Fundamentally, these methods use the derivative as an estimate of the slope of the function at any time and predict the next value of the function as a linear excursion with this slope.

At the new value, prediction backwards is made and appropriate corrections employed if the original and predicted values do not agree. The correction procedure varies among the several methods, but they are all designed to converge upon the true value of the function within some stated accuracy limits.

Stability Analysis

There is an important analytic area that can be pursued when analytic solutions for the system model cannot be found. This is the matter of system stability. It may be of interest to discover how the system will behave if it reaches the neighborhood of an equilibrium point. An equilibrium point is defined as the set of values of the system variables at which the rates of change are zero—and thus a point at which the system does not change over time. However, since there is always "noise" in any real system, displacements from the equilibrium point will generally occur. If after displacement, the system returns to the equilibrium point, it is said to be stable; if it diverges, it is unstable; and if it remains in the neighborhood of the point (say, oscillates about it) it is marginally stable. A great deal of information about system behavior can be obtained from an analysis of its stability at all equilibrium points.

To investigate stability, one first solves for the values of the equilibrium points by using the simultaneous equations:

$$\frac{dx_1}{dt} = f_1(x_i, t) = 0$$

$$\frac{dx_2}{dt} = f_2(x_i, t) = 0$$

$$\vdots$$

$$\frac{dx_n}{dt} = f_n(x_i, t) = 0$$

Then, a linearized model for small perturbations, Δx_i, in the x_i is obtained by constructing the Jacobean matrix:

$$\begin{pmatrix} \frac{d\Delta x_1}{dt} \\ \frac{d\Delta x_2}{dt} \\ \cdot \\ \cdot \\ \cdot \\ \frac{d\Delta x_n}{dt} \end{pmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \cdots & \frac{\partial f_2}{\partial x_n} \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \cdots & \frac{\partial f_n}{\partial x_n} \end{bmatrix} \begin{pmatrix} \Delta x_1 \\ \Delta x_2 \\ \cdot \\ \cdot \\ \cdot \\ \Delta x_n \end{pmatrix}$$

and evaluating it at the equilibrium point. The behavior of the system in the neighborhood of the equilibrium point is equivalent to that of the linearized model.

To illustrate, consider the Lotka-Volterra model:

$$\frac{dH}{dt} = f_1 = (b\text{-}dP)H \qquad b,d,r,m > 0$$

$$\frac{dP}{dt} = f_2 = (rH\text{-}m)P$$

Equilibrium points E_1 and E_2 are at:

$$(b\text{-}dP)H=0$$
$$(rH\text{-}m)P=0$$

$$E_1: \begin{cases} H=0 \\ P=0 \end{cases} \qquad E_2: \begin{cases} P = \frac{b}{d} \\ H = \frac{m}{r} \end{cases}$$

The Jacobean matrix is:

$$J = \begin{bmatrix} b\text{-}dP & \text{-}dH \\ rP & rH\text{-}m \end{bmatrix}$$

$$\text{at } E_1: \qquad J = \begin{bmatrix} b & 0 \\ 0 & \text{-}m \end{bmatrix}$$

The eigenvalues are:

$$(b-\lambda)(-m-\lambda) = 0$$
$$\lambda^2 - (b-m)\lambda - bm = 0$$
$$\lambda_1 = b,\ \lambda_2 = -m$$

Thus, $\Delta x_1 = c_{11} e^{bt} + c_{12} e^{-mt}$
$\Delta x_2 = c_{21} e^{bt} + c_{22} e^{-mt}$

where the c_{ij} depend upon the initial values of Δx_1 *and* Δx_2. Since each function contains a term of the form e^{bt}, an exponential that grows with time, the Δx_i become greater as time increases, and the system diverges from the equilibrium point. Thus, we are concerned with an unstable equilibrium.

At the second equilibrium point, E_2, the following result is obtained:

$$J = \begin{bmatrix} 0 & \frac{-md}{r} \\ \frac{rb}{d} & 0 \end{bmatrix}$$

The eigenvalues are:

$$\lambda^2 + \frac{md}{r} \cdot \frac{rb}{d} = 0$$
$$\lambda^2 + mb = 0$$
$$\lambda_1 = + \sqrt{-mb}$$
$$\lambda_2 = - \sqrt{-mb}$$

This is a different case from any of the previous ones. Since the quantity under the radical is negative, the eigenvalues are complex conjugates and the solution is

$$\Delta x_1 = C_{11} \exp(\sqrt{mb}\, it) + C_{12} \exp(-\sqrt{mb}\, it)$$

$$\Delta x_2 = C_{21} \exp(\sqrt{mb}\, it) + C_{22} \exp(-\sqrt{mb}\, it)$$

where i is the imaginary value $\sqrt{-1}$. By an equation of Euler, complex conjugate exponentials can be reduced to the real functions:

$$\Delta x_1 = c_{11} \sin \sqrt{bm}\ t + c_{12} \cos \sqrt{bm}\ t$$
$$\Delta x_2 = c_{21} \sin \sqrt{bm}\ t + c_{22} \cos \sqrt{bm}\ t$$

These are oscillating functions and imply that the disturbance neither grows nor decays, but that the system oscillates about the equilibrium point. Thus, we have discovered that there is some neighborhood in which this system demonstrates marginal stability.

In general, the non-linear system will be unstable if any of the eigenvalues of the linearized system has a positive real part, stable if all possess negative real parts, and marginally stable if any (complex conjugate) roots are purely imaginary. The presence of roots with positive real parts can be ascertained from application of Routh-Horwitz criteria to the polynomial equation, eliminating the need to solve the equation for the values of the roots. This and other methods for examining system stability can be found in Ogata *(1967)* and Bowers and Schultheiss *(1958)*.

System Identification by Perturbation

A particularly powerful method for discovering the form of the system model has resulted from the development of linear system theory. Basically, the time response of a linear system to a diagnostic perturbation contains all the information necessary to identify the system model. This is true only for linear systems. However, for many purposes, such as prediction, or even regulation, a linear model will yield sufficient accuracy, and the appropriate linear model (for some operating range) can be constructed in this way.

