interact according to dynamics as in (3.2). The three population equations of the form (3.6), together with an equation of the form (3.2) in which

$$A_n = W_{RR} N_n \tag{3.7}$$

and similar relations apply to B_n and C_n, comprise the model. Georghiou and Taylor conduct a series of numerical experiments to analyze the effect of various factors on the rate of increase of resistance. These factors include controllable variables such as pesticide dose, selection threshold, scheduling, and maintenance of refugia; and uncontrollable variables such as degree of dominance of the resistant gene, and rate of migration of the pest (this latter was also studied by Comins in an early paper (1977a)). They conclude that the maintenance of refugia, where a portion of the population is left untreated, may significantly retard the growth of resistance. They point out that resistance growth may also be retarded or even eliminated in a population with a high rate of migration, if the resistance gene is recessive.

The models of Comins and Georghiou and Taylor do not include the dynamics of the crop. If intraseasonal scheduling is to be a part of the modeling study, then such crop dynamics are an essential part of the model. Gutierrez et al. (1979) study a model for the interaction of the Egyptian alfalfa weevil and cotton. These models are quite realistic in that they include as dynamic variables the adult and larval weevil populations, gene frequency of the resistance gene, and a measure of the state of the cotton plant. These equations are quite complex in their form and we do not reproduce them here; rather we describe them qualitatively.

Adult weevils are assumed to enter the field only by immigration so that the number of adults $N_{A,n}$ at time n (time is measured in units of degree days in most agricultural models since all rates are temperature dependent) is given by

$$N_{A,n+1} = N_{A,n} f_A(n, p_n, x_n) \tag{3.8}$$

where f_A is a time dependent function taking into account immigration and death, p_n is the frequency of the resistance gene, and x_n is the pesticide application intensity at time n. Larval population N_z depends on prior adult population, on the frequency of the resistance gene, and on the pesticide spray rate through a complicated function, which we write as

$$N_{z,n+6} = f_z(N_{A,n}, x_n, p_n) \tag{3.9}$$

where the assumption is that larvae emerge six time periods after eggs are laid.

The frequency p_n of the resistance gene follows the random mating dynamics described by (3.2). The survivorships are modeled by

$$A_n = C^{-\alpha_{RR} x_n} \tag{3.10}$$

and similarly for B_n and C_n. The dynamics of the cotton plant are described by an equation of the form

$$L_{n+1} = f_L(N_{z,n}, N_{A,n}, n) \tag{3.11}$$

where L_n represents the dry leaf mass per unit area of the cotton.

The problem of maximizing long-term grower profits, as a discounted sum of the cotton, less pesticide costs, could in principle be solved by dynamic programming. The complexity of this type of solution is avoided by assuming that the grower follows a myopic strategy of simply trying to maximize his profits in each year. Gutierrez et al. (1979) examine the effect of the grower's knowledge of the level of resistance to the pesticide in the population. They find that when pesticide resistance is taken into account, the optimal myopic behavior is to gradually reduce the level of pesticide application, thereby slowing the growth of resistance.

Shoemaker (1982b) gives a dynamic programming solution for a model similar to that of Gutierrez et al. Her formulation of the model is more detailed than that of Gutierrez et al. in that it specifically includes the effects of weather and of parasitization of the pest insects. In order to reduce the model to a manageable form, she makes certain simplifying assumptions which allow her to formulate the dynamic programming problem in terms of four variables representing pest population level, resistance gene frequency, level of parasitization, and weather. She considers the case of univoltine (i.e., having only one generation per year) pests, and formulates the decision problem in terms of a binary decision on the application of pesticide (spray or no spray), along with an optimal date of harvest. By using some ingenious simplifications based on linearities in the model she is able to reduce the dynamic programming problem to a tractable form. Her results provide an estimation of the economic threshold, that is, the intensity of pest infestation that warrants pesticide application. If the economic threshold is exceeded, then pesticide should be applied. Under proper weather conditions, however, pesticide application may be avoided by harvesting the crop early. Shoemaker's model provides an estimate of the proper conditions for this latter strategy.

The models of Gutierrez et al. (1979) and Shoemaker (1982b) are dramatically different from those of Comins (1977b) and Georghiou and Taylor (1977a). The latter are formulated in relatively simple terms and have a significant analytical component,

while the former are quite detailed and are intended to provide precise numerical predictions, at the expense of providing insight into the interactions that lead to these predictions. If mathematical models are to be used as a management tool in which the grower simply provides as input his observations of the relevant parameters and the model responds with an optimal strategy, such models will have to be detailed and precisely calibrated. Efforts are currently underway to provide such models to growers of a variety of crops (Huffaker (1980)).

