HISTORY AND RELEVANCE OF BEHAVIORAL ECOLOGY
IN MODELS OF INSECT POPULATION DYNAMICS

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The object of studying population dynamics is to acquire a precise description of population behavior. Early models of population systems ignored or oversimplified relevant biological data, and because there was an incomplete representation of the biological (life history) processes that collectively drive the behavior of insect populations, the models were inadequate. Although there have been many advances in models of insect populations since the 1930's (Nicholson 1933, Nicholson and Bailey 1935), and these models have gradually become more biologically realistic, insect population system models have been slow to incorporate good quantitative descriptions of behavioral attributes of individuals. For example, single, fixed values are often used to describe rates of insect development, feeding, mating, oviposition, and mortality. Therefore, the realism in population models is often less than that desired or possible, and less than that necessary for accurate accounting of changes in population sizes.

What models of insect populations need is a greater incorporation of models of insect behavior (Krebs and Davies 1978). This will improve our models of insect predation, parasitism, and population dynamics. Currently, insect population models omit such important phenomena as the switching of prey sources (Holling 1966, Hassell 1978), interspecific interference or avoidance (Hassell 1971), and immigration decisions. By noting how their models are being used, behavioral ecologists can gain insight into how to make behavioral models more realistic with respect to their representation of resource constraints and mortality. Perhaps behavioral models could be incorporated into process-oriented models of population systems as submodels of insect behaviors which influence rates of population processes.

In this paper I will briefly review the history of insect population dynamics models, showing their gradual incorporation of behavioral/ecological elements. Also, I will give some examples of why such incorporation is necessary if insect population models are to be used in a predictive manner to aid pest management decisions. Thirdly, I will suggest some ways by which behavioral ecology can become a more explicit part of insect population modeling.

Population models describe how the numbers of individuals in a population change over time in a defined space. A predictive model describes how population numbers will change given an initial state of the population and set of environmental conditions. Over the past 50 years population models have evolved to become very complex mathematical representations, and

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computer simulation often is necessary to approximate solutions to the equations. The need for greater incorporation of biological detail into population models grew out of the desired applications for population models. Recent emphasis on pest management has demanded more reliable predictions of population status and behavior. Consequently, an evolution is occurring from general population models describing trends, to specific population models designed to accurately predict how the population will affect a resource. Five principle stages in the evolution of population models are: (1) general single species models, (2) two-species models without age structure, (3) matrix models with age structure, (4) process-oriented population system models, and (5) multiple species community system models.

The exponential and logistic growth models (Malthus 1798, Verhulst 1838, Pearl and Reed 1920; see discussion in Wilson and Bossert 1971) were the first population models in which explicit mathematical representations were used to predict population changes, and states at future times. These models used a single differential equation to describe such changes:

\[
\frac{dN}{dt} = rN, \quad \text{Exponential Growth}
\]

and

\[
\frac{dN}{dt} = \frac{r(K-N)N}{K}, \quad \text{Logistic Growth}
\]

where \( r \) is the intrinsic rate of increase, \( N \) is the number of individuals in the population and \( K \) is the carrying capacity of the environment.

These general models had great conceptual value in forcing scientists (and others) to become more aware of the importance of resource constraints on the behavior of individuals and the dynamics of populations. However, both models were biologically oversimplified in that they assumed that all individuals in the population are the same age, and breed continuously. Variable rates of reproduction, survival and resource utilization were ignored in both models.

In the late 1920's and early 1930's two-species population models began to receive attention. The predator-prey model (Lotka 1925 and Volterra 1926) and the host-parasite model (Nicholson and Bailey 1938) used two differential equations to describe changes in two interacting populations. Like their predecessor single-species models, two-species models assumed that all individuals in the population behaved alike. Numbers of encounters of prey (hosts) and predators (parasites) were assumed to be directly proportional only to prey density. Searching efficiency of the predator was assumed not to be influenced by other predators or other environmental conditions. Except in a very limited set of initial conditions, such models are inherently unstable and quite unrealistic for use in pest management applications because efficiencies of predators and parasites of pest species usually are influenced by both abiotic and biotic conditions. Rates of predation and parasitism can vary widely depending upon behavior of individuals in response to local weather conditions and the presence or absence of intra- and interspecific competition among natural enemies. For generalist predators and parasites, rates of mortality inflicted on pest species can be influenced heavily by the densities of alternate prey (non-pest species) or competitor predators and parasites.
Hassell and Varley (1969) modified the Nicholson-Bailey model by incorporating a coefficient to represent mutual interference among parasites. As parasite density increases searching efficiency of parasites decreases:

