CHAPTER

General Principles for Developing Landscape Models for Wildlife Conservation

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Models are abstract descriptions of systems or processes (Starfield and Bleloch 1991, Haefner 1996). In other words, a model is a formal framework for organizing and synthesizing existing knowledge about an ecological system. Models have become pervasive tools in natural resources management, large-scale planning, and landscape ecology (Shenk and Franklin 2001, Scott et al. 2002). Models help address fundamental questions about wildlife habitat relationships and habitat management. For example, models are useful for evaluating the potential impacts of management alternatives (Morrison et al. 1998, Larson et al. 2004, Shifley et al. 2006), predicting species occurrence (Scott et al. 2002), and assessing economic implications of management decisions (Haight and Gobster, this volume).

Landscape models take many forms, including statistical models that quantify relationships and patterns among variables (e.g., Niemuth et al., this volume; Hepinstall et al., this volume), conceptual models that offer a qualitative construct of a system, and simulation models that project landscape features into the future (e.g., He, this volume; Oliver et al., this volume). Landscape models can produce output that is as difficult to analyze and understand as data from the original system. For examining and presenting the results from landscape simulation models, ecologists need tools that facilitate interpretation of complex multivariate patterns (Shifley et al., this volume). For this reason, visualization tools are often used with landscape models because they make complex data easier to understand (McGaughey 1997, 1999).

Because of the usefulness and widespread application of models, researchers and decision makers should be well informed about potential strengths and limitations of these models. Here, we review principles underlying the construction and use of models, with an emphasis on their application to large-scale wildlife conservation planning. In addition to outlining general principles of modeling, we offer advice about using models in an adaptive management framework, addressing uncertainty, and making models useful and transparent. We also encourage a focus on viability and population objectives (Johnson et al., this volume) in modeling and we present a broadened concept of viability for species of conservation concern and game species as an important measure in understanding wildlife response in large landscapes. To communicate results from landscape models, we need tools for visualizing these results. Therefore, we end the chapter by briefly discussing some basic theory, dangers, and utility of visualization software. We refer readers to other relevant papers and books, such as Box (1979), Starfield and Bleloch (1991), Hilborn and Mangel (1997), Starfield (1997), Williams et al. (2002), Shenk and Franklin (2001), and Scott et al. (2002), that further discuss philosophical considerations of modeling in natural resources.

USES OF MODELS

Modeling has become widespread in natural resources management because models can be incredibly useful and practical tools. Johnson (2001) defined three categories of purposes for models: explanation, prediction, and decision making.

1. *Explanatory models* are used to describe or decipher the workings of systems. Such models attempt to identify the mechanisms involved in the system.
2. *Predictive models* are used to forecast future states of systems or results of management actions. Prediction is a common use of landscape models and allows the user to determine the potential impacts of various proposed management actions (e.g., Shifley et al. 2006). The opportunity to ask "what if?" questions is especially attractive to natural resource managers.
3. *Decision-support models* are used to identify management strategies that will produce desired results. Optimization techniques are one useful example of decision-support models used in planning resource management (Moore et al. 2000).

A given model may be used for more than one purpose. For example, habitat suitability models may be used to investigate the relative importance of key habitat characteristics and simultaneously predict future habitat suitability. Many of the habitat suitability and population models discussed in this book and elsewhere are decision-support models that allow managers to assess the relative trade-offs of management actions.

PHILOSOPHY OF MODELING

In this section, we summarize general principles that modelers and end users should consider when working with models, regardless of the model purpose. We re-emphasize points frequently made in introductions to modeling, especially Starfield (1997).

Every Biologist Constructs Models

Some biologists view modeling as a mathematical art of little relevance to real-world management problems. However, every biologist constructs models. Every scientist and manager has an intellectual framework of hypotheses about how his or her focal system is organized, what factors drive changes in key resources, how the system will respond to management actions, and what the major uncertainties and holes are in this framework. Whether these scientists and managers admit it, this framework is the basis for a conceptual model that can be translated easily into narratives, diagrams, pictures, equations, and even computer programs (i.e., into quantitative models).