A different application of mathematical modeling is to attempt to use the model to gain an understanding of the processes underlying the behavior of a complex system, and to use this understanding to provide general recommendations to the grower for strategies which, while they may not be optimal, are at least an improvement. For example, the model of Georghiou and Taylor (1977a, b) indicates that a useful way to delay the development of resistance in a pest population is to maintain refugia where a portion of the breeding population is spared from application of the pesticide. No attempt is made to precisely quantify the extent of such refugia.

The two applications of mathematical models described above are not mutually exclusive; indeed, they are complementary. The nature of the model used in each of the two applications is, however, quite different. While detailed models must generally be quite complicated, models that are intended to provide insight must generally be quite simple. An excellent example of the complimentary nature of such models is provided by studies of the spruce budworm. A team of workers at the University of British Columbia developed a detailed model of the dynamics of this pest in its interactions with the forest ecosystem of New Brunswick. Jones (1976) provides a description of the model. Using this model, forest managers can determine the effects of various management strategies. The model, however, is so complex that it provides little or no information as to why it behaves the way it does. Ludwig et al. (1978) developed and analyzed a simple version that simulates qualitatively the pest–ecosystem interaction. While their model does not provide precise information, it does provide insight as to what is causing the more complex model to behave as it does. It should be noted that a recent article by Royama (1984) questions the fundamental assumptions of the model described by Jones (1976).

Mangel and Plant (1983) and Plant et al. (1985) attempt to use the same sort of approach with a model for pesticide resistance. They begin with equations that are quite similar to those of Gutierrez et al. (1979), except that the equations are formulated in continuous time. The specific system that Mangel and Plant consider is motivated by the spider mite as a pest of cotton. Spider mites have a very high reproductive rate, so that outbreaks may occur very rapidly. For this reason, many growers typically treat for them prophylactically. Mites have as many as ten generations per growing season, so a continuous time model is most appropriate. The model ignores a number of complications, such as predation and pesticide induced fecundity, that are thought to occur with spider mites. This is done to focus on the development of resistance, which is generally independent of these effects except as they influence the intensity of pesticide application.

Mangel and Plant consider the events in a field that suffers immigration of mites from a nearby "pool," which may be weeds or a different crop, such as an orchard. During a given season time is measured continuously and the dynamics are described by differential equations. At the end of each season the crop is harvested and the initial conditions of the model for the subsequent season are set, based on the state of the variables at harvest time. Interseasonal time is therefore measured as a discrete variable, while intraseasonal time is measured continuously. Pests immigrate from

the pool to the field throughout the year. They establish colonies which then grow and reproduce. For simplicity the original immigrants are not counted in the population.

Mangel and Plant begin with a detailed model in which age is measured as a continuous variable and the population has genetics similar to those of (3.2). Through a series of simplifications they reduce the model to one in which the population has only one age class, and two resistance classes, resistant and susceptible. They show that the behavior of this simplified model is qualitatively identical and quantitatively similar to that of the more complex model. The equations of the simplified model for intraseasonal dynamics are

$$\begin{aligned} &\frac{dx_i}{dt}=\rho_i(t;t_s(n),\eta(n))x_i+\mu_i(n)I(t), \qquad i=\mathrm{R},\mathrm{S},\\ &\frac{dc}{dt}=\begin{cases} rc-v(t)(x_\mathrm{R}+x_\mathrm{S}), & c>0,\\ 0, & c=0,\end{cases} \\ &x_\mathrm{R}(0)=x_\mathrm{S}(0)=0, \qquad c(0)=c_0. \end{aligned} \tag{3.12}$$

Here the subscript denotes the resistance class (resistant or susceptible), $x_i(t;n)$ is the pest population of class i at time t in season n, ρ_i is the population growth rate, $I(t)$ is the immigration rate, and μ_i is the fraction of members of the pool of susceptibility class i. The growth rate $\rho_i(t;t_s(n),\eta(n))$ depends on the time t_s and intensity η of applications of the pesticide in season n. The terms t_s and η are the control variables of the model. The variable $c(t)$ represents the amount of crop at time t, and $v(t)$ represents the rate of crop consumption per individual pest.

