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Limitations of Reductionist Approaches in Ecological Modeling: Model Evaluation, Model Complexity, and Environmental Policy

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ABSTRACT

Population ecology has traditionally relied on mathematically simple, and usually tractable, models to mimic the basic dynamics of populations. Parameters in these models are not generally tied to physiology, but reflect aggregate properties of individual behavioral and physiological characteristics. The models are therefore biologically naive, with little direct relevance to practical problems of resource management or risk assessment, although they may be useful as general descriptors of possible population behavior. Models with higher precision and greater biological realism include many more details of population structuring (e.g., age, size, genetics, spatial, dominance, and satiation level), but thereby require many more parameters and assumptions about interactions. These complex models may work well for accurately predicting future population sizes and structures under alternative scenarios for a certain time frame for the few species in which we are willing to invest the requisite financial and research resources. However, the structure of the dynamical systems underlying these complex models is such that analysis of the general behavior of the model is either precluded or requires intensive numerical experimentation. These difficulties, coupled with the fact that the models typically view the habitat environmental variables (physical and biotic) as static, diminish the utility of these reductionist approaches to problems on larger spatial or longer temporal scales. What is needed for problems of environmental policy may well be a hybrid of reductionist and "top-down" approaches. Reductionism can suggest appropriate alternative forms for macrodescriptors of large-scale systems, which may then be coupled to methods that query policymakers as to the level of accuracy they deem necessary to differentiate between the effects of alternative decisions. Evaluation procedures for these models will be quite different from those appropriate for models used mainly for development of general theory.

KEY WORDS

mathematical models, reductionism, aggregation, scaling

INTRODUCTION

> It is a common fallacy to confuse scientists' models of reality with reality itself. A model is a map. A map is not the territory it describes.
>
> Richard Casement, in *Man Suddenly Sees to the Edge of the Universe*

Despite tremendously rapid growth in the development of mathematical models over the past several decades, in application to hosts of scientific disciplines, relatively little attention has been paid to the actual practice of testing and evaluating models. It may be reasonably argued that for most of the physical sciences, in which carefully controlled experiments often lead to observations with small sampling errors, questions of model testing should be relegated to philosophers. In these disciplines, there is no great difficulty in comparing model results with new experiments; rather the concern is whether the model results are consistent with alternative experiments. In the ecological sciences, however, appropriate experiments to test a model may be difficult, if not impossible to perform, and often the data obtained have so large an inherent variation that they do not allow discrimination between several different models. It is often extremely difficult to control all variables that may be affecting a particular behavior of interest unless the experiment is performed under laboratory conditions. How readily laboratory results can be subsequently extended to field conditions, for which there are many more independent and dependent variables, is typically open to much interpretation by the researcher. For these reasons, careful attention to evaluation procedures is essential, particularly if the models are to be used for policy considerations. Yet relatively little work has been done on the development of reasonable agreed-upon procedures for testing models, either for practical applications or in theory.[1]

The lack of substantive work on model evaluation is evident by perusing most of the texts available on mathematical modeling. It is not unusual for these texts to say so little on the subject that it is not even listed in the index (e.g., References 2 through 5), or the comments are limited to parameter estimation and statistical goodness-of-fit (e.g., References 6 and 7). Only a couple of texts illustrate concern for model testing; although some carefully include it in a list of the important attributes of modeling,[8] the general attitude seems to be that the issue is not central to the modeling process. One of the exceptions is the text by Mesterton-Gibbons,[9] which is infused with the importance of testing models, but proceeds mainly by case studies. This offers little in the way of a general approach to model testing, though the author clearly stresses that one important criterion for models being applied in decision-making is their flexibility. France and Thornley[10] devote a brief chapter to model evaluation with emphasis on the importance of testing throughout the modeling process and the difficulty of defining precise criteria for model evaluation.

