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In Defense of Big Ugly Models

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SINCE THE INTRODUCTION OF MODERN, high-speed computers, there has been a divergence of approaches to modeling ecological systems. One path builds on the historical lineage of mathematical analysis pioneered by physicists and applied mathematicians. The objective of this approach is to build a model amenable to the classical tools of mathematical analysis. Such models generally have been referred to as *theoretical models*; for example, as used by May (1976) in his book, *Theoretical Ecology*. In an attempt to provide models amenable to the tools of mathematical analysis, and also to result in general descriptive power, theoretical models typically follow the principle of parsimony, which states that the modeling process should start with the simplest possible structure and include complexity only when absolutely necessary (Berryman et al. 1990, Royama 1992).

The other path has followed the route of computational power provided by digital computers. In this approach, there is neither the need nor the motivation for parsimony, and the objective is to provide a mechanistically detailed representation of the modeled system. Models developed through this approach generally are referred to as *simulation models*. In contrast to the *elegant* models that are the goal of theoretical ecology, these biologically explicit models tend to be complex mathematical descriptions—the big ugly models that are the topic of this article.

Although there is a continuum that ranges from clearly theoretical models on one hand (e.g., the Lotka/Volterra predator-prey equations), to complex simulation models of an entire insect life system on the other, the principal of parsimony results in qualitative criteria that serve to identify these two modeling approaches. In general terms, theoretical models consist of coupled differential or difference equations with only a few *state variables*¹ (typically less than 10, perhaps only 1), whereas simula-

tion models may contain tens or even hundreds of state variables. The number of parameters likewise differs between the two modeling approaches; the number of parameters in a theoretical model is typically less than 20 (often as few as 4 or 5), and a simulation model may contain hundreds of parameters. Interpretation of model parameters also tends to differentiate the two approaches. The principal of parsimonious structure in theoretical models necessitates that many system interactions either are ignored or their effects are combined, resulting in abstracted, composite parameters.

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The computational intensive, mechanistically detailed descriptions of simulation models tend to have parameters with straightforward biological/ecological interpretation. In fact, an underlying principal of the simulation approach is system description in terms of parameter values that can be measured directly. Qualitative characteristics that differentiate theoretical models from simulation models are discussed further in Berryman (1991) and Logan (1989a).

Systems analysis, a formalized procedure for the study of complex systems, typically has relied up on the construction and analysis of mechanistically based computer simulation models (Hall & Day 1977). This approach had its origin in the engineering sciences during the early 1960s. Many of the concepts of systems analysis were established in Forrester's (1961) influential publication, *Industrial Dynamics*. For a book with such an unpromising title, *Industrial Dynamics* (and the principles so lucidly

stated by Forrester) has had a profound influence on the science of insect ecology. Based on the principles outlined in this book, the most ambitious ecological research program to date was launched under the auspices of the International Biological Program (IBP).² The IBP represented a massive influx of resources into ecological research, including an entomological component that became known as the *Huffaker Project* (Huffaker 1980). Central to the research philosophy of the IBP was the development of large-scale, computer simulation models. The modeling approach of the IBP was embraced fully by the Huffaker project; of 12 specific objectives, 7 were related directly to the development of simulation models (Stone 1989).

At first, the application of simulation models was endorsed by the entomological community at large. This statement is supported by the profound influence that the Huffaker project had on the concepts of pest management as they evolved during the 1970s and early 1980s, including the Adkisson project (Frisbie & Adkisson 1986), which succeeded the Huffaker project, and the various big bug programs that were sponsored by the USDA Forest Service (e.g., Brookes et al. 1978). Publications on the topic in influential periodicals, such as the *Annual Review of Entomology* (Ruesink 1976) and *Science* magazine (Coulman et al. 1972), are further evidence of the influence that systems analysis and simulation models have had on pest management in general. The initial infatuation with complex simulation models, however, began to wane during the 1980s, initiating a trend that has continued to the present. An indication of the extent of this disenchantment is exemplified in recent articles by A. A. Berryman (1991) and A. M. Liebhold (1994), both of whom are quantitatively oriented insect ecologists.