The multiseasonal management problem may be stated as

$$\begin{aligned} &\text{maximize} \quad J=\sum_{n=1}^{n}\gamma^{n+1}[C(T;n)-c_p\eta(n)],\\ &\text{subject to} \quad \mu_\mathrm{R}(n+1)=h(\mu_\mathrm{R}(n),t_s(n),\eta(n)) \end{aligned} \tag{3.13}$$

where γ is a discount factor and the function h is obtained by solving (3.12) in season n. Mangel and Plant show that a useful approximation to the problem may be obtained by fixing η for all n. Plant et al. (1985) obtain solutions to problem (3.13), using this approximation, by dynamic programming. Several qualitative conclusions may be drawn from these solutions. One is that as the discount rate increases, the optimal strategy moves closer to that of applying the pesticide at the single season optimal time t_s^* in each season. The susceptibility of the pest population to the pesticide may be regarded as a nonrenewable (or slowly renewed) resource (Hueth and Regev (1974)); from this perspective the effect of the discount rate may be interpreted as an example of the fact that as the discount rate increases, the optimal strategy for extracting a resource moves to one of extracting it as rapidly as possible.

For moderately high values of the discount rate the best strategy is to apply the pesticide at time t_s^* during the early seasons. The high relative value of the crop in the early seasons due to discounting of later crops outweighs the cost of increased resistance in later seasons. When a significant fraction of the population becomes resistant, the best strategy is to apply the pesticide earlier than the single season optimal. This gives time for immigration of susceptibles to dilute the resistant population. As the time horizon is approached, the best strategy is again to spray at the single season optimal time t_s^*, since there is nothing to be gained by spraying at another time.

The optimal strategy evidently depends on the values of the discount rate and the time horizon. In general the grower does not know these values with any precision. This motivates the formulation of a closed loop strategy that, although possibly suboptimal in a deterministic setting, is nevertheless preferable in actual practice to an open loop strategy. Such a closed loop strategy could be to spray at the optimal time t_s^* when there is no evidence of declining yield due to pesticide resistance, and to spray earlier when resistance buildup begins to cause a reduced yield. Simulations using such a strategy do indeed provide for an increased total discounted profit over the time horizon.

In conclusion, the work of Plant et al. (1985) provides a method of interpreting the results obtained from simulations involving more complex models. While large scale models are essential in the development of precise predictions about a system, simplified models can, at the expense of quantitative accuracy, provide qualitative insight into the workings of both the more complex simulation models and the real system that they are intended to simulate.

4. Estimating the state of infestation: scouting and trapping. One of the key principles of the integrated pest management concept is that intervention should not occur until the pest population has reached the economic threshold, that is, the level at which the cost of treatment is economically justifiable. Adoption of this concept necessitates some means of estimating both the economic threshold and the level of infestation of a particular insect pest in a crop. There are at least two possible ways of estimating the population of pests of a given species in a particular location. One way is to employ scouts to sample the plants, either by visual inspection, by using a sweep net, or by removing certain plants to insepct them in a greater detail. The second way is by setting out traps that contain a species specific attractant and inspecting them regularly. This is particularly appropriate for highly mobile insects or for pests whose economic threshold is so low that their presence implies intervention. In this section we review research in both of these state estimation methods. We first discuss the application of sequential sampling theory to the method of scouting along rows of crops. We then examine the type of information that may be gleaned from trapping studies.

The objective in crop scouting is typically to estimate the mean number of pests per plant. This statistic is then compared with a predetermined economic threshold and if the mean population exceeds the threshold intervention is begun. The traditional method for determining the appropriate decision under these circumstances is the sequential probability ratio test of Wald (1945). One of the first to discuss the application of sequential sampling to a biological problem was Oakland (1950), who showed how it could be used to estimate the average number of tapeworm cysts in a batch of whitefish. Since then there have been numerous papers describing sequential sampling plans for insect pest control. We cannot give an exhaustive list of these publications, but a sequential sample might include Waters (1955), Allen et al. (1972), Sterling (1976), and Onsager (1976). The latter papers contain many other references.

In the sampling of insect populations in a crop, one often assumes that the population's spatial distribution may be represented by a negative binomial (Bliss (1956)). This distribution involves two parameters, the mean n and an exponent k. It is characterized by (Anscombe (1950)):

$$\Pr\{x=r\}=\left(1+\frac{n}{k}\right)^{-k}\frac{\Gamma(k+r)}{r!\,\Gamma(k)}\left(\frac{n}{n+k}\right)^{r}. \tag{4.1}$$

The value of k reflects the degree of overdispersion (i.e., aggregation) of the population. The smaller the value of k, the more aggregated the population. As k approaches infinity, the distribution approaches a Poisson distribution, while as k tends to zero, the distribution becomes logarithmic (Bliss (1956)). Natural populations almost always yield a small value of k, indicating aggregation.