An admitted difficulty faced by any modeler is the possibility of a conflict of interest in the testing of a model that the same modeler may well have spent a great deal of time and effort developing. Some authors[11,12] argue that criteria for model testing should be specified before model construction begins to ensure that bias does not creep into the evaluation process. In practice, this suggestion is rarely followed in ecology, and the literature is full of models that have never been tested in any substantive way. As Hall and DeAngelis[13] point out, "the testing of the adequacy of models vis-a-vis reality seems to us to be poorly developed and often deliberately and arrogantly ignored." As the quote from Casement indicates, models sometimes take on a life of their own, obscuring the purposes for which the model was ostensibly derived. This can lead to potential misuse of the model by individuals who merely pull a model off the shelf

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when needed without taking care that its use is compatible with the assumptions on which it was originally based.

The main objective in this chapter is to point out the dependence of model evaluation procedures on the problem to which the model is intended to be applied. The author suggests that useful classifications of models based on application and leading to different evaluation criteria are models for theory development; models for specific, carefully delineated systems; and models for policy decisions. The discussion includes ways in which this relates to other classification schemes (e.g., the generality-realism-precision continuum of Levins[14]), and point out some of the difficulties inherent in the application of highly reductionist models based upon the behavior of individuals. Another key point concerns the general inattention of the scientific community to the criteria that policymakers use in making decisions concerning biological systems, in particular the economic, social, and political implications.

MODEL EVALUATION

A wide variety of terms are used by different authors in discussions on model evaluation, including the term *evaluation* itself. Others include testing, accuracy, verification, validation, corroboration, desirability, domain of applicability, certification, realism, tuning, and curve-fitting. This plethora, and the very different meanings assigned to the terms by different researchers, contributes to the lack of agreement on what constitutes effective evaluation. Most authors point out that evaluation is coupled to the purposes for which the model is being constructed. The variety of reasons for constructing models thus leads to differing criteria for evaluation. Several terms are defined for the purpose of this chapter.

Verification. The model behaves as intended, in that the equations correctly represent the stated assumptions. The equations are self-consistent and dimensionally correct, their analysis is error free, and any computer coding has been carried out correctly.[11-15] France and Thornley[10] use the term *testing* synonymously with verification in this sense, as does the present author. In contrast, Jeffers [16] uses *verification* to indicate that a model behaves in ways that broadly fit expectations of how the modeled system behaves, while Shugart[17] uses it to indicate that the model has been investigated to ascertain if it can be made consistent with some set of observations. In the usage of Shugart,[17], verification therefore becomes specific to a particular data set, while in that of Jeffers,[16] it is specific to the modeler.

Validation. The model behavior is in agreement with the real system it represents with respect to the specific purposes for which the model was constructed. Inherent in this is a notion of both accuracy (that is how far apart in some metric the model behavior is from some components of the real system), as well as a domain of applicability (a prescribed set of conditions over which the model is intended to apply). A variety of measures of the domain of applicability have been introduced in theory,[18] but these seem to be of little use in real applications. The metric chosen to specify model accuracy would depend on the purposes for which the model was constructed. For example, if model output consists of a time-dependent vector variable $\mathbf{X}(t) = (X_1(t), \ldots, X_n(t))$ and the data to which the model is being compared were $(x_1(t_1), \ldots, x_n(t_1)), \ldots, (x_1(t_k), \ldots, x_n(t_k))$ for some time points $(t_1, \ldots, t_k)$, then a general form of a metric would be

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$$\Psi\,[X,x) = \sum_{j=1}^{k} \sum_{i=1}^{n} f_{ij}(X_i(t_j) - x_i(t_j))$$

A typical choice for the f_{ij} functions would be a time-weighted least squares such as $f_{ij}(y) = w_i \omega_j y^2$. Here, the ω_j represents relative weights in time so that if emphasis were desired on more recent times, for example, the ω_j would be increasing functions of j. If comparisons were only desired at a single time, then all the weights ω_j would be set to zero, except at that time. The w_i represents relative weights of the different output variables. The above choice of $f_{ij}(y)$ assumes multiplicative effects of the time vs variable weights, though more complicated models could be chosen.

For example, it may be important for a model to determine the occurrence of rare events, one of which could be a population bottleneck; in this case the form of the f_{ij} would not be as above but depend only upon times t_j for which $x_i(t_j)$ is below some preassigned threshold. Such a circumstance may have occurred in the case of the passenger pigeon, due to the interaction between social effects and population size. In situations with limited data, investigators have utilized a variety of Monte Carlo schemes.[19] These involve resampling randomly from a data set split into a calibration component and one used for validation.