Berryman compares and contrasts the relative strengths and weaknesses of theoretical and simulation models. In his analysis, the theoretical approach was far

¹State variables are the defining variables of a modeled system and describe the status or state of the system at any particular point in time. Changes in values of state variables define the temporal dynamics of the system

²Total U.S. funding for the IBP was more than \$55 million in 1970s dollars (J. T. Callahan, personal communication).

superior to the simulation approach, not only for basic ecological inquiry, but also in the prediction, management, and policy-making arenas. Berryman goes on to discuss Douglas-fir tussock moth outbreaks, and contrasts his theoretical model of this interaction to a large simulation model. In Berryman's opinion, the theoretical model resulted in superior predictive power and significant ecological insights that were lacking in the simulation model. By implication, Berryman generalizes this specific example to characterize the relationship between theoretical models and simulation models. In broad terms, Berryman's article is a strong advocacy of abstract theoretical models and an equally strong condemnation of large, complex simulation models. As contrasted to Berryman's article, Liebhold's article is focused more narrowly on the management application of specific simulation models in forest insect and disease pest management. In his analysis, the simulation approach is found wanting. Liebhold concludes that "there is little evidence that these systems models have significantly contributed to solving either applied or theoretical problems." Liebhold concludes his article with a strong advocacy for starting with a simple model and introducing complexity only if needed. Once again, the general tone of Liebhold's article is one of advocacy for simple models and condemnation of large simulation models.

This article in defense of big ugly models is not exactly a rebuttal of either Liebhold or Berryman's articles; in fact, I share many of their concerns and agree with much of what they have to say. Rather, my intent is to provide a counterpoint to their view. Both Berryman and Liebhold begin with the proposition that simulation models have made valuable contributions to insect ecology, but then go on to describe failures of large simulation models and raise questions regarding the basic validity of systems analysis as a modeling approach. In contrast, I will first acknowledge that large modeling efforts have not always lived up to their expectations, but will then go on to point out where large, complex models have made significant contributions to basic ecological understanding and will detail circumstances where this approach is both appropriate and valuable. In particular, my concern is that Liebhold's and Berryman's articles could be interpreted (and may have been intended) as a general condemnation of large simulation models and the systems approach. This would be a case of condemning a valuable research tool because it has not always fulfilled its promise. There is the danger of throwing out the wash with the water. I also take exception to Berryman's casting of the

two different modeling approaches as a polemic, with complex simulation models on one hand versus simple theoretical models on the other. Both modeling approaches can be and, in fact, have been used effectively in consort. In my opinion, their concordant application holds far greater potential for furthering ecological understanding than either of them applied alone.

In this article, I first will discuss several examples in which simulation models provided insights that would be difficult to gain through other modeling approaches. Then I will discuss possible reasons for the failure of the simulation approach in some past applications. Finally, I will consider future applications of big ugly models.

Examples of the Power of Simulation Model Applications

Complexity Versus Simplicity. Central to both Berryman's and Liebhold's articles is the inference that somehow simplicity is *good* and complexity is *bad* (the terms are my choice). This seems a curious notion. No