One frequently-used sampling procedure, called sampling with a common k, is to assume that the value of k is a fixed parameter determined by the species and location. One then does a preliminary, fixed size sample to obtain an estimate for the value of k. Unfortunately, in actual practice k is often found to depend on n (e.g., Sylvester and Cox (1961)). This increases the number of preliminary samples that must be conducted and complicates the formulation of the probability ratio test. The problem of mean dependent k may be avoided if the economic threshold is sufficiently low that n_1 is relatively small.

Allen et al. (1972) provide a good description of what might be considered the "standard" application of sequential sampling to insect pest population estimation. Two alternative hypotheses are tested. Hypothesis H_0 is that there is an average of n_0 or fewer insects per plant, and hypothesis H_1 is that there is an average n_1 or more insects per plant, with $n_1 \geqq T_E > n_0$ where T_E is the economic threshold. The average values n_0 and n_1 are computed from the distributon (e.g., (4.1)). The scout walks along the row and periodically counts the number of insects on a plant. He maintains a record of the cumulative number of insects counted, T_m, and the number of plants sampled, m. After each count is recorded the scout must decide from among three options: accept hypothesis H_0, accept hypothesis H_1, or take another sample.

An efficient procedure for selecting from among these options has been derived by Wald (1947).

Wald begins by assuming that there is a known prior probability g_0 that H_0 is true, and a prior probability $g_1 = 1 - g_0$ that H_1 is true. Let g_{im} denote the posterior probability of H_i after m observations, and $p_{im}(x)$ denote the probability function in the m-dimensional space under hypothesis H_i. Then Bayes theorem gives

$$g_{im} = \frac{g_i p_{im}(x)}{g_0 p_{0m}(x) + g_1 p_{1m}(x)}. \tag{4.2}$$

The procedure for selecting among the alternatives proceeds as follows. Choose two numbers d_0 and d_1 between $\frac{1}{2}$ and 1. Hypothesis H_i is accepted if $g_{im} \geqq d_i$, for $i = 0$ or 1. If neither of these inequalities are satisfied, another observation is made. Wald shows that these events are mutually exclusive and exhaustive. The inequalities $g_{0m} \geqq d_0$ and $g_{1m} \geqq d_1$ are equivalent to

$$\frac{p_{1m}}{p_{0m}} \leqq \frac{g_0}{g_1} \frac{1-d_0}{d_0} \tag{4.3}$$

and

$$\frac{p_{1m}}{p_{0m}} \geqq \frac{g_0}{g_1} \frac{d_1}{1-d_1}, \tag{4.4}$$

respectively where $p_{im} = p_{im}(x)$. It is from (4.3) and (4.4) that the name "sequential probability ratio test" is derived.

Since the prior probabilities g_0 and g_1 are rarely known, in actual practice one selects two constants, A and B, with $B < A$, and acts according to the following

procedure: accept H_0 if $p_{1m}/p_{0m} \leqq B$; accept H_1 if $p_{1m}/p_{0m} \geqq A$; and make an additional observation if $B < p_{1m}/p_{0m} < A$.

To select the constants A and B, one considers the possibilities for error. There are two types of errors that may occur. One, called an error of the first kind, is to accept H_1 when H_0 is true; the other, called an error of the second kind, is to accept H_0 when H_1 is true. Let Q_i be the event that H_i is accepted, and let $P_i(Q)$ be the probability of event Q conditioned on the assumption that H_i is true. Then $P_0(Q_1)$ is the probability of making an error of the first kind, and $P_1(Q_0)$ is the probability of making an error of the second kind. The constants A and B are selected to keep the probabilities of these errors at specified levels, in particular, to establish the equations $P_0(Q_1) = \alpha$ and $P_1(Q_0) = \beta$, where α and β are exogenously given error rates.

To relate α and β to A and B, Wald (1947) first establishes that $P_i(Q_0 + Q_1) = 1$ for $i = 1, 2$, i.e., that with probability 1 either H_0 or H_1 is ultimately accepted. It follows from the definition of A and B that $P_1(Q_1) \geqq AP_0(Q_1)$ and $P_1(Q_1) \leqq BP_0(Q_0)$. But $P_0(Q_0) = 1 - \alpha$ and $P_1(Q_1) = 1 - \beta$. Therefore

$$\frac{\alpha}{1-\beta} \leqq \frac{1}{A}, \qquad \frac{\beta}{1-\alpha} \leqq B. \tag{4.5}$$

Wald suggests replacing the inequalities in (4.4) with equalities to obtain as an approximation

$$A = \frac{1-\beta}{\alpha}, \qquad B = \frac{\beta}{1-\alpha}. \tag{4.6}$$

The sequential probability test is therefore the following: Accept H_0 if $p_{1m}/p_{0m} \leqq \beta/(1-\alpha)$; accept H_1 if $p_{1m}/p_{0m} \geqq (1-\beta)/\alpha$; take another sample if $\beta/(1-\alpha) < p_{1m}/p_{0m} < (1-\beta)/\alpha$. In practice these tests are usually accomplished by taking the logarithms of both sides of the inequalities and thereby expressing them in terms of the parameters of the distributions $p_{im}(x)$. This avoids computational overflow or underflow problems.