There are multiple potential purposes for formalizing one's intellectual framework into a model, whether conceptual or quantitative. Regardless of whether one constructs a landscape simulation model or draws a diagram on the back of a napkin, constructing a model forces biologists to confront their assumptions about the system and the support for these assumptions. It prompts them to consider the most critical uncertainties inhibiting scientists and managers from better understanding the system. It can act as a framework for integrating new information and is a tool for more rigorous thought about the system (White 2001). Finally, it forces the biologists to expose hypotheses and assumptions to critiques from others. In the case of complex, high-profile management decisions, a manager may be unable to recommend and defend (perhaps in court) a course of action without well-developed quantitative models (Swartzman 1996, Starfield 1997, Walters and Martell 2004:3–4).

Models Are Useful Despite a Lack of Data or Understanding

As frameworks for the organization and synthesis of existing information, "all models are wrong, but some are useful" (Box 1979). Ultimately, we seek a sophisticated, accurate understanding of natural systems, precise estimates of important parameters and their dynamics, and good knowledge about the specific effects of various management alternatives. In such an optimal situation, we might have at least moderate confidence in model predictions, even though there is still significant uncertainty. For example, even biologists who are skeptical about most models are comfortable using predictive results in this situation

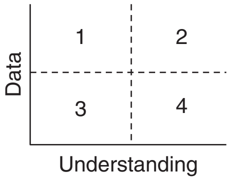


FIG. 1-1

A classification of modeling from Holling (1978). The x-axis represents understanding of a system (from limited to complete), and the y-axis represents the quality and quantity of data (from incomplete to adequate) that are available for use in model-building. Ecological models typically are based on limited data and incomplete understanding of systems, and thus fall in region 3 (Starfield and Bleloch 1991).

(e.g., daily weather forecasts produced from atmospheric models) despite knowing that such forecasts are often inaccurate.

However, in wildlife habitat modeling, we usually possess limited data and an incomplete understanding of the system (Holling 1978; Fig. 1-1). Models can be especially useful tools for decision making and for prioritizing efforts to address these gaps in our understanding. The argument that modeling should not be used unless data are adequate is just as misguided as arguing that no new management actions should be tried unless we completely understand the system and can predict the specific effects with high certainty. Managers have to act in the face of uncertainty; models help them make as defensible a choice as is currently feasible. Similarly, researchers have to justify why they are proposing studies of a particular aspect of the resource. Model building helps us evaluate the relative importance of various influences on a system and identify data that should be collected (Starfield 1997; Shifley et al., this volume).

Models Should Be Constructed for Specific Purposes

A model can be seen as a structural framework for our current knowledge and as a tool for exploring uncertainties in our knowledge. To create a useful framework or tool, we need clear, specific objectives for the modeling effort. The purpose of the model should determine its structure; scope, resolution, and complexity; its user interface and output; and how it is evaluated (Starfield 1997, Nichols 2001, Kettenring et al. 2006).

In defining the purpose for the model, we should address multiple issues:

1. Who are the intended end users of the model? What are the technical skill levels of these end users?
2. How will the model be used: for evaluating management alternatives, determining high priorities for future research, communicating what we know to other stakeholders, or simply clarifying for our own benefit what we know and need to learn about the system?

3. What spatial and temporal context do we want to explore? For example, do we care about breeding season patterns only, modeling short-term forecasts or long-term dynamics, a specific management area or an ecological province?
4. How will the model be evaluated?
5. Are we building the model for long-term use? How will it be updated as our understanding of the system improves?

Predicting the Future Is a Lofty Goal

Ecological systems are driven by factors with high variability and unpredictability, and observed ecological patterns are shaped partially by random processes (e.g., Hubbell 2001, Fuentes et al. 2006). Modeling experts understand that even the best model rarely can accurately forecast the future condition of natural systems (e.g., Boyce 2001, White 2001, Walters and Martell 2004:10–11), except sometimes over short time spans. In the face of this variability, the predictive value of models usually comes not in forecasting the expected future condition of a resource, but in projecting a range of potential conditions given the likelihood of different stochastic events (Clark and Schmitz 2001). However, with increasing time, previously undocumented events or misunderstood processes are likely to move the system beyond a range of variability predictable from our current knowledge (but see Brook et al. 2000).

Therefore, why bother with predictive, quantitative modeling at all? First, short-term predictive accuracy sometimes is an important goal for management. For example, when using spring-collected data to set autumn hunting regulations each year, we want highly accurate model-based predictions about what fall abundance will be that year. Second, we learn a great deal by making specific but inaccurate predictions and assessing why our underlying hypothesis was inadequate. Biologists should fear acting on ill-defined assumptions and weak logic far more than acting on inaccurate predictions and incomplete models. Certainly, we should not be over-confident in our predictions; we have to weigh the risks of acting on a wrong prediction versus the risks of inaction and other alternatives. For this reason, having a model and its output account for known sources and magnitudes of uncertainty is important. Third, we can make defensible management decisions by comparing the predicted results of various management alternatives. Moreover, we may be able to predict the relative benefits of these alternatives far more accurately than we can predict specific outcomes of each (Beissinger and Westphal 1998, Walters and Martell 2004:5).