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one will argue that there are indeed complex problems. Do complex problems necessarily require complex solutions? Perhaps not, as pointed out by Berryman. On the other hand, some complex problems probably do require complex solutions. There is nothing inherently wrong with complex models, just as there is nothing inherently correct with simple models; it is more a question of appropriateness. The question should be, what is the most appropriate approach for the particular problem at hand? A particular strength of the detailed simulation model is that it provides the flexibility to test hypotheses regarding mechanistic pathways and interactions. For example, currently we (Logan and Amman 1986, Bentz et al. 1991) are developing a model of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, population-level response to weather. The current model represents the population response in a mechanistic fashion, with stage-specific developmental rates, temperature-dependent recruitment, and stage-specific, cold-temperature mortality. The model has 80 or more parameters, clearly a complex model

by Berryman's terms. Yet, for a specified annual temperature regime, the model will result in either exponential growth or exponential decay of the population. In other words, the entire behavior of these 80 or more parameters could be captured by one simple parameter, the per-capita instantaneous rate of population growth! It seems unavoidable that the principle of parsimony would demand us to forsake the big ugly model in favor of the theoretically sound Malthusian model. Unfortunately, by doing so, we would also lose the ability to test for subtle interactions between seasonality, developmental thresholds, phenology, mortality thresholds, etc., all of which are critical to address important weather- and climate-related issues such as changing climate scenarios. Although the elegant theoretical model may capture the behavior of the complex simulation faithfully, it does little to improve our understanding of how seasonal changes in weather or climate will effect mountain pine beetle populations.

Multiple Causality. There are other inherent limitations to initiating ecological inquiry from the principle of parsimony, particularly by the process of using a priori defined theoretical models as the basis for interpreting time-series data. The risk is, as with any inductive argument, that observed population time-series patterns may result from a variety of causes. For example, the cycles that are diagnostic of delayed density-dependent population processes can also result from autocorrelation in an exogenous factor (Williams & Liebhold 1994). In more general terms, there may be an infinite number of mathematical relationships that are indistinguishable over a limited extent of their domain.

Simulation models can add substantially to the complex, inductive process that attempts to ferret out ecological causality. Mechanistic models that are based on the best information available can add credibility to a particular interpretation of observed population data. As an example, I developed a mechanistically detailed simulation model of the predator-prey interaction between *Tetranychus mcdanieli* McGregor, and *Metasenus occidentalis* (Nesbitt) Logan (1976). This complex simulation model was based on data from independent laboratory studies and published literature and, as such, represented the current state-of-knowledge involving this interaction. Running the model, which was parameterized from independent data, under prevailing environmental conditions, resulted in prey-predator cycles that were similar to the observed outbreak cycles. The inference was that the current state-of-knowledge was sufficient to explain patterns similar to those

observed in the field. Based on the supporting evidence from the simulation model, a more analytically tractable theoretical model was used for the analysis of dynamical systems properties (Wollkind & Logan 1978). This process differs from the type of inference discussed by Berryman in that the resulting population cycles were an emergent property rather than a property derived from a curve-fitting process.

Emergent Properties and Hierarchical Structure. An emergent property is defined by Allen & Starr (1982) as "...properties of higher levels in the system that are not obvious from the properties of the parts." An application in which the simulation approach resulted in an important ecological insight as an emergent property is provided by Bentz et al. (1991). This work involved development of a simulation model of mountain pine beetle phenology constructed from individual level, temperature-dependent, developmental data. When the resulting model was run under prevailing annual weather conditions typical for mountain pine beetle habitat, a univoltine seasonality emerged from the relationships between stage-dependent developmental rates and developmental thresholds. To my knowledge, this result is the only mechanistic demonstration for direct control (seasonal temperatures alone, Danks 1987) of univoltinism in a temperate-zone insect. Direct control of seasonality is an ecological insight, by the way, that has important implications for the nondiapausing mountain pine beetle. The important point is that an appropriate seasonality (a population-level response) resulted from the interactions of stage-specific developmental parameters (an individual-level process).

The emergence of properties, such as univoltinism in mountain pine beetle, is a basic property of hierarchical structure. Strictly speaking, an emergent property can result only from estimating parameters at a level lower in the hierarchy than the one of interest (Allen & Starr 1982). As such, discovery of emergent properties is a important potential with most simulation approaches, and one that is not possible when estimating parameters for population-level models from population-time series.

