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

Louis J. GROSS
University of Tennessee
Department of Mathematics and
Graduate Program in Ecology
Knoxville, TN 37996-1300
U.S.A.

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Limitations of Reductionist Approaches in Ecological Modeling:

Model Evaluation, Model Complexity and Environmental Policy

Louis J. Gross
Department of Mathematics and
Graduate Program in Ecology
University of Tennessee
Knoxville, TN 37996-1300

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, though 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 (age, size, genetics, spatial, dominance, satiation level, etc.), but thereby require many more parameters and assumptions about interactions. These complex models may work well (in terms of being accurate predictors of future population sizes and structures under alternative scenarios for a certain time frame) for the few species for 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. Coupling these difficulties with the fact that the models typically view the habitat environmental variables (physical and biotic) as static, diminishes 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 approaches, to indicate alternative appropriate forms for macrodescriptors of the system on these larger scales, with top-down approaches which query the policy-makers 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 a tremendously rapid growth in the development of mathematical models over the last several decades, in application to hosts of scientific areas, relatively little attention has been paid to the actual practice of testing and evaluating models. It might be reasonably argued that for much of the physical sciences, in which carefully controlled experiments can often lead to observations with small sampling errors, questions of model testing should be relegated to philosophers. Here there is no great difficulty in comparing model results with new experiments, but rather the concern is with how many alternative such experiments the model is consistent. 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 which may be affecting a particular behavior of interest unless the experiment is performed under laboratory conditions. How readily the lab results then can be 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 there has been relatively little work 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. 2, 3, 4, 5] or else limit the commments to parameter estimation and statistical goodness-of-fit [e.g. 6, 7]. Only a couple of texts illustrate concern for model testing; even though some carefully include it in a list of the important attributes of modeling [e.g. 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 criteria 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.

There is an admitted difficulty faced by any modeler due to the possibility of a conflict of interest in the testing of a model that the 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 which have never been tested in any substantive way at all. 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 above 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 when needed without taking care that the use to which it is being put is compatible with the assumptions on which it was originally based.

One objective in this paper is to point out the dependence of model evaluation procedures on the context for which the model is intended to be applied. I suggest that a useful classification of models which leads to different evaluation criteria is: models for theory development; models for specific, carefully delineated systems; and models for policy decisions. How this relates to other classification schemes (e.g. the generality-realism-precision continuum of Levins [14]) will be discussed, and along the way I'll 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 which policy-makers use in making decisions concerning biological systems, in particular the economic, social and political implications. I begin with a quick overview of some of the work on mouel evaluation.

MODEL EVALUATION

A wide variety of terms are used by different authors in discussions on model evaluation, including: evaluation, 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, illustrates the lack of agreement as to 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. For the purposes of this paper, I will use tne following definitions:

Verification: model behaves as intended, in that the equations used 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, and I will as well. In contrast, Jeffers [16] uses "verification" to indicate that a model behaves in ways which broadly fit your expectations of how the system being modeled does behave, 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: 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 $\boldsymbol{X}(t)=(X_1(t),\dots,X_n(t))$ and the data to which the model is being compared were $(x_1(t_1),\dots,x_n(t_1)),\dots,(x_1(t_k),\dots,x_n(t_k))$ for some time points $(t_1,\dots,t_k)$, then a general form of a metric would be

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

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 represent relative weights in time so that if emphasis were desired on more recent times, for example, the ω_j's 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's represent relative weights of the different output variables. The above scheme assumes multiplicative effects of the time versus variable weights,

though more complicated models could be chosen.

For example, it might be important for a model to determine the occurrence of rare events, one of which might be a population bottleneck, in which case the form of the f_{ij}'s 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 a situation with limited data, a variety of Monte-Carlo schemes have been investigated which involve splitting the data into a calibration component and one used for validation [19].

Calibration: use of data to determine parameters of the model so that the model behavior is in agreement with this particular data set. This is also called curve-fitting or model tuning and involves many areas of statistics tied to parameter estimation. Inherent here is also a notion of model accuracy, though only in the restricted sense of providing agreement to the particular data set.

Corroboration: a set of data independent of that used to construct and calibrate the model is in agreement with 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 versus those constructed as calculation tools or for prediction has been discussed by a number of authors [20, 21, 13].

Evaluation - validation plus attention to a variety of criteria, including appropriateness to objectives, utility, plausibility, elegance, simplicity, and flexibility [10]. There is not therefore a set of simply objective criteria for evaluation, but a number with different weightings assigned to each through the preferences of the investigator. It is the emphasis in the evaluation criteria which serves 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 in the generality-realism-precision continuum they occur [14], with no one model capable of satisfying all three completely. At the outset of a modeling project, some decision is made regarding where in this continuum the resulting model should be aimed. 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 make up the majority of the subject of mathematical ecology, with emphasis on generality, a slight amount of realism, and typically very little precision. Evaluation criteria here are tied more to biological reasonableness, rather than 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 ones. Parameters in these models are often far removed from observable biology. Thus the coefficients in a Lotka-Volterra type model are amalgams of many physiological and population-scale processes, with far too much effort wasted in ecology trying to estimate them. 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.