Useful Versus Truthful Models

The process of model evaluation and validation is a critical step in modeling (Johnson 2001; Shifley et al., this volume). However, this evaluation should focus not on how well the model captures "truth" (verification), but how well the model performs for its intended purpose (Oreskes et al. 1994; Starfield 1997; Shifley et al., this volume). Even when quantitative prediction is the primary objective of modeling, accuracy can be judged only in terms of the desired use of the model. For example, when one is predicting occurrence of below-freezing nightly temperatures, specificity (correctly predicting frost episodes) of 70% might be fine for southern Canada in October but terrible for Florida fruit-growing areas in February. Our primary purposes for modeling usually are to quantify major uncertainties about the system and to provide a framework for improving our understanding of the system. In the context of resource management, a "good" model is one that promotes a better decision than could be made without it (Starfield 1997, Johnson 2001).

Model Complexity and Credibility

Because of uncertainty surrounding our knowledge of the system and limited data, the use of complex models may not improve one's understanding of a system. Occam's razor is a logical guiding principle in habitat suitability modeling: the simplest model that is consistent with existing knowledge is likely to be most appropriate and is most likely to produce reliable insights. Models should be no more complex than necessary to capture the key relevant features of the system. That is, one should construct the simplest model that fulfills one's purpose adequately (Starfield 1997, Nichols 2001; for a contrasting view see Walters and Hilborn 1978:168).

When a more complex model produces different results than a simpler model, it is easy to assume that this means the complex model is more realistic (more "truthful"). This is a dangerous assumption. Increased complexity does not guarantee increased accuracy. As model complexity increases, the necessary assumptions multiply, and the body of data needed to parameterize the model is stretched thinner. Small errors that would have minor effects in a simple model may propagate; the uncertainty in the model output may be far greater than the sum of the uncertainties in the input parameters (Haefner 1996:186–187). With careful simulations and sensitivity analyses, the modeler can examine how dependent model results are on the additional assumptions and parameter values needed for the complex model (Bekessy et al., this volume). However, this requires an honest assessment of the degree of uncertainty about values for which data are extremely limited. This uncertainty may be far greater than the range of variability from a few published studies.

Often, model development should proceed incrementally starting with a general, very simple model. For example, a landscape habitat model could consist simply of a cover-type map and expert rankings of suitability for each cover type. If possible, each step up in complexity could be added as a new module that can be turned on or off easily; sometimes separate incremental models will be required (e.g., adding a vegetation simulator; adding a subroutine to account for spatial arrangement and size of patches when estimating suitability, incorporating demographic simulation to model density rather than qualitative suitability). At each step, the model can be explored, tested, and compared with simpler models before adding additional complexity. Logistically, this approach often helps point out errors in the structure or calculation of the more complex model, particularly if the two models can be used to run nearly identical scenarios. Scientifically, this approach helps the modeler be explicit about the purpose of the additional complexity, additional assumptions needed, and data limitations.

Consider Alternative Models

When only one model is built, modelers and users risk getting too attached to the model and its assumptions, and too forgiving of its faults. Instead, biologists should simultaneously construct and compare two or more competing models, each based on alternative hypotheses about the system being modeled (Holling 1978:100–101, Nichols et al. 1995, Haefner 1996:22, Mangel et al. 2001, Conroy and Moore 2001, Hill et al. 2007). Such models may differ in their underlying structure or may form a nested set of models (e.g., models with and without density-dependent effects on population growth). The multimodel approach can be seen as a direct extension of having multiple working hypotheses (Platt 1964, Ford 2000:290).

Comparing multiple models helps users to clearly examine effects of alternative assumptions about the system, check for structural and computation errors, and compare projected effects of alternative management policies. It may have intuitive benefits when there are multiple stakeholders with differing views about the ecological dynamics of a resource and likely effects of management actions (Williams et al. 2002:663–684, Conroy and Moore 2001).