Calibration. This refers to the use of a data set to estimate parameters of a model, resulting in model behavior that is consistent with this data set. This is also called curve fitting or model tuning and involves many areas of statistics tied to parameter estimation. Also inherent is a notion of model accuracy, although only in the restricted sense of providing agreement to a particular data set.

Corroboration. The model is in agreement with a set of data independent of that used to construct and calibrate the model. This is one aspect of validation. It is quite different from the notion of corroboration of a scientific theory.[11] The issue of differences between models constructed to elaborate a theory vs those constructed as calculation tools or for prediction has been discussed by a number of authors.[13,20,21]

Evaluation. This term comprises validation plus attention to a variety of criteria, including appropriateness to objectives, utility, plausibility, elegance, simplicity, and flexibility.[10] Therefore, no set of simply objective criteria for evaluation exists, but a number with different weightings assigned to each through the preferences of the investigator. It is the areas emphasized in the evaluation criteria that serve to differentiate the modeler, who is often primarily interested in either theory development or a particular scientific question, from the manager or politician who is in general answerable to the public for decisions influenced by the model.

EVALUATION CRITERIA FOR DIFFERENT TYPES OF MODELS

One classification scheme for models considers where along the generality-realism-precision continuum they occur,[14] because no single model is capable of completely satisfying all three criteria. At the outset of a modeling project, a decision is made regarding where on this continuum the resulting model should be focused. This is intimately tied with the purposes for which the model is being constructed, and the evaluation criteria are chosen accordingly.

Models for theory development comprise the majority of the subject of mathematical ecology, with emphasis on generality, a slight amount of realism, and typically very

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little precision. Evaluation criteria here are tied more to biological reasonableness, rather than to biological reality, for the objective is to produce a theory for general patterns of nature.[20] Validation here takes the form of qualitative comparisons with nature rather than quantitative comparisons. Parameters in these models are often far removed from observable biology. Far too much effort in ecology has been wasted in trying to estimate model parameters such as the coefficients in Lotka-Volterra type models. If estimable at all, these coefficients would result from complex interactions of many physiological and population-scale processes. The models serve useful qualitative roles, but trying to squeeze them into a role for which they are not suited is a wasted effort. Calibration and corroboration are not appropriate for these models, for the objective is typically to investigate how model behavior varies qualitatively over what is viewed as a reasonable parameter space.

In a number of instances, however, models developed having mainly theoretical goals have proven to be useful in extensions to particular problems with close ties to observable biology. One example includes the McKendrick-von Foerster formulation of a population structured by age, size, or physiological state. This partial differential equation model is very general in form and serves as a basis for the theory of continuously structured populations. Yet it has been shown to be quite useful as a means to couple toxicological effects on individuals to population scale phenomena (see Chapter 49). Very simplistic epidemic models have been extended in a host of ways to analyze specific instances of disease spread, with varying success,[22] and simple host-parasite models have been extended to apply to several case studies of macroparasite infection and spread.[23] Other examples include the applications of very general reaction-diffusion models to many situations of animal movement.[24] Here, applications to particular field situations typically involve discretizations of the underlying partial differential equation or random walk model being approximated.[25] Thus, theoretical models not only are important for the development of general paradigms, but often lead to more realistic extensions closely coupled to biological data. This requires a step back from the generality of the original model, however, along with an attendant increase in model complexity and size of parameter space.

Models for specific systems (e.g., a given fish stock in a particular region, or a particular mammal population in a forest) are typically tied to data sets that, though often very limited, provide some guidance for choosing possible validation criteria as well as possible model formulations.[26] It makes little sense to construct a model with detailed social structuring in the population, if there are no data available to estimate the nature of this structuring. Population models of this sort are typically based around some method of fancy bookkeeping, particularly discrete age-structured models used for wildlife populations. The assumptions about the mortality and fecundity relationships in these models are typically the weakest components, and the most difficult to validate. Nevertheless, it is these components that detail the coupling between individuals and the population-scale effects of external environmental factors.[27] Evaluation criteria, therefore, may need to be more stringent in application to some model components than to others.