There are three diagnostic perturbations: the impulse, step, and sine functions. The second is the most appropriate for biological population systems and consists of an abrupt change in the level of a system variable. The behavior of the system subsequent to this abrupt change is examined, and from the graphical or numerical results the values of exponents and constants can be calculated. These imply certain relationships among the basic variables and define these relationships uniquely in a differential equation model. An example of a step function in a predator-prey system would consist of an abrupt addition of a given number of either organism. A negative step could also be employed, such as the removal of some of the predators in a plant-herbivore-predator system.

There is a large number of other diagnostic methods for model identification that derive from systems theory—many of which have not yet been employed in biological investigation. A particularly interesting introduction to the subject is contained in Milsum *(1966)*.

Conclusion

The intent of this paper has been to provide a brief introduction to constructing and solving dynamic population models. Some examples have been presented to illustrate the basic approach. A great deal has been left out. No mention has been made of stochastic elements in such models, nor has anything been said about the utilization of the models for pragmatic purposes. Emphasis has been placed on how the model reveals the structure of the system, which will be the principal aim of many investigators. Those of us who are interested in resource management and optimization of yield, or the subsidiary problem of minimization of damage, need system models for this purpose. Given good population system models, we can explore in a meaningful way modification of the destructive effects of the pest, or devise an optimum strategy to obtain yields in spite of its effects. This is another topic, requiring for its solution models of a different organizational system, but which is no different in concept from the problems discussed above. The point that needs general recognition from population dynamicists is that it is both necessary and relatively easy to approach their systems from a dynamic point of view.

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MODELING FOREST INSECT POPULATIONS— THE STOCHASTIC APPROACH

by R. C. CHAPMAN, Mathematical Statistician, Northeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Upper Darby, Pennsylvania.

ORDINARILY, phenomena such as growth of a population or changes in the qualitative character of a population are not open to immediate observation in all their details. Usually we observe only a few external manifestations of the phenomenon, i.e. the inputs and outputs of a black box.

When we view a complex phenomenon—complex in the sense that we do not fully understand what is occurring—we attempt to explain it by using mechanisms that, through experience or imagination, appear simple or elementary. These simple mechanisms we use to explain a phenomenon are sometimes, perhaps often, only apparently simple.

This paper is not a review of probability theory nor an advocation for the general use of probability techniques by entomologists. Rather, it is an attempt to demonstrate the utility and the power of probabilistic models. Probabilistic and deterministic models will be contrasted to illustrate the fundamental differences between the two types of mathematical models. The level and tone of the presentation is a compromise between a desire for some mathematical sophistication and a realization that such sophistication would completely negate the utility of this paper as an introduction for the non-mathematically inclined.

A model may be defined as a set of hypotheses representing a class of phenomena as a particular combination of elementary mechanisms. Thus, a model is a hypothetical structure composed of elementary mechanisms joined by a set of hypothesized relationships.

The introduction of mathematics into the modeling process represents a logical step in the evolution of a science. Mathematical models have assumed some acceptance because: (1) the symbols are easily manipulated; (2) definition is precise i.e., lack of ambiguity; and (3) subjective judgment is reduced in the evaluation of the hypothesized relationship. In the remainder of the paper, a model will always refer to a mathematical model.

The elementary mechanisms that we invoke in building the structure of the model may be deterministic or probabilistic. A model is deterministic if a particular mechanism implies that every variable in the system is a function of the others.

For example, consider Thompson's *(1922)* model for a parasite-host system. The fraction of the host population attacked by the t^{th} generation is

$$f = \frac{p R^t}{h - p \frac{(R^t - R)}{(R-1)}}$$

where

f = fraction of host population attacked by the t^{th} generation.
p = number of parasites initially present $t = 0$.
h = number of hosts initially present $t = 0$.
t = generation.
R = ratio of reproductive power of parasite to host.

Knowing any four of the five parameters of the model we can solve for the fifth. The model states that beginning with the same number of hosts, h, parasite, p, and ratio of reproductive power R at the t^{th} generation we will always have the same fraction f of host population parasitized.

If at least one variable is a chance or random variable then the model is probabilistic. For example, consider a stationary population subject to chance immigration. The immigrants after arriving remain in the population. The number of individuals in the population at time t is given by

$$N_t = N_o + I_t$$

where

N_o = number of individuals in the population initially, $t = 0$.
I_t = number of individuals who have immigrated at or before time t.

N_t = number of individuals in the population at time t.

The number of individuals in the population at time t is a random variable because the number of immigrants at or before time t is subject to chance variation. The term random implies that the process under consideration (immigration) is in some sense probabilistic.

In the last 50 years deterministic models have been developed for a wide variety of biological phenomena. The increasing development of probabilistic models in the past twenty years is due to the failure of deterministic models to provide a description of all the phenomena one may wish to study. Deterministic models fail to take into account the role of chance fluctuations in the development of the process. For example, the competition experiments of Park *(1948)* with flour beetles showed that under a given set of initial conditions the same species did not always survive.

The main appeal of deterministic models appears to lie in their relative mathematical simplicity not in their philosophical foundation. Any debate between the advocates of deterministic and probabilistic models revolves around the economics of model construction and analysis, not on the theoretical applicability of the stochastic model. The advocates of deterministic models find some support for their position in the fact that *sometimes* when a population is large, a description of the deterministic type is equal to the expected value of the probabilistic model.

Both deterministic and stochastic models must satisfy Neyman's *(1960)* criteria of "broad applicability" and "identifiability of details". Broad applicability refers to "the possibility of deducing from the model verifiable consequences relating to categories of observation other than those for which the model was constructed." Identifiability of details refers to identifying in the empirical world elements that correspond to hypothetical entities in the model.

The subsequent comparison of probabilistic and deterministic models closely follows a discussion by Lucas *(1964)*.