Models Should Be Transparent

Models should be completely transparent in their objectives, assumptions, model structure, data used, mathematical details, and limitations. Unless users of a model are examining a test scenario in which they know what the outcome should be, these users can tell little about the quality of a model from its output. This is particularly true in landscape habitat models, where colorful maps created using geographic information systems (GIS) may give us undue confidence in the underlying model. Both modelers and model users share blame for the frequent situation in which a model is treated as a black box and the user is encouraged to worry only about running the model and interpreting the output, not about the model itself. Just as we can fully assess the results and discussion of a scientific paper only after critically examining the methods, we can assess the value of a model only by carefully considering the model formulation—structure, assumptions, calculations, and data sources.

When a model is constructed for other users, it should be documented well enough to (1) provide a sufficient recipe for the model such that another modeler could rebuild the model from scratch and replicate its output (or at least reproduce similar average values and variability in results for stochastic models); and (2) provide a clear description of the purpose and hypotheses guiding the model, the assumptions involved, the ecological spatial and temporal domain for which the model was constructed and validated, a description of how the model was evaluated and tested, and a discussion of its potential limitations (Benz et al. 2001, Kettenring et al. 2006).

Modelers need to document explicitly what data were used for constructing and parameterizing the model, and model users need to critically assess limitations in these available data. Citing the data sources is an obvious step, but a citation title tells the user nothing about the sample size, sampling limitations, or temporal duration of the study. Usually, one can get only a vague idea of the study location and timing (e.g., spring versus fall) from the citation title. Therefore, adequate documentation for a model usually should provide more details about studies critical to the model, including the study area, habitat types or ecological province, sample size, season, temporal duration, sex and age classes addressed, and any strong criticisms of the study (e.g., occupancy estimated naively rather than with models accounting for detectability). Last, transparency regarding the visualization process and procedures is important in understanding whether images accurately project model results. This discussion suggests that modelers must spend significant time documenting their models. However, model users share equal responsibility for demanding adequate documentation. These users need to assess carefully the model's assumptions, data support, and limitations before focusing on interpreting model output.

Use of Models from Other Regions Should Be Done Judiciously

Biologists need to use great caution when using generic models or models developed for other regions or purposes. Models are developed to meet specific objectives and are influenced by available data, knowledge of the system, and assumptions, which makes them difficult to apply universally. Although many general models are structurally similar (e.g., matrix models for demographic analyses; Caswell 2001), specific models are uniquely suited for specific regions and applications. When adapting existing models to a new situation, biologists need to assess the compatibility of that model's purpose, assumptions, and data requirements with the details of their own problem (Kettenring et al. 2006; Probst and Gustafson, this volume). In some cases (e.g., Landscape Management System; Oliver et al., this volume), one may refine a general model for local applications by inputting site-specific data. However, the user still must be cautious that the underlying assumptions and relationships in the model are appropriate for the situation at hand.

Even if the objectives of the existing model are fairly close to those of the current situation, the biologist must evaluate whether specified relationships are appropriate and relevant to the new system, and that parameters in the model can be estimated precisely. For example, Mladenoff and Sickely (1998) applied a resource selection function model developed for wolves (*Canis lupus*) in the upper Midwest United States to the Northeast United States to project the suitability of wolf habitat. In doing so, there is an implicit assumption that the important features (e.g., whether or not variables such as road density or prey type) and their form and strength of the relationships that affect the suitability of wolf habitat in Wisconsin translate to potential wolf habitat in New England.

Managers Should Be Involved in Model Construction

A management-oriented model is built to help managers determine the course of action to take, the risks associated with alternative actions, and the uncertainties that must be addressed to make better decisions. Increasingly, managers should see modeling as an invaluable tool for the scientific component of management, and model building should be an art they practice regularly on their own computer or notepad (Starfield 1997). We believe that managers should be involved heavily when management-oriented models are constructed.

Constructing large-scale, complex models usually requires a modeling team, including a manager. To construct useful management-oriented models, the modelers need clear management objectives or a range of objectives, clearly defined management options, detailed understanding of the populations and landscapes being modeled, and clear ideas about how the models can be used to improve subsequent management decisions. Usually, the manager is best able to supply much of this expertise, and educates the rest of the modeling team (Kendall 2001). In some cases, the manager may not be accustomed to heavily quantitative, partially data-driven, structured approaches for decision making. Therefore, part of the modeling process will be spent educating the manager to consider how the model can be most useful. In either case, the resulting models will be useful only if the manager is an integral part of the modeling group throughout all stages of model development (Clark and Schmitz 2001).