\[ H_{t+1} = F H_t e^{-Q t(1-m)} \]
\[ P_{t+1} = P_t(1- e^{-R t(1-m)}) \]

where \( H \) and \( P \) are the numbers of hosts and parasites, \( F \) is the net rate of host increase, \( Q \) is the quest (searching area) constant and \( m \) is the mutual interference constant.

The significance of this two-species model was that it recognized that searching behavior of parasites must be incorporated into the model in order to achieve population stability. That is to say, behavior of individuals is an essential feature regulating the dynamics of a population. Although this result may be viewed as an admission of the real world, it was still only a small one. In the Hassell-Varley model the representation of searching area was given by a single parameter value which was not adjusted in accordance with the real behavioral attributes of the parasite or host. Incorporation of the “mutual interference” parameter added a great deal of realism to the Nicholson-Bailey model, but a mechanism for dynamically changing the level of mutual interference as a function of observed behavioral attributes of individuals was lacking.

The Leslie (1945) and Lefkovitch (1965) matrix models divided the population into age classes, with age (or stage) specific survival and reproductive rates. Population performance was assumed to be a summation of performances of each age class, and average survival and reproductive rates were used for each age class. Behaviors of individuals within a class were assumed not to affect rates of survival and reproduction, although biological knowledge tells us that often behavioral attributes of individuals can dramatically affect both survival and reproductive success.

![Diagram of relationships between abiotic factors, physiological and behavioral responses of individuals, and population performances.](image-url)
In an attempt to overcome the assumptions of static rates of survival and reproduction within an age class of a population, process-oriented population system models have evolved. In process-oriented models, modeling focuses on the biological processes that occur during the life cycle and which account for changes in the age structure of a population. Rates of processes can be represented by average values or by complex submodels incorporating knowledge of thermodynamics and behavioral ecology (Sharpe and De Michele 1977, Stimac 1977, Logan et al. 1979). Fig. 1 describes how rates of biological processes are governed by both physiological and behavioral responses of individual organisms. The rates of these processes are necessary for making predictions of population performances. Fig. 2 shows some examples of population processes that are modeled for an insect population. Rates of mating, oviposition, feeding, development and mortality can be influenced by behavior of individuals. Consequently, each process may require a detailed submodel with many equations in which knowledge of behavioral ecology is incorporated. This process-oriented modeling approach offers a logical common ground for traditional behavioral and population ecologists to unite efforts. Behavioral attributes can be altered by population densities and population density changes can be modeled using feedback from changes in behaviors of individuals. For polymorphic populations, the number of state-variable chains (boxes with stages in Fig. 2) can be increased with linkages among morphotypes.

Population models such as shown in Fig. 2 can be linked together through a resource base to form multiple species community system models (Fig. 3). For example, a model of the soybean crop/pest community has been conceptually represented as a five level crop/pest/natural enemy species hierarchy (Stimac and Barfield 1979). Each module in the hierarchy can be a process-oriented population model, describing changes in popula-
Fig. 3. A conceptual model of a soybean crop/pest/natural enemy community. (Modified from Stimac and Barfield 1979.)

...tion numbers as a function of physiological and behavioral responses of individuals to variations in abiotic and biotic factors. Although such a model may involve derivation of thousands of equations, the modeling approach offers the opportunity to incorporate all relevant knowledge of behavioral and population ecology into a single system model. A great advantage to the community system model is that it can be used to examine how behavioral changes in individuals of one population (or subpopulation) affect population or community performance.