Of all applications of ecological modeling, the author believes the uses in policy analysis have the poorest record of results obtained for efforts expended. A graphical scheme to illustrate the situation is shown in Figure 1. The horizontal axis corresponds to a simple bounded set of possible decisions. The solid line portrays a modeling effort producing what might be considered superb results for a particular policy decision. In this case, any particular policy chosen results in an easily understood outcome that is completely deterministic. This outcome results from a biological analysis of the situation, with higher values corresponding to stronger negative effect on the population in

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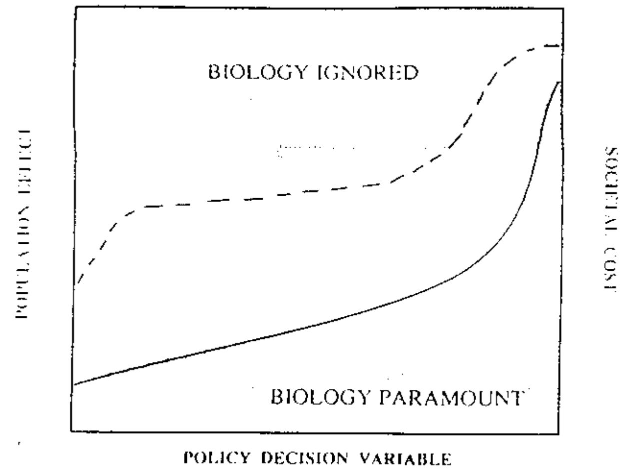

FIGURE 1. Scheme to illustrate the combination of social and political concerns (dashed curve) along with scientific criteria (solid curve) affecting a policy decision. Social cost and population effect are not on commensurate scales.

question. Thus, a rational decision may be made based upon some acceptable level of the outcome. Possible examples are population size remaining given a certain amount of habitat destruction, population size as a function of mean toxicant concentration per unit area of habitat, or fraction of suitable habitat remaining to a species after a given land-use scheme is implemented.

The difficulty with the preceding analysis is that typically quite different criteria, not included in the biological assessment of effects, are applied in making the policy decision. Figure 1 (dashed line) illustrates the effects of the policy decision on social factors such as loss or gain of jobs, expenditures to maintain the local economy, infrastructure or bureaucracy needed to carry out the decision, and the opportunity costs associated with these expenditures. These could just as well be political costs, such as the perceived political advantage to the decision-makers of carrying out a particular policy, including gain of financial support from certain constituents. The dashed curve corresponds to a particular societal cost function. The solid and dashed curves are not commensurate quantities; combining them in some way involves multiple-criteria optimization and construction of a utility function that makes assumptions about the effects of alternative combinations. Societal costs act to effectively constrain policy responses in many instances, in particular to the endpoints of the policy decision set.

Several possible scenarios are illustrated in Figure 1. The upper shaded region indicates a threshold such that if the social costs are within this area, these costs completely determine the policy choice with any possible population effects being ignored. Similarly, the lower shaded region illustrates a situation in which biological factors completely outweigh any political or social concerns, and policy choice is determined completely by biology. Cases corresponding to these situations are readily available. The recent controversy regarding the use of Alar on apples[28] illustrates that when direct effects of toxicants on humans are perceived to be large, policy decisions can be made based entirely upon social factors, independent of the biological data, which in this case indicated minuscule relative health effects on the population. As an alternative to this example of policy action being taken according to political and social factors,

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consider the case of the spread of resistance to antibiotics in bacterial populations endemic among humans. Here, despite the fact that many researchers feel that the widespread use of antibiotics in animal feed has fostered the development and spread of new bacterial strains with quite damaging human health effects, governmental agencies have taken very little action on the issue, except to request further studies.[29] This is one example of a common property resource overutilized for the benefit of one component of society but not rational from a total society viewpoint.[10] Although in general one may believe that an analysis of recent past policy decisions would indicate that it is situations involving direct effects on human health for which the biological impacts (the solid line in Figure 1) take precedence over the political, this may not always hold true. Certainly, direct human effects would more frequently take precedence relative to effects on other species.