There are a number of instances however in which models developed with 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 an age/size/physiological state structured population. 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 the paper by Hallam and Lassiter in this volume). 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 a number of 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 which is being approximated [25]. All of these illustrate that not only are theoretical models important for development of general paradigms, but they often lead to more realistic extensions which are closely coupled to biological data. This requires a step back from the generality of the original 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, a particular mammal population in a forest, etc.) are typically tied to data sets which, though often very limited, provide some guidance as to the validation criteria possible to choose as well as the 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. It is the assumptions which go into the mortality and fecundity relationships in these models which are typically the weakest component, and the most difficult to validate. It is these components which detail the coupling between individuals and the effects of external environmental

factors at the population scale [27]. Evaluation criteria therefore might need to be more stringent in application to one model component than to others.

It is the area of models for policy decisions that I believe has the poorest record of results from effort expended of any area within ecological modeling. A graphical scheme to illustrate the situation is shown in Figure 1. The horizontal axis corresponds to a simple bounded set of possible decisions. Here we view a modeling effort as producing what might be considered superb results for a particular policy decision. In this case, an easily understood outcome (the solid line in the figure), which is completely deterministic, for any particular policy chosen. This is meant to represent the outcome from a biological analysis of the situation, with higher values corresponding to stronger negative effect on the population in question. Thus a rational decision might be made based upon some acceptable level of the outcome. Examples might be 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 above is that there are typically quite different criteria, not included in the biological assessment of effects, which are applied in making the policy decision. Several possible results are illustrated in Figure 1. These are meant to illustrate 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. They could just as well be political costs, including the perceived political advantage to the decision-makers to carrying out a particular policy, including loss or 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 which makes assumptions about the effects of alternative combinations. The societal costs act to effectively constrain the 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, 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 apparent. The recent controversy regarding the use of Alar on apples 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, 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, there has been very little in the way of action by governmental agencies on the issue, except to request further studies [28]. This is one example of a common property resource which is overutilized for the benefit of one component of society but is not rational from a total society viewpoint [29]. Though in general one might believe that an analysis of policy decisions over the recent past would indicate that it is situations involving direct effects on human health for which the biological impacts (the solid line in Figure 1) take precedent over the political ones, I am not at all certain this would hold. Direct human effects certainly would more frequently take precedence relative to effects on other species though.

Situations for which the social and political factors fall into the region bounded between the two dotted curves are the ones in which our models have been least successful. In part this is due to the ignorance of these social factors in the way we structure our models. What may appear to the biologists to be very large effects may well appear very small when viewed in a policy framework taking account of social factors. The level of detail of our models must therefore take account of the level of indifference to details imposed not by biology, but by external factors. Dealing with externalities is a standard difficulty in bioeconomics but with little agreement as to how to do so [29].

The above illustration is of course highly simplified. The policy decision space is often not representable as a single variable, and there are multiple biological criteria which might be applied as well as social and political ones. The above view assumes the world is deterministic, while often we can do no more than specify outcomes with certain probabilities, or in a mean sense. Probabalistic explanations introduce difficulties both in the analysis of models as well as in their explanation to policy-makers. The above view is also a static one, ignoring both the dynamics of the system being modeled as well as the adaptive nature of policy decisions. A large body of literature suggests that in situations with very limited data, corresponding to much of resource management, policies leading to very contrasting outcomes may be highly useful methods to increase the accuracy of the models as well as their utility [30, 31]. There are large potential errors in the prediction of ecosystem effects of toxicants induced by uncertainties in extrapolation from limited data sets [32]. Another aspect of the information effects of policies is the potential for a policy to change the nature of the social and political factors which are operating. A primary

mechanism for this change is education.

REDUCTIONISM AND ENVIRONMENTAL POLICY

A natural tendency in the application to policy concerns, or to specific management situations, of models derived for general theory is to add complexity to increase the potential precision and to allow for calibration and corroboration through the introduction of detailed sub-models. Many of the detailed single and multi-species models take this approach. It is one alternative to strictly empirically based models such as those for habitat indices, or statistical models which are coupled to a particular data base. As noted above, this has led to useful results in a number of situations. It also requires a much larger data base, or many more assumptions about particular model forms. These models have limitations however, since 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 for which the assumptions of uniformity within a class break down (e.g. if population sizes are low so that a class consists of few individuals) are not readily handled by these extensions of theoretical models. Thus there are ongoing a number of attempts to model populations as interacting individuals, tracking each individual separately in a simulation format [33].

The new individual-based models have great appeal for a number of reasons. First, explicit behavioral rules can be specified at the individual level and there is no need to make ad hoc assumptions about the effect of these behaviors at the population scale - this comes out of the model. Secondly, they are relatively easy to construct once the behavioral rules are specified, since one is essentially doing a dynamic bookkeeping from that point, though it should be noted that efficient algorithms to handle this for the large numbers of individuals being simulated are not easily obtained. Thirdly, 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 rub in the above is that these models quickly grow to require enormous numbers of assumptions about individual behavior for which there is little available evidence. They are numerical and not qualitative, so determining the effects of a poorly understood assumption requires large numbers of 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 would imply a great future for these in policy applications since 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 as to what is really desired by the manager in the decision

process.

Yet, I would argue that policy applications of these models is 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. Since they are themselves large Monte-Carlo simulations, sensitivity analyses of these models are quite computer-intensive. One essentially must Monte-Carlo a Monte-Carlo.

It is my 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 should be robust in the sense that the outcomes are not highly sensitive to the details of individual behavioral assumptions. This leads to suggested forms for a top-down approach. Here, one starts with the manager and attempts to ascertain levels of indifference to model outcomes. This provides a means to scale the amount of reductionism necessary to meet the goals of the manager, and doesn't waste effort dealing with minute details of biological processes if these are second or third order effects in the scheme of social and political constraints acting.

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FIGURE LEGENDS

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. See text for further explanation.