MATHEMATICAL MODELLING IN ECOLOGY
AANCHAL

ABSTRACT:
Most ecological and evolutionary problems have their basis in changes in the number of organisms. This is one reason why mathematics is an important tool for ecologists and evolutionary biologists. Another one is the overwhelming complexity of ecological systems. An ecosystem often contains hundreds or thousands of species that interact in a complex food web. All species are different and they change continuously - evolution never stops! By formulating mathematical models of ecological and evolutionary processes we can to some extent study the behavior and even understand systems that are this complex.

INTRODUCTION:
Ecology is the science which deals with interactions between living organisms and their environment. Historically it has focused on questions such as:

- Why do we observe certain organisms in certain places and not others?
- What limits the abundances of organisms and controls their dynamics?
- What causes the observed groupings of organisms of different species, called the community, to vary across the planet?
- What are the major pathways for movement of matter and energy within and between natural systems? Historically, mathematical models in ecology have been used largely to provide qualitative explanations for patterns in nature. A classic example of this approach was the effort to use competition models to explain species diversity (Diamond and Case, 1986). Simple competition models showed that species that utilized the same resource can coexist under the right circumstances (Begon et al.,1996). This theoretical observation, however, leads to much controversy over the general issue of whether competition structures natural communities.

  This kind of general statement about nature is arguably of little importance for problems of resource management. Perhaps as a consequence, modeling efforts in many applied fields, especially pest management, have often rejected simple mathematical models in favor of giant simulation models (Onstad, 1988). Simulation models have hundreds of parameters and state variables, take years to construct, and are often so complex that they can take pages to describe. Such models represent the opposite extreme from the simple models used in academic research, in that they attempt to sacrifice understandability for ecological realism.
- The last few decades, however, have seen increased interest in applied questions among academic ecologists, and the resulting research has begun to suggest an alternative use for simple mathematical models (Hilborn and Mangel, 1996). Specifically, simple mathematical models can be used as statistical hypotheses much as linear models have been used in classical statistics
- Moreover, current research suggests that many sets of ecological data cannot statistically justify complex models. That is, although nature may appear to be complicated, real data often cannot prove that more complicated models give a better description than simpler models (Hilborn and Mangel, 1996). Whether this is because nature really is simple, or because our data are noisy, is irrelevant for many practical purposes. The fact is that, if we want useful quantitative descriptions of nature, it is typically the case that we need fewer than 10 parameters
- Current work in ecological modeling thus emphasizes close connections between theory and data, and the use of mathematical models as statistical hypotheses about nature. As a result, models that were once viewed as being of only intellectual interest may well become useful in pest management. To make this point concrete, I will review my own work on a virus disease of a forest pest, the gypsy moth *Lymantria dispar.*

- Ecological models of insect diseases began with a simple model by Anderson and May (1981), which started with a model for human epidemics and added population dynamics of insects and pathogens. Anderson and May used the model to make the general point that pathogens may drive the dynamics of forest insects capable of significant outbreaks such as the larch budmoth, *Zeiraphera diniana*. Further research on this and other insects has instead suggested first that single-factor explanations for forest insect population dynamics are probably generally insufficient, and second that pathogens are not always important players in the population dynamics of forest insects (Hunter and Dwyer, 1998). Nevertheless, even though the original generalization is too sweeping, features of Anderson and May's model have been useful for understanding insect pathogens.

- Specifically, Anderson and May's model assumed that the rate of horizontal transmission of the virus increases linearly with the density of the pathogen. This assumption provided a useful quantitative hypothesis, and it is nonetheless interesting even though data show that it is often incorrect. For example, data for the transmission of the gypsy moth virus reject a linear model but cannot reject a nonlinear model (Dwyer et al., 1997). Additional experiments, however, suggested that this nonlinearity arises because of variability among the host insects in their susceptibility to the virus, and a model that allows for this variability can accurately predict the timing and intensity of virus epidemics (or epizootics) in naturally occurring gypsy moth populations. Surprisingly, the resulting model requires only four parameters.

- Although this model arose from efforts to answer questions of basic research, it is beginning to have practical applications. For example, efforts are being made to genetically engineer this and other viruses. Consequently, a question of environmental concern is, "Will engineered virus strains outcompete wild-type strains, thereby altering the ecological balance between host and pathogen?" Because the model can predict epidemics from experimental transmission data, it can be used to assess the risks of releasing engineered strains before any such strains have been released (Dwyer et al., in press). Preliminary work has suggested that at least one deletion mutant of the gypsy moth virus is unlikely to be a superior competitor, and work is now advancing to apply the model to assess commercially produced strains of the nuclear polyhedrosis virus of the cabbage pest *Trichoplusia ni.*

More concretely, gypsy moth populations tend to be very patchily distributed, so that a major challenge for managers is identifying which populations need to be controlled and which are likely to collapse. Because the virus model can be used to predict which populations are likely to have severe virus epidemics, it can assist in identifying which populations are likely to collapse.