Situations for which the social and political factors fall into the unshaded region are those in which our models have been least successful. In part this is due to the ignorance of social factors when structuring our models. What may appear to the biologists to be very large effects may well appear very small when viewed in a policy framework that takes account of social factors. The level of detail of our models must therefore take into account the level of indifference to details imposed not by biology, but by external social factors. Dealing with externalities is a standard difficulty in bioeconomics but with little agreement as to how to do so.[30].

Figure 1 is, of course highly simplified. The policy decision space is often not represented as a single variable, and multiple biological, social, and political criteria may be applied. The underlying view of Figure 1 assumes the world is deterministic, while often we can do no more than specify outcomes with certain probabilities, or in a mean sense. Probabilistic explanations introduce difficulties both in the analysis of models as well as in their explanation to policymakers. The view of Figure 1 is also static, ignoring both the dynamics of the system being modeled as well as the adaptive nature of policy decisions.

Key data are typically not available for many resource management problems. Uncertainties in extrapolation from limited data sets can lead to potentially large errors in predicting ecosystem response to external inputs such as toxicants.[31] In such situations, one goal of a management policy could be to explicitly attempt to force the system into very contrasting outcomes. A policy that leads to large deviations from a mean response of a system can be highly useful because it provides a method to evaluate the applicability of a model under very different circumstances. This process of adaptive management is a particularly useful means to quickly increase the accuracy and utility of models in situations with very limited data.[32,33] Another aspect of the information effects of policies is the potential for a policy to change the nature of currently operating social and political factors, primarily through education.

REDUCTIONISM AND ENVIRONMENTAL POLICY

A natural tendency in applying models derived for general theory to policy concerns, or to specific management situations, is to add complexity to increase potential precision and allow for calibration and corroboration, through the introduction of detailed submodels. Many of the detailed single species and multispecies models take this approach. It is one alternative to strictly empirically based models such as those for habitat indices, or statistical models coupled to a particular database. As noted above, this has led to useful results in several situations. It also requires either a much larger database or many more assumptions about particular model forms. These models have

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limitations, however, because they typically amalgamate all individuals within some class (age, size, physiological state, etc.) and assume uniformity within this class. Situations with strong neighborhood effects, or whose assumptions of uniformity within a class break down (e.g., population sizes are so low that a class consists of few individuals) are not readily handled by these extensions of theoretical models. Thus, there are a number of ongoing attempts to model populations as interacting individuals, tracking each separately in a simulation format.[34,35]

The new individual-based models have great appeal for a number of reasons. First, they allow explicit behavioral rules to be specified at the individual level and do not require ad hoc assumptions about the effect of these behaviors at the population scale. Second, such models are relatively easy to construct once the behavioral rules are specified, since essentially dynamic bookkeeping is done from that point. (It should be noted that efficient algorithms to handle this for simulations involving large numbers of individuals are not easily obtained.) Third, they naturally provide a means to handle individual interactions and neighborhood effects, and Monte Carlo methods provide for analysis of situations with small population sizes.

The problem is that these models quickly grow to require enormous numbers of assumptions about individual behavior for which the available evidence is limited. They are numerical, not qualitative, so determining the effects of a poorly understood assumption requires numerous simulations. Validation of the submodels is precluded without a vast amount of field observations of individual behavior. A saving grace of these models is that they are relatively easy to explain to managers since the key objects are individual organisms rather than more abstract population mortality and fecundity schedules. This implies a great future for these models in policy applications, because a key limitation in the use of models by managers may be the ability to understand, at some level, how the models are constructed. Understanding on the part of the manager may lead to more ready acceptance of the model results as well as feedback from the manager in the decision process.

The author would argue, however, that policy applications of these models are generally premature, mainly due to the enormous number of poorly understood assumptions from which the models are constructed. The parameter space may be so rich that essentially any result desired can be obtained through judicious choices of the parameters. Because the models require large Monte Carlo simulations, sensitivity analyses of these models are quite computer intensive. To determine how sensitive the model output is to a parameter, one must essentially conduct a Monte Carlo analysis on a Monte Carlo simulation by varying the parameter within some range and observing how model output is affected.