A probabilistic model is defined by the relation

$$P_R[Y \leq y] = (\underline{\psi}, \underline{X}; \utilde{y})$$

where

Y is a random variable and

F is a probability distribution with arguments y and column vector parameters ψ and X

$\underset{\sim}{\psi}$ is a vector that is invariant over a class k of situations

$\underset{\sim}{X}$ is a vector that varies over the class k.

For example, consider the familiar normal linear regression model

$$f(y, \alpha, \beta, \sigma^2, x) = \frac{1}{\sqrt{2\pi\sigma^2}} \left[\exp - \left(y - \alpha - Bx\right)^2 \Big/ 2\sigma^2\right]$$

$$P_R\left[Y \leq y\right] = \int_{-\infty}^{y} f(y, \alpha, \beta, \sigma^2, x)\,dy$$

where $f(y, \alpha, \beta, \sigma^2, x)$ is the probability that the random variable Y assumes a value y.

It will be assumed that the probabilistic elements are written in the form

$$Y = \Delta(\underset{\sim}{\psi}, \underset{\sim}{x}) + \epsilon$$

The subscript tilde $\sim$ denotes a column vector. Thus $\underset{\sim}{X}$ is a column vector $\{x_1, x_2, \ldots x_n\}$ having n elements.

The random variable $\underset{\sim}{X}$ will be treated as an input or independent variable and y will be considered as an output or dependent variable.

$$\begin{aligned} \Delta(\psi, X) &= \int_{-\infty}^{\infty} y \; dy \; F(\underset{\sim}{\psi}, \underset{\sim}{X}, y) \\ &= E(y \mid \underset{\sim}{\psi}, \underset{\sim}{X}) \end{aligned}$$

This is the expected value or mean of the random variable.

The probability distribution of ϵ, the deviation from the expected value, is given by

$$P_R(\epsilon \leq e) = F(\underset{\sim}{\psi}, \underset{\sim}{X}, e + \Delta(\underset{\sim}{\psi}, \underset{\sim}{X}))$$

where $e = y - \Delta\ (\underset{\sim}{\psi}, \underset{\sim}{X})$.

The expected value of the deviation is zero.

$$\begin{aligned} E(\epsilon \mid \psi, X) &= E(y\text{-}\Delta(\underset{\sim}{\psi}, \underset{\sim}{X}) \mid \underset{\sim}{\psi}, \underset{\sim}{X}) \\ &= E(y \mid \underset{\sim}{\psi}, \underset{\sim}{X})\text{-}\Delta\ (\underset{\sim}{\psi}, \underset{\sim}{X}) \\ &= 0 \end{aligned}$$

The probabilistic model has deterministic aspects, the form of the probability distribution and the values taken on by ψ and X.

Consider a deterministic model, i.e. a model with no chance mechanism, of the form

$$\gamma=\Delta^*(\underset{\sim}{\varphi}^*\underset{\sim}{X})$$

where γ corresponds to the expected value of the output variable y.

Because real data never follow γ exactly an additional term ε^* is needed to account for the deviations from the model. The model becomes

$$y=\gamma+\varepsilon^*=\Delta^*(\underset{\sim}{\psi}^*\underset{\sim}{X})+\varepsilon^*$$

In order to make a probability statement about the deviation, it is assumed that ε^* follows some cumulative density function

$$P_R[\varepsilon^*\leq e^*] = F^*(\underset{\sim}{\beta}, \underset{\sim}{X}, y)$$

where β is a column vector of parameters invariant over the class of situations. The column vector of parameters β is used instead of ψ because often very simple assumptions are made about F^*. For convenience ε^* is often assumed to follow a normal distribution or some other well tabled distribution. The assumption that

$$E(\varepsilon^*|\underset{\sim}{\beta},\underset{\sim}{X})=0$$

is not always justified. For example, consider the use of the deterministic model

$$y=X_1\beta_1+\varepsilon^*$$

when the "true" model is in fact

$$y=X_1\beta_1+X_2\beta_2+\varepsilon$$

The deviation ε^* is obviously equal to $\chi_2\,\beta_2 + \varepsilon$ and its expected value is

$$E(\varepsilon^*|\beta_1,X_1)=X_2\beta_2$$

not zero unless $\beta_2 = 0$.

Although Δ^* and ψ^* may have the same form as Δ and ψ this is not always so. In the deterministic Lotka-Volterra equations the derivatives of the first moments are functions of products of means. In the stochastic analogy developed by Chiang *(1954)* the derivatives of the first moments are functions of means of products.

The difference between the two types of models revolves around the role of the probabilistic element in the model. In the stochastic model the probabilistic element is an integral part of the model. In the deterministic model the probabilistic element is added because of the nature of the real world. It is not mandatory to attach a probabilistic interpretation to the deviations. There is nothing to prevent a researcher from using the sum of squared deviations from the model or any other statistic to classify a model as good, bad, or indifferent. Intuitively we are inclined to say a model with a small sum of squared deviations is better than a model with a larger sum of squared deviations. But how much better? The probabilistic interpretation of the deviations is an attempt to say how much better under the assumptions of F^*, the cumulative density function assumed for ϵ^*.

For any given deterministic model it is generally possible to construct a variety of stochastic analogs. For example, the deterministic logistic does not distinguish between the situation where the intrinsic rate of increase represents purely reproductive growth and the situation where the intrinsic rate of increase represents a net balance between births and deaths.

If the intrinsic rate of increase represents a purely reproductive growth, a modified pure birth process[1] may be used as a stochastic analog of the deterministic model. When the intrinsic rate of increase represents a net balance between births and deaths a modified birth-death process[2] may be used as a stochastic analog.

In the preceding paragraph, two stochastic processes were introduced. A stochastic process may be defined as a process that may occur in the real world that has some probabilistic element involved in its structure. The phrase conventionally refers not

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[1] A pure birth process is a stochastic process in which it is assumed that each individual in the population acts independently and is subject to a birth rate λ. It is assumed that there is no death, no migration, and the population and the environment are homogeneous. In the pure birth process the number of births in a population of size $N(t)$ at time t is assumed to be $N(t)\ \lambda$. In the modified pure birth process the number of births in the population at time t is $\lambda N(t)\ (K-N(t))$, where K is the carrying capacity of the environment.