If the mean population density varies over a fairly wide range, it may be advisable to abandon the sequential probability ratio test. A second sequential test, called sequential estimation, has been developed by Anscombe (1949) and, independently, by Kuno (1969). This method exploits the observation (e.g. Taylor (1971)) that in natural populations the variance of a population sample may frequently be expressed effectively as a function of the mean. As before, let n denote the mean number of insects per plant, and assume that the variance may be expressed as a function $f(n)$ of the mean. Let T_m denote the cumulative total of insect counts after sampling m plants. Suppose that T_m is plotted as a function of m. The problem is then to determine the equation of a curve $y = F(m)$, called the boundary curve, such that when the plot $y = T_m$ crosses the curve $y = F(m)$, the mean n is estimated with a given coefficient of variation. Anscombe (1949) shows that if the mean is estimated by

$$\hat{n} = \frac{F(m_1)}{m_1} \tag{4.7}$$

where m_1 is the value of m at which the crossing occurs, then under certain conditions $\hat{n}$ is asymptotically normally distributed with mean n and variance $f(n)/m_0$, where m_0 satisfies

$$n = \frac{F(m_0)}{m_0}. \tag{4.8}$$

Anscombe implicitly assumes that a solution m_0 of (4.8) exists, i.e., that the sampling process terminates in a finite time. In practice the sampling process is of course always terminated at some point, with a decision being made arbitrarily if no acceptable estimate has been found at that point.

Therefore the equation for the standard error of the mean is

$$\frac{1}{m} f\left(\frac{y}{m}\right) = a^2 \tag{4.9}$$

where a^2 is the variance of the estimate. To estimate n with a coefficient of variation b, one divides (4.9) by the sample mean, i.e., by $(y/m)^2$. Substituting $b^2 = a^2/(y/m)^2$, the equation of the boundary curve becomes

$$\frac{m}{y^2} f\left(\frac{y}{m}\right) = b^2. \tag{4.10}$$

The primary condition that these equations be valid is that the probability of intersecting the boundary curve be small when m is small. For example, if a Poisson distribution is assumed, then $f(n) = n$, so to estimate n with a specified variance a, (4.8) yields $y = a^2 m^2$. Since this curve passes through the origin, it must be moved upwards near $m = 0$. Allen et al. (1972) work out a sequential estimation plan using the assumption that $f(n) = c_1 n + c_2 n^2$. As with the sequential probability ratio test, a preliminary survey must be conducted, in this case, to estimate c_1 and c_2. Strictly speaking, (4.10) is valid only if m is fixed in advance. However, Anscombe (1952) shows that for large m the error introduced by implementing the estimation procedure sequentially is small. In addition, (4.10) may be derived by Bayesian arguments, which are insensitive to the stopping scheme.

A third estimation technique intended explicitly for agricultural insect surveys has been developed by Wilson and his collaborators (Wilson et al. (1983)). Retaining the notation of the previous paragraphs, let $\bar{n}$ denote the sample mean number of insects per sampling unit, i.e.,

$$\bar{n} = \frac{1}{m} \sum_{i=1}^{m} x_i \tag{4.11}$$

where x_i is the number of insects counted on the ith sampling unit. Suppose first that $\bar{n} < T_E$, the economic threshold. Suppose for the moment that m is fixed. By the central limit theorem we have for large m

$$\Pr\left\{-Z_{\alpha/2} < \frac{\sum x_i - mn}{\sqrt{mf(n)}} < Z_{\alpha/2}\right\} \simeq 1 - \alpha \tag{4.12}$$

where $Z_{\alpha/2}$ is the standard normal variate. We implicitly assume that the variance may be described as an exact function f of the mean n. Wilson et al. use the variance-mean formula, developed by Taylor (1971),

$$f(n) = \mu n^{\nu}. \tag{4.13}$$

Equation (4.12) may therefore be written

$$\Pr\{\bar{n} - Z_{\alpha/2}\sqrt{\mu n^{\nu}/m} \leqq n \leqq \bar{n} + Z_{\alpha/2}\sqrt{\mu n^{\nu}/m}\} \simeq 1 - \alpha. \tag{4.14}$$

To ensure with confidence $1 = \alpha$ that the population is below the economic threshold, we require that

$$Z_{\alpha/2}\sqrt{\mu n^{\nu}/m} = T_E - \bar{n}. \tag{4.15}$$

Equation (4.13) then becomes

$$\Pr\{2\bar{n} - T_E \leqq n \leqq T_E\} \simeq 1 - \alpha. \tag{4.16}$$

In addition to providing an interval estimate for n, (4.16) ensures that the probability of an error of the first kind is at or below α.