These studies demonstrate several advantages of using simple mathematical models. First, compared to the logistic expenses of performing experiments and collecting data, the cost of constructing, simulating, and analyzing models is very low. Second, models can allow us to extrapolate between small-scale field and lab measurements and the dynamics of populations. The gypsy-moth-virus model, for example, uses as input only the initial density and frequency of infection of gypsy moths in the field, and measurements of disease transmission and kill rates from small-scale lab and field experiments. The model can nevertheless predict the timing and intensity of virus epidemics in naturally occurring gypsy moth populations on 3–10 hectare plots with great accuracy across a wide range of densities (Dwyer et al., 1997; Dwyer et al., in press). This ability to extrapolate across scales means that the model can be used to predict the outcome of large-scale releases of engineered viruses from measurements before such releases are carried out. Third, by focusing on simple explanations for what superficially appear to be complex natural phenomena, simple mathematical models provide useful testable hypotheses. Moreover, the success of the gypsy-moth-virus model, which includes only four parameters, suggests that many natural phenomena are simpler than they initially appear

Mathematics, as the language of science, allows us to carefully phrase questions concerning each of the above areas of ecology. It is through mathematical descriptions of ecological systems that we abstract out the basic principles of these systems and determine the implications of these. Ecological systems are enormously complex. A major advantage of mathematical ecology is the capability to selectively ignore much of this complexity and determine whether by doing so we can still explain the major patterns of life on the planet. Thus simple population models group together all individuals of the same

species and follow only the total number in the population. By ignoring the complexity of differences in physiology, size, and age between individuals, the models attempt to compare the basic dynamics obtained from the model with observations on different species. As a next step, additional complexity, associated with introducing different age classes for example, is included. How the inclusion of such additional complexity affects the predictions of the model determines whether this additional complexity is necessary to answer the biological questions you are interested in.

Mathematical models in physiological ecology are often compartmental in form, in which the organism is assumed to be composed of several different components. For example, many plant growth models consider leaves, stem and roots as different compartments. The models then make assumptions about how different environmental factors affect the rate of change of biomass or nutrients in different compartments. These models are typically framed as systems of differential equations with one equation for each compartment. Population models are used to determine the effects of different assumptions about the age, size, or spatial structure of a population on the dynamics of the population. Mathematical approaches include differential equations (both ordinary and partial), integral equations, and matrix theory. Models for communities are often framed as systems of ordinary differential equations, with separate equations for each of the interacting populations. Additional models apply graph theory to elucidate the topological structure of food webs, the links which determine who eats who in a particular community.

- The above has focused on the use of mathematics to formulate basic theory in ecology. There are also many applications of mathematical and computer models to very practical questions arising from environmental problems. This includes the entire field of ecotoxicology, in which mathematical models predict the effects of environmental pollutants on populations and communities. The field of natural resource management uses models to help set harvest quotas for fish and game, based upon population models similar in form to those mentioned above. Conservation ecology uses models to help determine the relative effects of alternative recovery plans for endangered species, as well as aid in the design of nature preserves.

Modeling is vitally important in making ecological predictions, and whether this takes the form of abstract mathematical equations or computer simulations, the basis is still mathematical. Quantifying ecological data is often done with metrics that turn raw measurements into ecologically relevant information. Statistics is also extremely important in ecology, since we have so much data to crunch; many of the greatest advances in 20th century statistics came about thanks to ecologists.

Since math is so ubiquitous in ecology, I'll just give a few simple, unsophisticated models from one field in ecology: Population dynamics.

$$dx/dt=x(\alpha-\beta y) \quad dx/dt=x(\alpha-\beta y)$$

$$dy/dt=-y(\gamma-\delta x) \quad dy/dt=-y(\gamma-\delta x)$$

These are the Lotka-Volterra equations of population dynamics. x is prey, y is predators, and the rest are constants describing their simple interactions.

The basis of these equations is the idea that population change is birth rate minus death rate (assuming no migration). An increase in the prey population will provide more food for predators, causing their population to increase; this puts more strain on prey, causing their populations to decrease, and predators to follow.