As the population approaches the carrying capacity, the birth rate declines.

[2] A simple birth-death process assumes that a population composed of homogeneous individuals acting independently is subject to a birth rate λ and a death rate λ. The modified birth-death process assumes that the population fluctuates between two limits N_1 and N_2, $N_1 < N_2$, where N_2 corresponds to the saturation level. As the population approaches N_2 the death rate increases and the birth rate decreases. The reverse is true, as the population approaches N_1.

only to the actual process but also to its mathematical representation. The simple birth process and the birth-death process are examples of an important class of stochastic processes known as Markov processes. A Markov process is a process with the property that knowing the state of the system at time t, knowledge of its past behavior does not alter the probability of any particular future state.

Although many, if not most, biological processes are non-Markovian the Markov assumption serves as a useful approximation in many instances. Markov-type assumptions are inherent in the construction and analysis of many deterministic models, such as

$$S=P_1P_2P_3 \ . \ . \ . \ P_i$$

where

$S =$ generation survival

$P_i =$ survival rate in the i^{th} stage.

Curent analyses of models of this type treat survival in the i^{th} stage as a function only of the number entering the stage and mortality forces acting in this stage. This type of analysis ignores the influence of past behavior or experience on survival in the i^{th} stage.

The difference between probabilistic and deterministic models sometimes becomes apparent when one considers the ultimate extinction of the population. In the simple birth-death model with birth rate λ and the death rate μ the probability of ultimate extinction is

$$\lim_{T \rightarrow \infty} P_R \left[X(t) = 0 \mid N_{(o)} \neq 0\right] = \begin{array}{l} 1 \text{ if } \lambda \leq \mu \\ 0 \text{ if } \lambda > \mu \end{array}$$

where

$N(o)$=the number of individuals in the population at time zero

$X(t)$ = the number of individuals in the population at time t.

If birth rate is less than the death rate, extinction is expected. It is surprising, however, that when the two vital rates are equal, extinction is also certain.[3] Although extinction is certain when

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[3] A mathematical proof of this phenomenon may be obtained by considering the gambler's ruin problem. (*Feller 1957*)

the vital rates are equal, the expected ultimate population size is N(0). This apparent anomaly occurs because although a few populations will rise to very high values, most populations will be extinguished at very low values so that a constant mean is achieved. Bailey *(1964)* comments that this result indicates that fallacy of attaching too much attention to stochastic mean values even when they exactly equal the corresponding deterministic quantities.

A population in which the intrinsic rate of increase represents a net balance of births and deaths may approach the saturation level K, by (1) increasing the mortality and preserving a constant mortality, or (2) decreasing fertility and maintaining a constant mortality, or (3) by some combination of (1) and (2). Therefore, the approach toward the saturation level may be represented by a variety of models.

Leslie *(1958)* investigated the two extreme situations for populations with stable age structures. He concluded that the imposition of a force of mortality independent of the age distribution, when fertility remains constant and mortality is a linear function of the number present at time t, will result in sigmoid population growth. If the initial population is not *stable* there may be considerable departures from the logistic, although population growth will still follow a sigmoid form. The age structure models Leslie studied show dampened oscillations. Bartlett *(1957)* pointed out that under certain conditions the modified stochastic birth-death process continued to show undampened fluctuations with an amplitude depending on the population size. Feller *(1939)* showed that in the stochastic version of the logistic, fluctuations have in the main the effect of diminishing the rate of population growth.

The subsequent paragraphs are devoted to the development of stochastic models for populations subject only to the risk of death. The first model illustrates the theoretical assumptions and the methodology of model construction. An example of the applicability of the stochastic model to a particular entomological phenomenon is shown. The problem of competing risks is briefly considered.

Assume that a homogeneous isolated population is subject only to the risk of death. At time $t = 0$ the population is composed of $N(0)$ individuals. Each individual acts independently and is subject to the same risk of death. the probability of death of an individual in the interval $(t, t + \Delta t)$ is

P_R (death in the interval $(t, t + \Delta t)$ alive at t) $= \gamma_t \Delta_t + 0(t)$ where γt is the force of mortality, i.e. instantaneous death rate.

The probability of being alive at time $t + \Delta t$ is given by

$$P_R(t + \Delta t) = P_R(t) \cdot (1 - \gamma_t \Delta_t + 0(\Delta_t))$$

where

$P_R(t)$ = the probability of being alive at time t

$1 - \gamma_t \Delta_t + 0(\Delta_t)$ = the probability of surviving the interval $(t, t + \Delta_t)$

After some mathematical manipulations, which may be found in any elementary text on stochastic processes (for example *Parzon 1962*), we obtain

$$P_{R(t)} = \exp(-\int_0^t \gamma_t d_t)$$

as the probability of survival to time t.

The average or expected number of individuals alive at time t is

$$\begin{aligned} E(N(t)) &= N(0) \cdot Pr(t) \\ &= N(0) \cdot \exp(-\int_0^t \gamma_t d_t) \end{aligned}$$

If the force of mortality is constant the expected number of individuals alive at time t is $N(0) \cdot \exp(-\gamma t)$.

Utilizing the assumptions that each member of the population acts independently and is subject to the same force of mortality γ_t we obtain

$$P_R \left[\begin{array}{l|l} N(o) - k & N(o) \text{ alive} \\ \text{individuals} & \text{at time} \\ \text{alive at} & t = 0 \\ \text{time } t & \end{array} \right] = \binom{N(o)}{N(o) - K} P_R(t)^{(N(o)-K)} \cdot (1 - P_R(t))^{K}$$

as the probability at time t exactly $(N(0) - K)$ individuals will be alive. The form of this equation is recognizable as the binominal probability law.

Let us now consider the hunger component of the predation model of Holling *(1966)* as a real life phenomenon.

$H = HK(1\text{-}\exp(- AD \cdot TF))$

where

H =hunger level in grams of food to satiate an insect at any given time.