In the process-oriented system models, submodels of each biological process can vary in complexity. With greater complexity in submodel structure, more biological knowledge is required. Since acquisition of biological knowledge is costly, one strives to incorporate only the necessary amount of knowledge required to obtain adequate behavior of the model. How does one judge what biological detail is necessary? With process-oriented system models, structural sensitivity analysis helps make such judgments. Given a mathematical representation of a population (Fig. 2) or community system (Fig. 3), the sensitivity of each population to changes in behavior of individuals governing a process can be examined. The general procedure for performing structural sensitivity analysis of the population model is to select a life history process, change the structure of the mathematical submodel representing that process, then examine the impact of the change on population age structure and dynamics.

Processes for which a small change in the structure describing the process (or behavior of individuals governing the process) yield a large change in population dynamics are extremely sensitive to behavioral changes. The more sensitive a process is to changes in behavior of individuals, the greater the need for incorporation of behavioral ecology into the model describing the process. Myers (1976) examined the influence of egg batch size and clumping of egg batches on population performance and stability of an insect population with an exhaustible food resource. Both egg batch size...
and clumping of egg hatches are determined by the oviposition behavior of individual females. Therefore, using a population model in which the structure of the oviposition submodel was changed in accordance with changes in egg laying behavior of female moths, the author was able to examine the "importance" of oviposition behavior. The results showed that population size and stability were highest when egg batch size was as large as could be supported by the average food plant or slightly larger if larval dispersal occurred. Clumping of egg batches on food plants increased population stability when egg batches were small. Similarly, Stimac (1977) used a process-oriented population system model to perform a sensitivity analysis of oviposition for the cinnabar moth, Tyria jacobaeae (L.). Egg loading on host plants was varied between 20 and 200 and population performance was evaluated in terms of percent biomass change of the host plant after one year. Egg loading varying between 40 and 200 eggs per plant showed only a 10-15% change in biomass of the host plant but at 20 eggs per plant more than a 300% increase in host plant biomass was observed. Whether the dynamics of cinnabar moth and its host plant fluctuated violently (unstable) or showed low amplitude fluctuations (stable) depended upon oviposition behavior of female moths. Because cinnabar moth dynamics were found to be so sensitive to egg laying patterns, one can conclude that a population model used to evaluate the biological control potential of the cinnabar moth against its weedy host plant, Senecio jacobaea L., should include an oviposition submodel with a detailed description of egg laying behavior of females.

From the analyses of Myers (1976) and Stimac (1977) it is obvious that average seasonal values representing complex behavioral/ecological processes can lead to serious inadequacy of predictive population models. Other population processes subjected to dramatic changes from behavioral responses of individuals are: (1) dispersal and migration; (2) mating success and mate selection; (3) predation, parasitism, and host selection; and (4) feeding site or host plant selection. Behavior of individuals governing these processes can be heavily influenced by environmental conditions and can change drastically over a short interval of time. Therefore, a predictive population model used for pest management applications can require incorporation of knowledge of behavioral ecology for one or all of these processes.

Finally, the essence of behavioral ecology is the understanding and use of natural selection theory. Recognizing that environmental pressures result in the natural selection that drives population change and evolution (e.g. pesticide resistance), a critical question is, can population models be made to predict what will happen evolutionarily when we put pressure on an insect population? An affirmative answer to this question depends upon the ability of population and behavioral ecologists to unite their efforts for purposes of constructing population system models which contain realistic descriptions of behavioral attributes of individuals.

**Summary**

There has been a historical trend in population models toward incorporation of greater biological detail in descriptions of life history processes responsible for population changes. This evolution has been driven by the knowledge that population performance is a function of both physiological and behavioral responses of individuals to environmental conditions. Ignor-
ing or oversimplifying critical biological components can lead to poor
descriptions of population changes, and models of little utility. For example,
the categorical use of mean values to represent population processes that are
subject to behavioral changes can lead to serious malfunctions in models, and
problems of interpretation. It is important that we make even greater use
of the knowledge and models of behavioral ecologists in dynamic models of
populations, especially if the population models are used in making pest
management decisions.

APPENDIX

For specific examples of how behavioral differences in feeding and migra-
tion can influence insect population performances, see the paper by Frank
Slansky, Jr. in this volume.

A state variable is a variable representing the value or state of an entity
at a particular time. For example, the number of eggs, larvae, or pupae
present at a site at time $t=0$, $t=1$, $t=3$, ..., $t=n$.

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