The format and output of models must carefully consider the targeted end user. For management-oriented tools, there often is a trade-off between user-friendliness and technical sophistication. One might program cutting-edge spatially explicit, data-driven landscape habitat models using completely open-source, free GIS and statistical software with state-of-the-art numerical tools. For some managers who are technically proficient, this might be ideal. Other managers might have no interest in installing and learning to use new programs. A more useful first step for them might be a spatially implicit spreadsheet-based model (with careful assessment of whether the simple model is adequate for their purposes) or a relatively sophisticated model in their preferred GIS package. Similarly, some users may require readily available help files to explain concepts that might be elementary to other audiences; they may pay more attention to simple graphical displays of output than complex graphs or numerical summaries. In any case, modelers and managers should collaborate carefully as models are developed to produce a user interface that will facilitate their application of the model.

AVOIDING UNRELIABLE MODELS

A key to successful modeling is the avoidance of common missteps that make models unreliable. Ineffective or unreliable models maintain the following characteristics (Starfield 1997):

1. *Explicit accounting for processes that are not relevant or well understood*. In an attempt to increase the utility of a model, there is sometimes a tendency to incorporate all processes, including those that are not necessary (in the context of model objectives) or well understood. One should only account for processes that are relevant and understood well enough to be included in the model. For example, in some landscapes, disturbances from insects might be of minor importance. In an attempt to be all inclusive, the modeler might be tempted to include an insect disturbance module when projecting habitat conditions, although it is not particularly relevant or important to the outcome.

2. *Dependence on parameters that cannot be estimated precisely*. Many parameters might be considered important, but some might be difficult to estimate with a meaningful degree of precision. Such imprecision compounds uncertainty and propagates error. With greater uncertainty, it becomes even more important to limit the number of input parameters (Mangel et al. 2001). Input parameters need to be estimated with enough confidence that they are helpful in the modeling process. It is also possible to consider other ways to structure the model that relies on parameters about which more is known (Nichols 2001). On the other hand, if the purpose of a model is to assess our understanding of a system, one needs to account for the full uncertainty in critical parameters, regardless of how great the uncertainty is.

3. *Dependence on too many parameters*. Much has been written recently in the natural resources literature about model parsimony (Hilborn and Mangel 1997, Burnham and Anderson 2002) and the dangers of over-fitting models. There is a direct trade-off between bias and variance and although richer models are preferred when the purpose is prediction, there are also practical considerations. When one is modeling large landscapes, additional parameters require additional data collection and synthesis, which can take considerable time and effort (Roloff et al., this volume; Shifley et al., this volume). Regardless of whether one is developing statistical models or models based on expert opinion, it is advisable to make models parsimonious.

4. *Uncritical application of pre-existing models*. Statistical models, such as resource selection functions, are specific to the data used to construct them (Hicks et al., this volume), and inferences made from them are limited by the sampling design used to collect the data (Mangel et al. 2001). In many cases, subtle differences in model structure, assumptions, or other issues affect whether a model is suitable for a new application in a new environment. For these reasons, applying models from one system to another should be done judiciously (Probst and Gustafson, this volume).

MODELS AND ADAPTIVE RESOURCE MANAGEMENT (ARM)

Managers and scientists should continually and systematically try to improve management by formally examining the outcomes of management actions and policies, and assessing how well they meet well-defined management objectives (Nichols et al. 1995, Taylor et al. 1997). Landscape models, like other models, are often developed with an incomplete understanding of system properties (Starfield 1997). Landscape models are best viewed within an adaptive management framework. Such an approach inherently acknowledges that (1) there is uncertainty in our knowledge of the system to be managed; (2) improving management decisions would be facilitated by a reduction in uncertainty; and (3) management decisions must be made and revisited periodically. Through adaptive management, alternative models are considered working hypotheses to be developed, evaluated, and refined as new data become available. Management prescriptions are treated as experiments and opportunities for learning by confronting model predictions with data from a purposefully designed monitoring program. Therefore, models serve as a mechanism to evaluate uncertainty and our understanding of the system; they also facilitate decisions based on the best available data. Last, models facilitate refinement of management actions as additional data become available. However, because of the complexity and variability inherent in ecological systems, appropriate model refinements are difficult to identify and incorporate in short time periods. Therefore, the Adaptive Resource Management (ARM) philosophy is an essential framework for scientifically defensible and effective management (Walters and Hilborn 1978). Several principles provide the background context for ARM:

1. Current management actions are based on hypotheses about what processes control the system being managed. Every manager and advising scientist is operating from models, based on these hypotheses, which predict how the system will respond to specific management actions and policies. These models may be conceptual or quantitative, formal or informal.