HK=maximum capacity of the gut.

AD=rate of digestion.

TF =time without food from complete satiation.

This model can be used to show the applicability of the probabilistic approach. For simplicity I have reformulated the model in terms of food remaining in the gut,

$$\begin{aligned} R &= HK - H \\ &= HK \cdot \exp[-(AD \cdot TF)] \end{aligned}$$

The revised model can be recognized as the expected number of units remaining in a population subject to a constant rate of decrease, AD. The probabilistic formulation of Holling's model not only provides the probabilities of occurence but also indicates the assumptions that are implicit in the model.

Let us now assume that an isolated homogeneous population is subject to risk of death by three mortality factors R_1, R_2 and R_3.[4] The factors are assumed to be acting contemporaneously on the entire population. Associated with each factor R_i is a force of mortality $\gamma_{\tau i}$. The sum of the individual forces of mortality $\gamma_{\tau i}$ is μ_τ, the total force of mortality.

In the interval $(t, t + \tau)$ the ratio

$$\frac{\gamma_{\tau i}}{\mu_\tau} = r_{ti}$$

is independent of time τ but is a function of the interval and the mortality factor R_i. Therefore, the absolute magnitude of cause-specific mortality may vary at any instant subject only to the restriction that it remain a constant proportion of the total force of mortality μ_t throughout the interval $(t, t + \tau)$.

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[4] The model for competing risk was developed by C. L. Chiang (1960): Fourth Berkeley Symposium on Mathematical Statistics and Probability, Vol. 4. 413 pp. Univ. of California Press. 1961.

Occasionally, we may be interested in the influence of a single mortality factor upon a population in the absence of competing risks—for example, how many individuals would be killed if a predator were the only mortality factor operating. Except under very special circumstances, this information is not available from field records. Commonly we observe mortality in populations subject to a multitude of mortality factors. If we wish to determine the mortality associated with a specific factor operating in the absence of other causes of mortality, we must build some theoretical relationship between the crude *probability of death* from factor i operating in the presence of other factors and the *net probability of death* from factor i operating in the absence of other mortality factors.

The simple death process discussed in the previous paragraphs is used to develop a theoretical relationship utilizing the assumptions that forces of mortality are additive and that within the interval $(t, t + \tau)$ the ratio $\frac{\gamma_{\tau i}}{\mu_\tau}$ is constant.

The crude probability of death from factor i in the interval $(t, t + 1)$ is

$$Q_{ti} = \int_t^{t+1} [\exp -(\int_t^\tau \mu_t dt)] \; \gamma_{\tau i} d\tau$$

where $\exp\left(- \int_t^\tau \mu_t d_t\right)$ is the probability of survival from t to τ, and $\gamma_{\tau i} \, d\tau$ is the instantaneous probability of death from factor i at time τ.

The net probability of death from factor i in the interval $(t, t + 1)$ when it is the only factor operating is

$$q_{ti} = 1 - \exp \; [- \int_t^{t+1} \gamma_{\tau i} d\tau]$$

If the assumption of a constant relative risk is introduced we obtain

$$Q_{ti} = \frac{\gamma_{\tau i}}{\mu_\tau} \int_t^{t+1} [\exp - \int_t^\tau \mu_t \, d_t] \; \mu_\tau d_\tau$$

$$= \frac{\gamma_{\tau i}}{\mu_\tau} \; q_t$$

as the relationship between the crude probability of death from factor i in the interval (t, t − 1), the forces of mortality γ_{ti} and μ_t and the probability of death in the interval q_t. The probability of death in the interval is of course equal to the sum of the crude probabilities of death.

The relationship between the net and crude probability of death from factor i under the *assumptions of the model* can now be obtained:

$$q_{ti} = 1 - \exp\left[- \frac{\gamma_{\tau i}}{\mu_{\tau}} \int_{t}^{t+1} \mu_t d_t \right]$$

$$(Q \qquad)$$

$$= 1 - P_t^{(Q_{ti}/q_t)}$$

Although the assumptions of the model for competing risks may be unrealistic for many populations, the model shows what assumptions are made and how they are used to build the desired relationship. The next step in the model building process is testing the adequacy of the model.

This particular model was selected for review because it has some relevance to life table construction and mortality models currently employed in entomology.

Population dynamics, models, and systems analysis are the magic words of quantitative forest entomology today. The success of model building and system analysis depends on the extent and organization of entomological kowledge. Elaborate mystical arrays of symbols are no substitute for carefully planned field and laboratory studies. Modeling should not only indicate possible mechanisms but also should indicate where additional biological knowledge is needed.

In this paper I have ignored the empirical models developed by massive data screening programs because although they may lead to good predictions, they are often difficult or dangerous to interpret in terms of underlying biological mechanisms. Screening and correlation programs are useful as fishing trips to locate interesting areas for further study. All too often such programs force the researcher to perform mental contortions to explain his observed relations in terms of a biological phenomenon. Philosophically such an approach to model building is repugnant because it tends to nourish the belief that given sufficient data in large enough quantities a computer can and will find the correct relationship. Access to an electronic computer is not a substitute for careful analytical thinking by the entomologist and statistician.

Simple models like the logistic have been very useful in biology because the parameters are often rather insensitive to small changes. The parameters represent a kind of average value or balance. The parameters are a function of the intrinsic and extrinsic factors associated with the population. Although simple models are intuitively appealing, the interpretation of their parameters must be done with care.