As with (4.10), (4.16) is valid only if the sampling procedure is implemented in such a way that m, the number of samples, is held fixed and the equation is used to compute α. While this is sometimes done in practice, often the rules are bent so that the procedure may be implemented sequentially. This is done by substituting the estimate $n \simeq \bar{n}$ into (4.14) to obtain a boundary curve equation of the form

$$m = \frac{Z^2_{\alpha/2}\mu\bar{n}^{\nu}}{(T_E - \bar{n})^2}. \tag{4.17}$$

An analogous sequential sampling procedure may be derived using Bayesian statistics (Plant and Wilson (1985)), which avoids the distinction between fixed size and sequential sampling procedures.

Each of these three sampling plans may be suited to a different situation. A detailed comparison of the three has not been made and would be a valuable contribution.

Having described state estimation based on scouting, we now turn to trapping. Insect traps are used to detect the presence of pest insects when scouting is not practical or when the economic threshold of the pest is so low that intervention occurs at pest population densities too low to be detected by scouting. For example, the State of California maintains traps for several insects, such as the gypsy moth and the Mediterranean fruit fly (medfly), that are not currently pests in the state and that the state wishes to prevent from becoming established.

A medfly population became established in Santa Clara County, near San Jose, during the late 1970s. Under climate conditions such as those of Northern California a medfly population can double every one or two weeks (Carey (1982)), so the Santa Clara population grew rapidly. It was the subject of an intense eradication effort from 1980 to 1982. In September 1982, after an expenditure of many million dollars, the population was declared eradicated.

During the height of the eradication campaign over 100,000 medfly traps were placed in areas susceptible to medfly infestation. These traps were used for two purposes: to indicate the presence of an infestation in a given area, and to delimit the extent of the infestation once it had been detected. The accurate delimiting of the extent of an infestation is an important part of an eradication program. If the extent is overestimated then pesticide treatment, sterile insect release, and the establishment of quarantines may be applied to areas that are not infested. The consequences of underestimating the extent are more serious. The eradication program may fail or be seriously set back if infested areas go untreated. For example, Lindquist and Nadel (1982) suggest that one primary reason the sterile insect technique (SIT) failed to eradicate the medfly in the Northern California campaign was that the infested area was not accurately defined. The original "epicenter" of the infestation was selected because the first medfly in Santa Clara county was found at this point. The actual epicenter was later determined to be some distance away.

The problem of using trap catch data to obtain good information about the presence and extent of a pest infestation may be divided into two subproblems: setting

out the traps in the best possible way, and interpreting the trap catch (or lack of catch).

The early theoretical work on insect trapping is concerned with using the traps to reduce, as opposed to detect and delimit, the population. Much of the theory is, however, similar for both questions. Wolf et al. (1971) develop a theory for determining the trap density required to reduce a pest population by a given fraction. They identify three parameters as necessary to estimate the performance of a trap placement strategy. These are (1) trapping areas, i.e., the effective area of a single trap; (2) trap performance, i.e., the fraction of insects within the trapping area that are caught by a single trap; and (3) trap density function, i.e., the relative degradation in performance with multiple traps due to overlap of trapping areas. Wolf et al. give experimental procedures that may be used to estimate the values of these parameters in the field. They also provide formulas showing how the trap density is related to the estimated population reduction.

Hartstack et al. (1971), drawing from the work of Wolf et al. (1971), attempt to establish a theory based on more realistic assumptions. They first use mark–recapture studies to estimate the performance of an individual trap. They express this performance by fitting their data to the equation

$$P=\frac{ER^2}{(x+R)^2}\cdot 100 \tag{4.18}$$

where P is the percentage recovery of pests released at a distance x, and E and R are parameters. Hartstack et al. identify E as the single trap efficiency and R as the effective radius of the trap. Using (4.18), Hartstack et al. derive formulas for estimating the density of insects in a given area, assuming this density is uniform. By assuming that traps operate independently, Hartstack et al. derive an expression for the probability that an insect will be caught by a grid of traps. This is an alternative to the trap density function of Wolf et al.