It is the author's belief that these highly reductionist models will be most useful in a policy sense if they provide means to suggest appropriate large scale macrodescriptors of systems. These macrodescriptors should be robust so that the outcomes are not highly sensitive to the details of individual behavioral assumptions. The best way to accomplish this is using a top-down approach. Here, one starts with the manager and attempts to ascertain levels of indifference to model outcomes. This approach provides a means to scale the amount of reductionism necessary to meet the goals of the manager, and reduces wasted effort dealing with minute details of biological processes, if these are second or third order effects in the scheme of acting social and political constraints.

SUMMARY

Models are not a panacea. In analyzing policy issues, models have two main uses: to allow investigation of system behavior under alternative assumptions when information is limited about key processes affecting the system; and (2) to provide a mechanism to predict system behavior under alternative management policies, possibly coupling this with criteria to determine optimal policy choice. Unless information is very detailed about a particular natural system, the investigation in the first use will be necessary before model results can be reliably applied to carry out the second use.

Just as modeling is an iterative process, so is social policy choice. The political process is often one of compromise that involves trade-offs for certain constituencies, made in an iterative manner. The objective is to couple this iteration with the iteration of the modeling process,—not with a single model, or even a single class of models, but rather with models that are most effective at each stage of the policy decision process. For example, the choice of national land-use plans would require models on much larger, regional, or global scales than the implementation of that policy at smaller, local scales. Managing particular forest systems according to local guidelines, taking account of local wildlife, recreational use, and wood product production, would require finer detail in any model being utilized. When averaged over large regions, these local guidelines would conform to the large-scale policy, but may on a small scale be quite diverse.

Models used at these diverse spatial scales would be quite different in form. The detail necessary at smaller scales can come from reductionist approaches, including individual-based models that mimic the behavior of numerous individual organisms to allow prediction of population and community behavior. On larger scales, the hope is that these reductionist approaches will suggest the form for less detailed models of sufficient realism to be applied under very differing policy alternatives. There has been little experience to date in developing large-scale models in this manner, yet they are a critical component of regional and global planning. If their development is also closely coupled to input from those responsible for policy decisions, our detailed knowledge of local biology will have been successfully integrated with the constraints imposed by social factors to produce a rational method of environmental social choice.

REFERENCES

1. Shugart, H. H., and R. V. O'Neill, *Systems Ecology*, Dowden, Hutchison & Ross, Stroudsburg, PA, 1979.
2. Maki, D. P., and M. Thompson, *Mathematical Models and Applications*, Prentice-Hall, Englewood Cliffs, NJ, 1973.
3. Beltrami, E., *Mathematics for Dynamic Modeling*, Academic Press, Orlando, FL, 1987.
4. Rose, M. R., *Quantitative Ecological Theory: An Introduction to Basic Models*, Johns Hopkins University Press, Baltimore, 1987.
5. Jeffries, C., *Mathematical Modeling in Ecology: A Workbook for Students*, Birkhauser, Boston, 1989.
6. Giordano, F. R., and M. D. Weir, *A First Course in Mathematical Modeling*, Brooks/Cole, Monterey, CA, 1985.
7. Edelstein-Keshet, L., *Mathematical Models in Biology*, Random House, New York, 1988.
8. Roberts, F. S., *Discrete Mathematical Models*, Prentice-Hall, Englewood Cliffs, NJ, 1976.
9. Mesterton-Gibbons, M., *A Concrete Approach to Mathematical Modeling*, Addison-Wesley, Redwood City, CA, 1989.
10. France, J., and J. H. M. Thornley, *Mathematical Models in Agriculture*, Butterworths, London, 1984.

9.