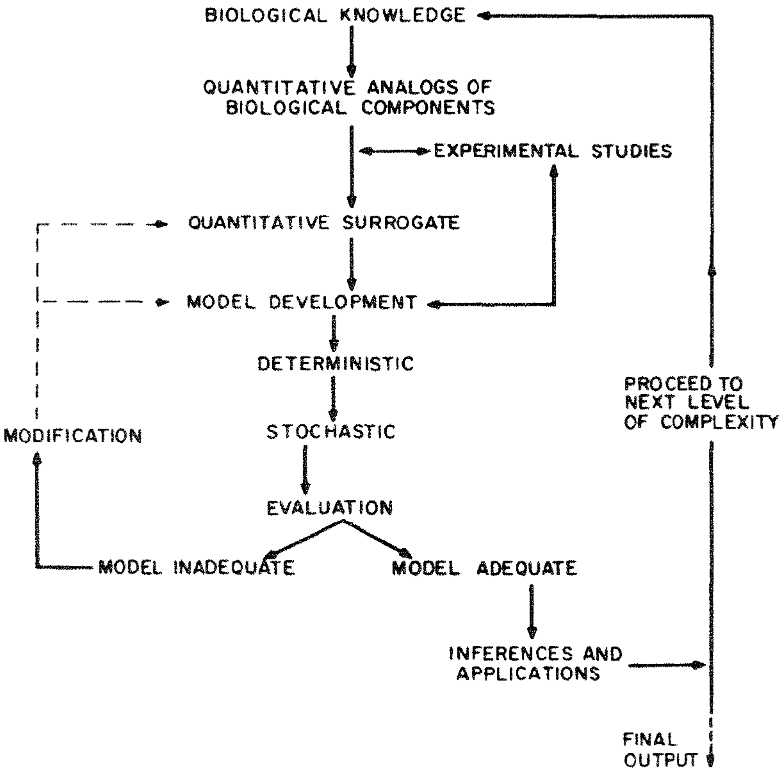

Figure 1.—Schematic diagram of model-building strategy.

Stochastic and deterministic models were compared to show the difference in their philosophical approach to modeling. The distinction between stochastic and deterministic models has been somewhat blurred because sometimes the expected value of the stochastic model is equal to the value of the deterministic model. But this is not always true. Is the entomologist interested in average behavior? Population explosions and extinction may be of greater interest than average behavior. Stochastic models with their embedded chance mechanisms appear to be more adequately suited to the study of such biological phenomena than the more classical deterministic models.

Because stochastic models often involve a more complex mathematical formulation, the economics of model construction and analysis must be evaluated in terms of future benefits. After it has been decided that the population dynamics of an insect are to be studied, the researcher must develop a strategy for model construction and analysis. Figure 1 illustrates a stepwise strategy that might be used for model development in forest insect population dynamics.

The relative mathematical simplicity of deterministic models is used to obtain an idea of the form of the interrelations of the variables. In the strategy diagrammed in figure 1, deterministic and stochastic models for restricted situations are initially developed for restricted situations. The restrictions are gradually relaxed to obtain models for more general situations. For example, initial lack of knowledge of the mode of action of predators and parasites will necessitate the use of crude submodels until sufficient information is available to build more realistic models.

Successful model building demands complete cooperation of entomologist and statistician. The entomologist supplies the biological knowledge about modes of action and interrelationships. The statistician uses the biological information to form a mathematical structure.

Empirical (predictive) models and rational (mechanistic) models, both deterministic and stochastic, are essential to the development of good population models. The complex interrelationships that we wish to understand require not only the mathematical and statistical ability of the statistician but also the genius of the biologist to design the studies needed to gain deeper insights into biological phenomena.

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SOME PRACTICAL FIELD PROBLEMS ASSOCIATED WITH SAMPLING OF SCARCE INSECTS

by F. B. KNIGHT, Professor of Forestry and Chairman, Department of Forestry, The University of Michigan, Ann Arbor, Michigan.

IT IS WELL for us now to review some sampling problems that we must face in gathering adequate field data for quantitative analysis. I've never seen a plan of research that wasn't changed to some extent once the field work commenced. Many plans are changed drastically because the conditions in the field just do not always provide the expected. This is why we enjoy working with field biology problems, perhaps. I shall not attempt to discuss all of the many practical field problems that we face. If insect population models are to be realistic, however, the problems of sampling the natural populations must be resolved to some extent. The sampling of scarce populations is particularly vexing. We are often faced with budget and manpower limitations, and we have difficulty in obtaining the statistical precision we desire.

We should make a real distinction between sampling for population dynamics research purposes and sampling for trend prediction in surveys. The requirements for the two are completely different. In the first we are attempting to define the real causes of population fluctuations. This perhaps will lead to more effective control procedures either by direct or indirect means. When sampling for trend prediction, we are involved more directly in applied forestry. Here we want to answer the related questions—is this population going to increase or decrease and will significant damage occur? I believe that often there is a tendency to mix the two approaches. Methods of trend prediction are generally developed from population research data, but in application these methods will differ somewhat from those carried out in population research. Survey evaluation procedures must be relatively simple, inexpensive to apply, and fast. It is obvious that they must also give reliable answers.

Before considering some specific examples pertaining to survey evaluations and sampling of scarce insects, it might be well to comment briefly on what I like to call "nonsense" statistics. Some research workers become so wrapped up with the idea that everything must be expressed in statistical terms that they fail to use common sense. One good example, and a simple one, is concerned with the analysis of variance. How often have you seen a complete analysis made for a comparison of two obviously different things? One should not waste his time making an analysis if the differences are so striking that he knows the results before he even starts the computations. A second type of "nonsense" statistic is as commonly seen and is much more serious. I'm afraid the computer has added to this problem; some biologists act as though they do not need to think if a computer is used to analyze their data. I refer here to the computation of correlations. Lots of things correlate. For example, in our climate the number of letters in the spelling of the months would correlate with mean monthly temperature. Most of the colder months have long spellings, the warmer months short spellings. We can compute such a correlation but all we end up with is nonsense. Why compute a correlation or talk about it if it has no relevance or usefulness? All too often the computer hands us correlations which are mathematically correct but are biologically meaningless. If a correlation cannot be defended on the basis of logic and biological common-sense then it probably is nonsense. When correlations are published they should be defended by sound biological reasoning. The computer only answers "yes" or "no" to a question. It is up to us to do the creative part of the research; we must answer the question "why?"