Obviously, the equations are a bit of an idealization. Ecologists have more sophisticated models - models that take into account the fact that prey don't have an unlimited food supply, that weather conditions may change unpredictably over time, that populations evolve, and that there's a hint of randomness to any natural process. But the Lotka-Volterra equations were a vital stepping stone to these models, and the fact that they reflect the periodicity of real-life population dynamics so well is a testament to their success.

Another mathematically interesting population dynamics model - this time, involving just one species - is the logistic map, most notably studied by mathematical biologist Robert May.

Being able to make mathematical predictions about ecological phenomena is essential, because these models inform us about what we should do to resolve problems and conserve biodiversity. Without them, we would just be groping through the dark.

Of course, the kinds of math one uses depend on the problems one wants to study. Pollination experts may use graph theory to model plant-pollinator networks. Evolutionary ecology often requires phylogeny reconstruction, which uses linear algebra. But nearly all ecologists use math, and most regret not taking more.

Modeling ecological complexity

The greatest challenge today, not just in cell biology and ecology but in all of science, is the accurate and complete description of complex systems. Scientists have broken down many kinds of systems. They think they know most of the elements and forces. The next task is to reassemble them, at least in mathematical models that capture the key properties of the entire ensembles. (Wilson 1998, p. 85)

As ecology has matured, our conceptual and theoretical models for how the world works have evolved from the very simple to the very complex (Levin et al. 1997). Simple models that ignore individual and environmental variation, species interactions, and transient dynamics try to capture generalities about systems and offer analytical tractability. However, these models are often insufficient for predicting realistic temporal and spatial patterns. Advances in mathematics, statistics, and computation help us to assess more fully the consequences of such simplifications and to incorporate more realism. In many situations, this translates into more complex models.

A challenge in modeling any system is the choice of level of detail. The challenge resides in identifying which details at one level of organization are driving phenomena at other levels, and which details can be ignored. In many cases, developing a suite of complementary models operating at different scales and levels of complexity will help elucidate the mechanisms underlying observed macroscopic patterns. However, building more detailed and complex models is not always better. Complexity typically demands additional data and computation time, and makes model results difficult to analyze. Researchers need tools for identifying the situations in which building detailed models will increase our ability to understand and predict the structure and dynamics of ecological systems. For example, recent statistical advances based on model selection (box 1) show substantial promise for distinguishing among alternative ecological hypotheses and theories. In general, situations that call for more detailed models will either require mathematical approximations of added complexity or advances in computer science that allow more efficient computation. In the following sections, we describe three areas in which advances in computational science may improve ecological theory by providing ways to incorporate increased biological complexity.

The advantages of simple models should theoretically be even greater in pest management. This is because questions of ecological research can often be phrased somewhat qualitatively, whereas questions of pest management research are ultimately economic and thus inescapably quantitative. I would therefore argue that the infrequent use of mathematical models in pest management is due to an overemphasis on complex simulation models. In addition to being more difficult to understand, such models are inherently more expensive than the simple models that I advocate here. Complex simulation models are therefore less likely to be tested, and in turn are less likely to be discarded in favor of better models. Hopefully simple mathematical models will eventually come to be as useful in pest management as they are in ecological research.

REFERENCES:

1.Anderson, R.M., and R.M. May. 1981. The population dynamics of microparasites and their invertebrate hosts. Philosophical Transactions of the Royal Society, Series B 291:51–524.

2.Begon, M., J.L. Harper, and C.R. Townsend. 1996. Ecology: Individuals, Populations, and Communities, 3rd edition. Cambridge, Mass: Blackwell Science.

3.Diamond, J., and T.J. Case. 1986. Community Ecology. New York: Harper and Row.

4.Dwyer, G., J. Dushoff, J.S. Elkinton, and J.P. Burand. In press. Host heterogeneity in susceptibility: Tests using an insect virus . In Virulence Management, U. Dieckmann, J.A.J. Metz, M. Sabelis, and K. Sigmund, eds. Berlin: Springer-Verlag.

5.Dwyer, G., J.S. Elkinton, and J.P. Buonaccorsi. 1997. Host heterogeneity in susceptibility and the dynamics of infectious disease: Tests of a mathematical model. American Naturalist 150:685–707.

6.Hilborn, R., and M. Mangel. 1996. The Ecological Detective: Confronting Models with Data. Princeton, NJ: Princeton University Press.

7.Hunter, A.F., and G. Dwyer. 1998. Outbreaks and interacting factors. Integrative Biology 1:166–177.

8.Onstad, D.W. 1988. Population-dynamics theory: The roles of analytical, simulation, and supercomputer models. Ecological Modeling 43(1"2):111–124.