Communication Between Field and Quantitative Ecologists. Irrespective of whether one dates the beginning of modern theoretical ecology from Verhulst's publication of the Logistic equation in 1845, or the independent rediscovery of that work by Pearl and Reed in 1920, the theoretical-modeling approach vastly predates simulation modeling and systems analysis. Apparently, theoretical models generated a great deal of interest from ecologists of the

day. An indication of this acceptance is Volterra's lengthy (38 pages) appendix in Chapman's (1931) *Animal Ecology with Especial Reference to the Insects*, which was perhaps the most widely used insect ecology text of the time. But why, when the theoretical modeling approach had predated the simulation models by almost 50 years, did simulation modeling and systems analysis strike such a responsive cord with ecologists of the 1960s? In my opinion, one important reason is the highly abstract nature of theoretical models. The language of higher mathematics, and in particular differential equations, is opaque to most field ecologists. Simplicity, opaqueness, and transparency are all relative terms. For example, the elegant mathematical simplicity of a system of coupled differential equations typically is opaque to the classically trained field ecologist. Conversely, the mathematically inelegant representation of an ecological interaction by a Forrester (1961) flow diagram will likely be intuitively clear to the same ecologist. Simulation models provide a common ground and overlap between disci-

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plines and scientists with little shared intellectual experience. If the quantitative scientist and the field ecologist can agree on a systems representation of particular ecological interaction, then there is a good chance that a more abstract model, amenable to mathematical analysis, can be developed that also maintains ecological credibility.

Even though many theoreticians have disdain for big ugly models, an existing simulation can provide the catalyst for further model refinement. The biologist, who feels comfortable in the simulation environment, can develop a detailed simulation of the system independently. This description, in turn, can inspire the theoretician to modify the model further and recast it in a more elegant form. Both gain through the process, or at least they can. This was clearly the case in the previously described analysis of the prey-predator relationship between *T. mcdanieli* and *M. occidentalis*. This work began in the early 1970s with the development of a complex simulation model of the

interaction (Logan 1976). The simulation model provided the inspiration for both the development of, and a verification check for, subsequent theoretical analysis that spanned the next 15 years (Wollkind et al. 1988). One of the best examples from the entomological literature of synergism between simulation and theoretical models is the well-known analysis of spruce budworm dynamics that occurred at the University of British Columbia during the 1970s (Ludwig et al. 1978). Development of a detailed simulation model preceded the theoretical analysis by several years, and provided a synthesis for the extensive database (Morris 1963) on budworm dynamics.

Why the Disenchantment with Simulation Models?

Unrealistic Expectations. If simulation modeling is such a laudable enterprise (as I contend it is), why is the approach so vulnerable to criticism by highly qualified insect ecologists, such as Berryman and Liebhold? This is an interesting question and its answer probably has as much to do with human nature as it does with either ecology or mathematics. One of the most important reasons for the disenchantment with simulations is that the approach never came close to meeting the expectations that were generated by its early proponents. The reasons for these unrealistic expectations were partially a result of the sudden availability of digital computers. In retrospect, the mainframe computers of the mid-1960s are primitive indeed, but when compared with the rotary Monroe calculator that was state-of-the-art for most ecologists of the time, the capabilities seemed unlimited. It really did seem possible that we could recreate nature inside a computer. I agree with Liebhold that, in retrospect, it was a naive expectation. Another, and perhaps even more important reason, is the nature of competitive funding that was becoming the dominant means to support research during the 1960s and 1970s. In the competitive-funding environment, it is necessary to paint as optimistic a picture as possible in order to increase the chances of success. The more administrative levels that must be sold on a research project, the greater the chance of building false expectations.