I am going back a few years in my own research to briefly comment on population research in contrast to research on evaluation methods. I know that all of you are familiar with sequential sampling, and most of you are aware that sequential sampling procedures were developed nearly 10 years ago for the Black Hills beetle, *Dendroctonus ponderosae*. You may not be aware of the objectives of the research that preceded the development of the method for this insect. The major objective of the research at that time was to develop an evaluation system for Black Hills beetle infestations. We were interested primarily in obtaining a practical method for measuring trends. Secondarily, we hoped to obtain a considerable amount of information on the population dynamics of the Black Hills beetle. We did not pin down the major causes of population fluctuations; we did not even identify many of them. We did develop a workable sequential sampling method for evaluating trends. I had hoped the work would continue on the evaluation method because it does need refinement. However, more of the work since that time has been on population dynamics rather than evaluation procedures.

Sequential sampling is one of the better procedures to use in predicting trends in populations. However, it is not a part of population dynamics research. It may be a product of such research but has very little usefulness in the research itself.

Now, to the main point, there are many problems associated with sampling of scarce insects.

Measurement of population numbers.—Often we hear comments on this problem, such as, "I sampled all plots in the usual fashion and counted no budworms, but I saw an occasional one on other branches" or "Between the two outbreaks of the southern pine beetle I never saw a beetle in the entire region." The problem is simply presented. How can we give statistics on populations without numbers? Granted, a greater amount of sampling would eventually give us quantitative data, but usually we are limited by the time and manpower available.

Identification of mortality factors.—When we do have a population that is measurable, we often try to evaluate the effects of mortality factors. By a great effort, perhaps, we collect 30 larvae and we find that 12 or 40 percent of them are parasitized. Statistically it is correct, and it fills in a slot in the life table. However, any biologist who considered that value for parasitism a valid one would be dreaming. A second collection of 20 larvae might be 90 percent parasitized. Which is correct for the population? The answer is neither one; we just cannot get precise measurements of population reductions with such meager samples. Then, if we add to this the need for separation of mortality factors, perhaps eight or ten parasite species, we are indeed on shaky ground.

Destruction of population by sampling.—When populations become scarce they are not spatially distributed in the same fashion for all species. This is not a very profound statement because the same is true for outbreak populations. However, the differences may be much more striking among scarce insects. Some of them, such as bark beetles, are fantastically clumped. One Black Hills beetle infested tree in two sections of land is not uncommon. The individual infested tree often contains as many beetles as the average tree in an outbreak situation. Thus, the insects present are confined to micro-portions of their total habitat. These favorable locations may not be unique; there may be many other favorable niches not occupied in the surrounding forests.

Knowing our populations, we are sometimes able to locate clumps of plentiful insects; but if we concentrate our sampling on these clumps, we cause a real change in that population. Our destructive sampling procedures may be the major mortality factor affecting that population! When populations are large we can assume that our sampling has no affect on the population but this is not so with scarce populations.

The foregoing are three of the real problems we face when attempting to sample scarce insects. What can we do? One fact is apparent, we just will not produce the comparative quantitative data that our analyses ask for. We are usually day-dreaming if we think we can. Yet we are working on a key part of the population dynamics problem and we need reliable information.

I believe the answer to the problem is to take a completely different approach. This approach is not entirely satisfactory to those who insist upon exact data that can be subjected to mathematical analysis. The approach also requires a patient and very talented research man. I am referring to direct careful observations followed by thorough subjective analyses based on a limited amount of actual data.

In some ways we have gone too far in our enthusiasm for exact quantitative data to support all statements. Some field research workers do not know how to make observations, they just never have done this kind of work. Many even feel guilty if they sit in one spot and record nothing for fifteen minutes. The researcher must spend hours observing and recording what he sees, especially when studying scarce insects. When he has completed his work and reports his results those results must be accepted as reliable. He should not be given the thumbs down comment, "Where are your data to prove it." That question is often the greatest deterrent to creative work that can be expressed. I don't advocate complete acceptance of every unsupported belief of the researcher by any means, but conclusions based on long hours of close observation are not just unsupported statements. In most cases quantitative data will be recorded but often not enough for the statistical precision desired. It is the responsibility of the research worker to point out clearly that he is working with sparse populations and must rely on subjective analyses. Then the reviewer should respect the judgment of the researcher (provided the work has been truly thorough).

Jack pine budworm research.—To illustrate the preceding comments on the usefulness of observations, we will briefly consider two projects. The first concerns studies on the jack pine budworm, *Choristoneura pinus*. In this project there were ample budworms for population measurement, but problems developed when we attempted to analyze predation by birds. In particular, we found it possible to get quantitative information on the resident birds. but impossible to assess the effect of non-resident individuals. We found by observation and some measurements that non-resident birds were consuming large quantities of budworms. These birds were mainly blackbirds, including the red-winged blackbirds, Brewer's blackbird and the cowbird. In one area a flock of 700 to 1,000 of these birds was feeding on budworms during the late larval and pupal stages. If normal sampling with minimal time for observation had been maintained, we possibly would not have noticed their activity. These birds were the major factor controlling populations of the budworm in the one area. This area was a special one in that the jack pine site was only about 600 acres in extent and was surrounded by lowlying areas where many blackbirds were nesting. Nevertheless, the findings illustrate the point that observational data are vital to research.

Saperda inornata and Oberea schaumii.—The second project concerns two insects which are apparently scarce at all times. They also occupy the same ecological niche but exist at such low levels in nature that they never seem to compete. Both are regulated at low levels by factors other than food availability. These insects infest aspen twigs or suckers in diameters ranging from ¼ to ¾ inch. Larvae of both insects bore in the twigs. Adults can be found from June until August, although the emergence period of both is completed in June. Their life cycles in the twigs differ. *Saperda inornata* develops in 1 or 2 years while *Oberea schaumii* requires 3 years from egg laying to adult emergence.

Our data on suckers infested illustrate the scarcity of the insects. These data on six areas involve careful inspection of 13,500 suckers each year; 2,250 in each area each year. Egg niche construction data are presented in table 1. The data for *Saperda inornata* are in terms of galls because this insect may lay more than one egg at a location. Biologically a gall in *Saperda* is equivalent to an egg niche in *Oberea* because it is rare for more than one adult to emerge from a single gall.