2. There is uncertainty about the current usefulness of these hypotheses (i.e., whether predictions arising from these hypotheses will be accurate).
3. Management effects and general changes in the system need to be assessed so that this uncertainty about current management actions can be reduced. This monitoring and assessment also ensures that hypotheses can be refined and expanded as management goals or ecological conditions (e.g., climate, presence of disease) change (Williams et al. 2002:231).
4. To justify and defend specific management actions and additional research, the manager needs to make explicit these hypotheses, models, and uncertainties.

In this context, quantitative management-focused models are an element of the ARM process. At the least, these models are a vital tool for predicting comparative outcomes of alternative management options. When used at a deeper level, they provide the central skeleton for an ARM program. The model set encompasses what we think we know about the system, helps us assess the risks of incorrect assumptions, and can help prioritize (e.g., through sensitivity analyses) which of these gaps in our knowledge are most limiting in predicting system behavior. Whenever there are multiple alternative proposed management actions and quantifiable management objectives for which we want to select an optimal management strategy, quantitative models facilitate structured decision making based on the predicted effectiveness and risks of each strategy (Nichols 2001).

Such models can be updated and improved continuously as new data accumulate (i.e., from monitoring or separate research) and as hypotheses are refined. Moreover, these models help us focus monitoring on variables and areas that are most information-rich in evaluating management effectiveness and for improving our models (Nichols and Williams 2006). Models are most useful when they focus on specific questions and do not incorporate unnecessary complexity. However, as information increases, ARM models may be expanded to incorporate all major ecological factors driving viability of the species in question, allowing useful predictions even if there are major changes in management objectives and the ecological environment beyond what was envisioned when the models were originally constructed (Holling 1978:66).

ADDRESSING UNCERTAINTY IN MODELS

In nearly all resource management situations, we have an incomplete or flawed understanding, and snapshots of data from systems characterized by high variation and unpredictability. These facts are not arguments against modeling. Instead, this uncertainty often is the primary rationale *for* constructing models.

Models are useful because they help examine this uncertainty and its potential causes. However, this requires that modelers and users think thoroughly about several major forms of uncertainty affecting model development.

Uncertainty in Our Underlying Hypotheses and in Model Structure

Regardless of model complexity, there will always be more than one plausible hypothesis about critical components and processes in the ecological system. Moreover, we may be able to represent a single hypothesis with several alternate models or equations (Ford 2000). We can address this uncertainty by having multiple working hypotheses (Chamberlin 1890), by specifying the contrasting assumptions and predictions of each hypothesis, and by representing each hypothesis with one or more models. Such models may be nested, differing only in which parameters are turned on or off (i.e., are allowed to affect the calculations) in each model. For example, a simple landscape suitability model focusing on patch type may be expanded by adding additional parameters to incorporate effects of patch size and inter-patch distance. Alternative models may be non-nested, with large differences in their underlying structure (e.g., comparing an expert ranking of suitability versus a metapopulation demographic model).

For some purposes, qualitative comparison of these alternate models may be sufficient. However, strategies for comparing and ranking multiple models, and making decisions in a multimodel framework, have been among the most important tools developed by quantitative ecologists over the last few decades (e.g., Holling 1978, Walters and Hilborn 1978, Burnham and Anderson 2002, Williams et al. 2002:643–864). Previously, biologists often focused on ranking the "best" model and then drawing inference only from that model. Variance estimates from this final top-ranked model are underestimates of the true uncertainty in parameter estimates (Harrell 2001). Rather than ignoring model-selection uncertainty, biologists can incorporate it to produce inference unconditional on any single model. For example, with statistical modeling, biologists can weight models by Akaike's Information Criterion (AIC; e.g., Burnham and Anderson 2002) and use these weights to produce unconditional estimates of parameter values and confidence intervals about these estimates. Whether by such objective criteria or by subjective expert rankings, prior model weights can be incorporated into Bayesian data analysis (e.g., Link and Barker 2006) or into a simulation approach to integrate output from multiple models producing compatible output.