Using a mathematical formulation similar to that of Hartstack et al., McClendon et al. (1976) designed a computer simulation of insect population reduction. The simulation computes the expected fraction of insects captured based on assumed insect responsiveness and on trap placement configuration.

Cunningham (1981) identifies three physical variables as being the control variables in selecting a trapping strategy. They are: trap density, attractant dose per trap, and attractant vaporization rate. He shows how experimental data may be used to generate a simple model to predict the fraction of insects trapped in a marked insect release–recapture study as a function of the dose per trap. Cunningham and Couey (1983) expand on the work of Cunningham. They report the results of marked release–recapture studies, analogous to those of Hartstack et al. (1971), with medflies. Cunningham and Couey show that the percentage recovery function of (4.18) may, in the case of medflies, be well fitted by an exponential decay function.

Mangel et al. (1984) consider theoretical aspects of trapping an insect population to gain information, rather than to reduce the population. They show that the trapping process may be approximated as a Poisson process and treat the Poisson parameter α as the single trap efficiency. The value of the parameter is proportional to the product of two other parameters: the fraction q of the population that is "trappable," and the effective area l^2 of the trap. Based on the single trap efficiency, and on the rate of spread σ of the population, Mangel et al. derive a Bayesian expression for the posterior probability that a region contains pests, given that none were trapped. The normalized

difference between this posterior probability and the prior probability of the presence of insects represents the amount of information provided by the traps.

The spatial extent of the region is assumed to be divided into square mile "cells." Thus, with a given dispersal parameter σ, the prior probability $p(i, j)$ is defined by

(4.19) $p(i, j)$ = Probability that another medfly is in cell with coordinates (i, j), given that a medfly was found in cell (0, 0).

The posterior probability is defined by

(4.20) $\hat{p}(i, j, n)$ = Probability that pests are present in cell with coordinates (i, j) given that there were n traps in this cell but no pests were trapped.

The amount of information provided by tapping is estimated from

$$\Delta = \left[\frac{p(i,j) - \hat{p}(i,j,n)}{p(i,j)}\right] \times 100, \tag{4.21}$$

which is the percentage reduction in prior probability caused by trapping. Mangel et al. plot Δ as a function of n for given values of σ and α. In this way they are able to estimate the trap density that provide, the greatest per capita information gain.

To examine the efficiency of various trapping patterns, Mangel et al. conducted Monte Carlo simulations of the trapping process. These were designed to simulate the events taking place during the first 48 hours after a medfly is detected. Within 48 hours of the detection of a medfly, protocol (Anonymous (1982a)) calls for the aerial spraying of malathion bait. Aside from the obvious killing of many flies, spraying distorts the infestation in complicated ways that are not clearly understood. Mangel et al. therefore restrict their considerations to the interval between the detection of the first medfly and the aerial spraying. They assume that all increased activity takes place in a 9-mile by 9-mile region centered at the detection point. Current protocol calls for the placement of 360 additional traps in a 9-square-mile region surrounding the detection point during the first 49 hours. The primary question is whether these 360 traps could be placed in a more efficient pattern.

In a simulation the infested region is a square, centered at (0, 0), whose perimeter is a randomly chosen odd number between 1 mile and 15 miles. The simulation runs for 100 units of time, so the time unit may be considered as .02 days. At each time unit a medfly becomes "trappable" in one of the cells in the grid. The infestation is assumed to be uniformly distributed so that at each time each cell is equally likely to contain the trappable fly. The fly appearing at the first time unit is automatically caught. The cell in which the first fly is caught is the center of a 9 by 9 grid that contains all the traps. There is no possibility of catching a fly outside the 9 by 9 grid; this corresponds to not inspecting traps outside this region during the two day interval. Within the 9 by 9 region traps are placed at a basic density of ten traps per cell, and then 360 extra traps are added in some pattern. Note that not all of the 81 cells in the 9 by 9 region around the epicenter need be in the infested region.

If a fly becomes "trappable" in a given cell in the trapping region, the probability that it will actually be trapped is assumed to be .02 times the number of traps in the cell. Thus for example, the fly is always trapped if there are 50 traps in the cell, and is trapped with probability .4 if there are 20 traps. The number and location of the flies trapped in 100 time units is recorded and the simulation is repeated.

Several patterns of trap enhancement were tested using this simulation procedure. These included the current practice of focusing the extra traps at the center of the 9 by 9 grid, placing them at the periphery of the grid, placing them uniformly across the grid, and placing them in a cross shape centered at the center of the grid. The results indicated that placing the traps near the center maximized the number of insects trapped, but that placing the traps at the periphery gave the best indication of the extent of the infestation. The cross shaped pattern was a good compromise, giving both types of information.