Lack of Predictive Power. One of the main points for criticism of simulation models in both Berryman's and Liebhold's articles has been the lack of predictive power. It is possible that this lack of success at prediction results from some basic flaw in the simulation process, as both authors contend. It also may be an indication of something much more basic. Recognition of instabilities in numerical solutions to differential

equations goes back at least to the 1920s; however, it is only recently becoming accepted that instability of a basically unpredictable nature (chaos) may be intrinsic to ecological structure. There are many reasons for expecting insect populations, particularly eruptive species, to exhibit chaotic dynamics. These reasons are discussed in more detail elsewhere (Logan 1991, Logan & Allen 1992). Suffice it to say that if complex nonlinear dynamics are widespread in insect-population systems, then we need to take a serious look at the whole concept of prediction. Lack of predictive power may in fact not be a criticism at all. To the contrary, it may be a common manifestation of real ecological systems and, therefore, anticipated in models that represent their dynamics.

Model Development Strategies. Another reason for the unfulfilled promise of some simulation models is the basic approach that often has been used to develop large detailed models. The majority of simulation models criticized by Liebhold were developed through a modeling process loosely patterned after the Adaptive Environmental Assessment approach described by Holling (1978). The basis of this process is a series of workshops that bring the leading experts in a field together with computer programmers and facilitators that are capable of bridging the gap between field ecologists and computer programmers. The objective of these intensive workshops is to produce a working systems model. Undoubtedly, this process has made significant contributions toward an enhanced ecological understanding, and several such contributions are documented in the original publication. However, the process also has resulted in at least several models of questionable value. Liebhold details some of the reasons why this process has failed. Several additional reasons come to mind.

First is the principle of model invalidation. Holling went to great lengths discussing the concept of model invalidation and stressed the importance of alternative model structures. The essential concept of invalidation and willingness to discard an existing model may be subverted, as Liebhold contends, by large simulation models. The investment in money, time, and careers becomes so great that it becomes increasingly difficult to discard the model. Developers of the model become its advocates rather than its evaluators.

Second, many of the models criticized by Liebhold were initially developed for the USDA Forest Service through extramural contracts to a consulting company. This approach has the obvious advantage of assembling talented modeling expertise to focus on a problem of immediate interest. However, it

has the liability of abdicating the responsibility for model development to those with vested interests that last only to the end of a specific contract. Rather than a one-shot investment with the model as a goal, experience indicates that the most useful models are those that have undergone an evolution of thought and a continued commitment by ecologists whose vested interests are in the system rather than the model per se.

Other concerns have resulted from application of the workshop format used in Adaptive Environmental Assessment to identify critical processes. In the initial and subsequent workshops, the general idea is to gather the leading experts in a particular problem area. Then, a variety of techniques are employed to determine the important variables and parameter relationships that define the model. In principle, this approach seems reasonable, and the techniques used effectively facilitate communication between workshop participants. In practice, though, it often has resulted in models that emphasize those variables and relationships that are advocated by the most forceful

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personalities among the workshop participants. The dynamics of the best advocate may work well in a court of law; however, it has proven less effective in the course of scientific investigation.

Additional factors have contributed to the disenchantment with simulation models. These include the fact that much of the original motivation for development of simulation models was didactic in nature, such as providing a forum for discussion, evaluation of state-of-knowledge, etc. Although these are unquestionably valuable to the scientific process, by themselves they are not likely to result in administrative recognition or publications. Therefore, many models (perhaps some of those cited by Liebhold) have gained a life of their own. The real value as a research tool has been subverted into that of a questionable value as a research product. Whatever the reasons, it is obviously clear that there is widespread disenchantment with large simulation models, even among those like Berryman who have been important contributors to large-scale

modeling efforts in the past (Berryman & Pienaar 1974, Raffa & Berryman 1986).