It may be tempting to see the multimodel approach as a problem that ultimately will be cured when we have collected sufficient data. Instead, we should recognize that most natural resource dynamics are the result of numerous varying influences. In a multimodel framework, each model may capture a particular element of "truth"—therefore, examining the composite picture of multiple models may be preferred to acting on a single “best” model (Hobbs and Hilborn 2006). Monitoring outcomes and using these data to continuously update and reweight our alternate models can facilitate decision making that incorporates what we know about system dynamics, our management objectives, and estimates of the current state of the system (e.g., Kendall 2001, Williams et al. 2002, Hill et al. 2007).

Uncertainty in Parameter Estimates

The purposes of a model should determine whether a deterministic or stochastic approach is appropriate (e.g., Kettenring et al. 2006). Stochastic models are intuitively attractive because even in complex situations, we can address uncertainty about which parameter values we should use, and we can account for natural variability in these parameters. In each model run we draw a random sample from the assumed probability distribution for each parameter. However, this requires that we have suitable (given the purpose of the model) input values for this distribution. Often, published estimates for some parameters may help us pick an average value for the parameter with some confidence. However, determining how much uncertainty we have about the parameter, or how much it varies spatially and temporally, is even more challenging.

In some cases, there is a tendency for modelers to be overly optimistic about the adequacy of the underlying data for estimating parameter uncertainty and natural variability. Parameter distributions (e.g., mean and variance) for input into stochastic models should be defined after an honest and careful consideration of limitations in available data. Modelers and model users need to carefully consider potential biases in reported parameter estimates and whether reported variances are adequate for capturing uncertainty in the current model. For example, failure to account for incomplete detectability will produce biased estimates of abundance, survival, and occupancy (e.g., MacKenzie, et al., 2006). Even in a modest local study, published estimates of a parameter and its uncertainty may be biased if the landscape was sampled nonprobabilistically (Anderson 2001) or if the study did not cover enough years to cover the temporal domain we are modeling.

Occasionally, published studies may overestimate process variability (e.g., yearly variation in juvenile survival). For example, in individual studies both process (e.g., temporal and spatial) and sampling (measurement) variability are often lumped into a single variance estimate. More frequently, estimates from a few studies may not capture the full range of temporal and spatial variation in the system being studied.

Even estimates from high-quality studies from other locations and times need to be used with caution. For complex and even some simple landscape models, local data for the focal species are usually insufficient for adequately parameterizing the model or even for guiding the structure of the model. For a wide-ranging species, the only suitable estimates of many parameters may come from other regions. For example, for all but the most heavily studied species, there are few studies which use rigorous telemetry or capture-recapture modeling to estimate dispersal rates through various landscape matrix conditions. Even the basic assumptions underlying a viability model (e.g., habitat variables included in estimating occurrence) may vary greatly among regions. Species with broad geographic ranges typically show surprising spatial and temporal flexibility and variability in habitat associations, demographic parameters, and responses to management actions (Wolff 1995, Converse et al. 2006, Murphy and Lovett-Doust 2007, Whittingham et al. 2007). Yet, even relatively simple habitat suitability models may rely heavily on relationships documented only from other regions.

Modelers should be explicit about sources of input-parameter values and assumptions made in converting published estimates into input values. When models must rely heavily on studies from other regions, modelers need to be very explicit about this, and end users need to be particularly cautious in evaluation and testing. If parameters are used from studies in other regions, the estimates of uncertainty about these parameters in these studies may be gross underestimates, given the additional uncertainty induced by transferring estimates among regions. In some cases, one may be able to better place bounds on the assumed parameter distribution by integrating comparable estimates from multiple systems or closely related species with similar life histories. In other cases, the modeler may need to use very conservative bounds on the parameter. If a conservative distribution would be ridiculously wide, the modeler may need to reduce model complexity to eliminate parameters about which we know too little, or the modeler may rerun the model under several carefully defined, plausible scenarios for the distributions of these parameters.

In most cases, formal sensitivity analyses—systematically examining how changes in input values affect model output—can be invaluable in assessing effects of parameter uncertainty and assumptions (e.g., Johnson 2001). For example, if model results are highly sensitive to parameters relying heavily on data from other regions, obtaining better within-region estimates of their values may be a high priority for additional research even if very precise estimates were available from other regions.