5. Summary and discussion. Our review is not meant to be exhaustive. Rather, our goal is to show the variety of analytical tools that appear in problems of agricultural pest control. It is unlikely that a "general theory" will ever be developed. Each specific problem requires an in depth study and detailed understanding of its unique features. The appropriate analytical tools are then chosen according to the needs of the problem. This, of course, is the way that the best applied mathematics and operations analysis is done.

In our discussion, we have broken the problem of theoretical analysis of pest management into three components. This subdivision is to a large extent artificial, since in actual practice the three areas influence each other considerably. It is, however, useful as an aid in fixing ideas. Because of the overwhelming complexity of agricultural pest management problems, there have been no individual works that consider the overall problem of pest management for a given crop (some, such as those listed in the introduction, do come close). For purposes of illustration, we conclude our article with a brief consideration of some of the effort that would be required to develop a complete analysis of a crop system.

For our exemplary crop, we choose the tomato. Our discussion draws heavily from that in Anonymous (1982b). In beginning the analysis, one might consider the problem of selecting from among various strategies for the management of some of the moth larvae that are major pests of this crop, such as the tobacco budworm, beet armyworm, and tomato fruitworm. These strategies include cultural practices such as discing immediately after harvest to destroy larvae and pupae; biological practices such as the release of parasitic wasps; and chemical practices such as the application of broad spectrum insecticides.

In analyzing the strategy selection problem one must be cognizant of the various possible tactics. For example, in the application of chemical insecticides, a common practice is to spray the field twice, once early in the season, and once late in the season. The early season spraying of a broad spectrum insecticide will, however, kill predatory insects as well as the target pests. The removal of predators may result in outbreaks of secondary pests such as mites and stink bugs, so if possible, this early application should be avoided. It will be possible to avoid the early application if a reasonable means of estimating the numbers and types of pest insects present is available. Such a means is given, for example, by Zalom et al. (1983).

In addition to the means of estimating the current population of each major pest, the grower must also have available a reasonable estimate of the level of economic damage that would be caused by that pest, thus enabling the grower to establish an economic threshold. We bypassed a discussion of the economic threshold in §§2 and 3 because the specific examples considered in those sections did not incorporate the concept. We therefore take up the matter now.

The notion of the economic threshold was first made explicit by Stern et al. (1959), who define it as "the population density at which control measures should be

determined to prevent an increasing pest population from reaching the economic injury level," where the economic injury level is the lowest population that will cause an amount of injury sufficient to justify the cost of the control. Headly (1972) provides the first attempt to quantify the idea. He constructs a simple mathematical model of the pest population density. In this model, the value of the crop as a function of pest population is a decreasing, concave function that reaches zero at a finite value of the argument. Cost of control is a monotonically decreasing, convex function of population density. The derivatives of these functions are equal at exactly one value of the population density, and it is this value that Headly defines as the economic threshold. The justification for this is that by maintaining the population at this level the farmer maximizes his profit. The problem with this definition is that in most cases of control by a pesticide the pest population cannot be *maintained* at a given level; rather, it increases to a certain level and is then drastically reduced by the application of the pesticide. Hall and Norgaard (1973) extend Headly's definition to take this fluctuation into account.

The determination of the economic threshold is one of the most challenging aspects of the modern theory of integrated pest management. The threshold varies from species to species, even among closely related species, from time to time, and from place to place. The literature does not contain much specific information on economic thresholds for tomato pests. The review article by Stern (1973), and the references therein, is a good source of information on the work involved in actually establishing the economic threshold for a given crop–pest system.

In summary, the development of a theory that would allow an adequate strategy selection procedure rests on a consideration of tactics and ultimately on the ability to successfully monitor the state of the crop. If a monitoring method is available, then the state estimation procedure generally involves a periodic sampling of the field to estimate the insect population. Pesticides are not applied until the population passes a predetermined economic threshold. If economically justified, cultural and biological means of control may be used to try to keep the population below this threshold. Mathematical models may be used to aid the farmer in establishing the economic threshold and to determine a suitable combination of chemical, biological, and cultural practices for a particular crop–pest system.

One of the primary reasons for the wholesale acceptance of chemical pesticides by farmers is that these pesticides provide a sure, simple means of controlling the crop damage done by pests (Perkins (1982)). Unfortunately, the ability to rely on this means of control is rapidly diminishing. The challenge for applied mathematicians is to aid in providing the theoretical tools necessary to provide an environmentally sound alternative to simple reliance on pesticides that is accceptable to the farmer.

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