Recommendations

In conclusion, Berryman and Liebhold have both pointed out deficiencies in several major simulation modeling efforts. We need to recognize that some simulation models, and perhaps some simulation-modeling approaches, have outlived their usefulness. We should not live with obsolete models any more than we should live with any other obsolete scientific instrument or tool. Serious evaluation of existing models (such as Berryman and Liebhold have provided) need to be made, and those that have outlived their useful life should be discarded. However, this should not be interpreted as a general condemnation of simulation models or the systems approach. As with any other worthwhile scientific endeavor, simulation techniques and approaches have evolved over time. Some have worked; others have not. Attempts to recreate the ecological world, in all its detail and complexity, inside a computer chip generally have not paid off, whereas well-defined and more narrowly focused simulations often have. It also is clear that the corporate approach to model building is easily subverted in practice.

There is once again a real need for research on the science of modeling. For at least the past 10 years, research on modeling per se has been unfashionable (and unfundable). Topics such as expert systems, individual based modeling approaches, hierarchical theory, and self-organizing systems are but a sample of ideas that could facilitate development of ecologically credible simulation models. Three research objectives should be to (1) produce more robust techniques for coping with the complex nature of ecological structure and organization, (2) develop ways to avoid cascading and confounding errors that are typical of large simulations, and (3) provide efficient tools that help to reduce the overhead associated with simulation-model development (Logan 1989b).

Although there is no question that theoretical and simulation models are quite different both philosophically and procedurally, I think it is counterproductive to present these differences as a polemic, with theoretical models on one hand and simulation models on the other. In practice, some questions are well suited to simulation approaches, whereas others are more amenable to theoretical analysis. Simulation models and systems analysis are particularly powerful tools that can facilitate communication between empirical and theoretical ecologists. Simulation models also clearly have demonstrated their value for testing hypotheses

regarding the importance (sensitivity) of mechanistic pathways in ecological structure. Attempting to build a simulation model is an efficient way to evaluate the depth of understanding regarding a particular ecological interaction. Theoretical models, on the other hand, provide the analytical tractability to test hypotheses regarding questions of stability, persistence, and dynamical structure. In some sense, simulation models are well suited to provide insights into the proximate nature of extant, well-defined ecological associations, whereas theoretical models are better suited to address questions of ultimate consequence (a distinction that has long been recognized [Levins 1966]). What is needed is a recognition of the differences between the two modeling approaches and development of techniques that capitalize on their particular strengths while simultaneously avoiding ill-suited applications that expose their weaknesses.

Both Liebhold and Berryman extol the virtues of simple model representation, and few would disagree with the statement that a model should be no more complex than is necessary to represent the ecological process in question. The problem is, however, in determining what is important and what is not. It is easy to cut too fine with Occam's razor. In my opinion, parsimony serves us better as a goal rather than a point of departure. In previous articles (Logan 1982, 1987, 1989a), I discussed a procedure that attempts to combine the descriptive and exploratory power of the simulation approach with the analytical power of the theoretical approach. Plant & Mangle (1987) further developed the concept of a concordant modeling paradigm. To summarize the composite-modeling approach (Logan 1989a): "In this approach, a simulation model is first developed that captures ecological complexity with sufficient resolution to satisfy the goals of precision and realism. Then, through a systematic process of simplification and aggregation, progressively more analytically tractable models are developed. This finally results in a model amenable to mathematical analysis. Throughout this process, procedures are followed that serve to maintain the link between simplified models and the more complex models from which they were derived, and thus to the actual ecological system of interest." The important concept is that the simple theoretical model is linked procedurally to the descriptive, intuitively obvious simulation model. The simple model is a resultant product rather than the point of initial inquiry, in direct opposition to the modeling procedure suggested by both Berryman and Liebhold. It is important to emphasize the usefulness of both modeling approaches,

the big ugly model as well as the elegant theoretical model.

Liebhold and Berryman each end their articles with truisms that are difficult to deny. I will end in the same vein: In our quantitative representations of ecological associations, we should avoid dichotomous and antagonistic classification of quantitative approaches. After all, a model is only a model. The net worth of a model should be measured by the insights it provides into ecological processes. Any approach that facilitates this process is valuable and worthy of consideration.

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