These data when carefully analyzed illustrate our need for

Table 1.—Number of egg niches or galls constructed by *Oberea schaumii* and *Saperda inornata* on aspen suckers, 1964 to 1966

	Egg Niches of *Oberea*			Galls of *Saperda*		
Area	1964[1]	1965	1966	1964	1965	1966
1	34	12	158	2	24	63
2	308	159	390	22	73	73
3	163	146	212	38	50	122
4	92	50	230	37	24	100
5	—	33	148	—	18	102
6	—	55	262	—	12	81

[1] In 1964 only 4 areas with 1,500 suckers in each were surveyed. The number was increased to 6 in 1965 and the sample was increased to 2,250 suckers in each area.

observation. In 1964 the amount of egg production was very low among the *Saperda* adults. The reason might have been apparent two years prior. We found it extremely difficult to find emerging *Saperda* adults in the spring of 1964. *Oberea* adults on the other hand were as common as in 1965 and 1966.

In 1965 we increased the sample size (1,500 to 2,250 suckers) and added two areas (5 and 6). Our counts dropped in the *Oberea* record but increased significantly in the *Saperda* record. Why? The emergence of adults of *Oberea* was as large as in 1964 and *Saperda* adults were much more common. They seemed as common as for both species in 1966. The answer to the question was revealed in our rearing studies in the field. The weather in 1965 was adverse. On two June dates in 1965 temperatures overnight reached lows below 25°F. About half of the adults died in our cages. Daytime temperatures through much of June and July were below normal.

In 1966, egg production of both species was high. Again weather was responsible. We had warm temperatures and very little rain throughout the egg laying period.

Only one life table has been completed for the tagged niches. The *Saperda* galls tagged in 1964 were removed after emergence was complete in June 1966. One *Saperda* adult emerged. This was certainly a small number on which to base many conclusions. Our data for the remainder of the study involves larger numbers but we know that emergence numbers will not be large. Therefore, we must rely on much observational information, with some quantitative data to support our conclusions.

I have not attempted here to describe procedures for studying populations of scarce insects. You are all well aware that different techniques are required in handling each problem encountered. We must study such insects and should not give up when the problems seem insurmountable.

We must keep our perspective in population dynamics research. We may enjoy studying insects but just the study of insects is not enough because our primary aim must be to produce healthy forests with a minimum of damage by insects. Population dynamics models must take in account the condition of the host tree which is often the most important factor involved. I am very suspicious of models which revolve around the insect, its parasites and predators, and climatic factors associated with changes in numbers. The two most important variables are the insect and the host. We must thoroughly understand the ecology of both if we are to solve the complex population problems ahead of us.

Finally, let's be critical of our own work but at the same time be willing and eager to accept new ideas and approaches suggested by others. Above all, we must take a few minutes each day to sit on that stump and observe what is happening.

QUALITY CONTROL IN ENTOMOLOGICAL SAMPLING

(Abstract)

by C. J. DeMARS, JR., Entomologist, Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Berkeley, California.

THE USEFULNESS of any sampling program depends upon (1) a clear idea of the question to be answered, (2) a consideration of the various elements which enter into effective sampling, and (3) a means of analyzing the data when collected.

The necessity of phrasing the right question seems so elementary when you see it written out, but it is the heart of the matter of getting started. The kind of question asked is the difference between the EXPERIMENTAL approach and the ANALYTICAL approach. Unfortunately, we are often embarked on an analytical mission equipped with only experimental tools.

The point of all population sampling, brood mortality measurement, population trend estimation, etc., should be to reach a decision about some hypothesis, or at least to frame one. We sample because we want to answer some question. The sessions which preceded this one presented many questions. When these are asked about field situations, they are answered by making sample estimates of some population parameter. Therefore, sampling is an important tool to be used in field work. Again, the point of sampling though, must be to answer our entomological or ecological question, not just to collect data.

The final analysis of these data, once obtained, is a huge problem area. It lends itself to treatment at a number of levels — graph plotting, "t" tests, analysis of variance, regression analysis, and other even more sophisticated techniques. These topics I will leave to those more competent than I am in statistics.

It is a consideration of the various elements which enter into effective sampling to which I will address myself — the accuracy, precision, efficiency, biological relevance, and ecological integrity of the system. I will first define and discuss what is meant by each of these, and then I will try to illustrate how these problems can be approached with examples from research.

The Problem

At the onset I would like to emphasize that the development of an effective sampling system lies in striking a balance between these various elements. There is often no perfect solution; I would venture to say that there is never a perfect solution. The key is balance.

Taking these elements from the top we have:

(a) *Accuracy.*—Human in nature, measured by correlation between different workers or different methods of estimating the same characteristics. Error here results from fatigue, carelessness, poor instruction, confusion about borderline case decisions, etc.

(b) *Precision.*—Statistical in nature, measured by sampling error, used in determining the sample size required to estimate a mean to a certain degree of confidence.

(c) *Efficiency.*—Economic in nature, involves matching resources to statistical needs for optimal effort.

(d) *Biological relevance.*—Biological in nature. Does the sample unit selected and its attribute—the thing counted, measured, identified, pickled, or what have you—have relevance to the question asked? Are you measuring the right thing? And, if so, is its character influenced by the size or shape of the sample unit chosen?

(e) *Ecological integrity.*—Ecological and statistical in nature. Does the definition of the sampling universe coincide (overlap, if you will) with the ecological "universe"? Are you looking at all of the relevant parts of the system you are examining?

The Approach (with reference to real sampling problems).

(a) *Accuracy.*—Dissection vs. radiograph analysis. Comparison of observers. Training.*

(b) *Precision.*—Analysis of variance of brood density measurements over the sampling universe.**

(c) *Efficiency.*—What size sample unit?**

(d) *Biological relevance.*—The effect of plot size on the variance: mean relationship. SAMSIM—a computer sampling simulator.

(e) *Ecological integrity.*—A critique of single parameter measurement.

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