11. Caswell, H., The validation problem, in *Systems Analysis and Simulation in Ecology*, Vol. 4. B.C. Patten, Ed., Academic Press, New York, 1976, pp. 313-325.
12. Overton, W. S., A strategy of model construction, in *Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories*, C. A. S. Hall and J. W. Day, Eds., John Wiley & Sons, New York, 1977, chap. 3.
13. Hall, C. A. S., and D. L. DeAngelis, Models in ecology: paradigms found or paradigms lost?, *Bull. Ecol. Soc. Am.*, 66, 339-346, 1985.
14. Levins, R., *Evolution in Changing Environments*, Princeton University Press, Princeton, NJ, 1968.
15. Levis, A. H., and I. S. Levis, Toward a conceptual framework for policy analysis modeling, in *System Theory Applications to Agricultural Modeling*, A. H. Levis and C. L. Quance, Eds., USDA Publ. ESCS-07, U.S. Department of Agriculture, Washington, DC, 1978.
16. Jeffers, J. N. R., *Modelling*, Chapman & Hall, London, 1982.
17. Shugart, H. H., *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*, Springer-Verlag, New York, 1984.
18. Mankin, J. B., R. V. O'Neill, H. H. Shugart and B. W. Rust, The importance of validation in ecosystem models, in *New Directions in the Analysis of Ecological Systems, Part 1*, Simulation Councils Proceedings Series, Vol. 5, G. S. Innis, Ed., Simulation Councils, LaJolla, CA, 1977, pp. 63-71.
19. Wegener, K. R., and R. F. Malone, A methodology for determining the predictive accuracy of mathematical models from a limited data base, in Analysis of Ecological Systems: State of the Art in Ecological Modeling, Developments in Environmental Modeling, Vol. 5, W. K. Lauenroth, G. V. Skogerboe and M. Flug, Eds., Elsevier, Amsterdam, 1983, pp. 75-80.
20. Levin, S. A., Mathematics, ecology, ornithology, *Auk*, 97, 422-425, 1981.
21. Loehle, C., Evaluation of theories and calculation tools in ecology, *Ecol. Model.*, 19, 239-247, 1983.
22. Aron, J. L., Simple versus complex epidemiological models, in *Applied Mathematical Ecology*, S.A. Levin, T. G. Hallam and L. J. Gross, Eds., Springer-Verlag, Berlin, 1989, pp. 176-192.
23. Dobson, A. P., The population biology of parasitic helminths in animal populations, in *Applied Mathematical Ecology*, S. A. Levin, T. G. Hallam and L. J. Gross, Eds., Springer-Verlag, Berlin, 1989, pp. 145-175.
24. Okubo, A., *Diffusion and Ecological Problems: Mathematical Models*, Springer-Verlag, Berlin, 1980.
25. Kareiva, P., Predator-prey dynamics in spatially structured populations: manipulating dispersal in a Coccinellid-aphid interaction, *Lect. Notes Biomath.*, 54, 368-389, 1984.
26. Cale, W. G., R. V. O'Neill and H. H. Shugart, Development and application of desirable ecological models, *Ecol. Model.*, 18, 171-186, 1983.
27. Emlen, J. M., Terrestrial population models for ecological risk assessment: a state-of-the-art review, *Environ. Tox. Chem.*, 8, 831-842, 1989.
28. Marshall, E., 1991, A is for apple, Alar, and . . . alarmist?, *Science*, 254, 20-22, 1991.
29. Wright, K., Bad news bacteria, *Science*, 249, 22-24, 1990.
30. McKelvey, R., Common property and the conservation of natural resources, in *Applied Mathematical Ecology*, S. A. Levin, T. G. Hallam and L. J. Gross, Eds., Springer-Verlag, Berlin, 1989, pp. 58-80.
31. O'Neill, R. V., R. H. Gardner, L. W. Barnthouse, G. W. Suter, S. G. Hildebrand and C. W. Gehrs, Ecosystem risk analysis: a new methodology, *Environ. Toxicol. Chem.*, 1, 167-177, 1982.
32. Ludwig, D., and R. Hilborn, Adaptive probing strategies for age-structured fish stocks, *Can. J. Fish. Aquat. Sci.*, 40, 559-569, 1983.
33. Walters, C., *Adaptive Management of Renewable Resources*, Macmillan, New York, 1986.
34. Huston, M., D. L. DeAngelis and W. M. Post, New computer models unify ecological theory, *Bioscience*, 38, 682-691, 1988.
35. DeAngelis, D. L., and L. J. Gross., *Individual-Based Models and Approaches in Ecology*, Chapman and Hall, New York, 1992.

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WILDLIFE TOXICOLOGY and POPULATION MODELING

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