Uncertainty in Whether the Model Works the Way It Is Intended

Regardless of the purpose of the model or the accuracy of model predictions, we need to carefully check that the model has adequately captured our underlying hypothesis, that the structure is logical and correct, that there are no mathematical mistakes, and that the model has been programmed correctly. Frequently, this is referred to as "verification" (e.g., Haefner 1996; Johnson 2001; Shifley et al., this volume). For example, our programming code may make simple or major mistakes (e.g., missing parenthesis, reading the wrong location for an input parameter). We may have incorrectly derived a mathematical equation. We may forget to initialize the random number generator for each run, producing the same set of random numbers for each simulation, or we may be using a generator which produces some duplicate streams of numbers because its period is too small for the number of simulations we are running.

Verification is an art rather than a rote process. The following are a small number of the many strategies the biologist/modeler can use for verification.

1. As the model is built, output the result of each calculation and any random number streams used for these calculations. Check that these make sense before proceeding.
2. Work through your code and assumptions with a colleague who has equal or higher experience with your programming language.
3. Compare a deterministic model to results generated from a stochastic version in which variability is turned off or set to nearly zero.
4. Replicate the model or submodels in both a user-friendly and more mathematically robust and efficient program (e.g., a desktop spreadsheet package versus programs such as R or MATLAB) and compare results.
5. Have target users explore model output, and evaluate whether it seems plausible, over a broad range of conditions within its intended domain of use.

Uncertainty and Biases Caused by the Model User

Regardless of how well a model has been constructed and evaluated, the intended users may use poor input data, fail to select correct program options, and misinterpret output. The modeler can take specific steps to reduce such problems, such as trying to minimize input errors with traps for inadmissible parameters. The modeler and intended users can work closely together to develop and evaluate the model. Most importantly, users must take responsibility for how they apply the model, rather than assuming their responsibility is simply to induce the model to produce output as quickly as possible. Visualization of model output is another potential source of uncertainty and bias in landscape planning models (see below).

VIABILITY AS A GENERAL MANAGEMENT METRIC

Landscape models used in conservation planning output different metrics of species performance that include habitat suitability (Dijak and Rittenhouse, this volume), the probability of occurrence (Hicks et al., this volume), relative or absolute population size (Niemuth et al., this volume; Johnson et al., this volume), and population trajectories or viability (Akçakaya and Brook, this volume; Bekessy et al., this volume). Along this continuum of performance metrics (see Larson et al., this volume), population trajectories and viability are the most ambitious goals.

Viability is a useful and effective concept in wildlife conservation (Beissinger and Westphal 1998; Beissinger et al., this volume). It developed out of concern for populations in danger of extirpation or extinction. The concept of viability is effective because consideration of values and risk, which are implied in nearly all definitions of viability, are fundamental to making sound management decisions (Akçakaya and Brook, this volume; Bekessy et al., this volume). We argue that viability, and its associated risk-assessment framework, is a useful concept in any population management situation. There is still value in indices of habitat suitability, but associating some measure of risk with those indices might aid planning efforts.

The concept of viability, due to its origin in conservation biology, has retained connotations relevant mostly to small population sizes, endangerment, and extinction. Land management agencies in the United States and elsewhere, however, have begun perpetuating a mandate of population viability for all desirable species. We propose expanding the concept of viability to be applicable to conservation planning for all species by including criteria in addition to population persistence so that it applies to all species and to populations of all sizes, integrates biological and human dimensions considerations, and is quantitatively explicit. There are three hierarchical levels of viability in our definition (Table 1-1). If a population is deemed viable at one level, it also satisfies criteria for viability at higher levels. The hierarchical structure of the definition allows explicit incorporation of multiple, potentially overlapping concepts of viability that are implicit in the variety of definitions currently available.

Table 1-1 Hierarchical Structure of a Comprehensive Definition of Population Viability

Level	Abbreviated Definition	Quantitative Assessment Criteria
Primary viability	Continued existence of a population	Probability of remaining extant (or going extinct) during a specified time interval
Secondary viability	Resilience of a population[a]	Probability of returning to a desired abundance or remaining extant given a specified reduction in population size or landscape condition
Tertiary viability	Ability of a population to provide desired benefits[b]	Change in the level of service provided, target population size

[a] *Includes the concepts of genetic diversity and adaptability inherent in previous definitions of viability.*

[b] *Benefits may be a harvestable surplus, recreation, aesthetics, an ecosystem function, or maintenance of secondary viability without direct human intervention.*

Primary viability.— Primary viability is the ability of a population to remain extant. It is nearly synonymous with the classical and most widely understood definition of viability. That is, the abundance of a viable population will remain above zero some higher quasiextinction threshold (Ginzburg et al. 1982). Primary viability refers to the persistence of a population (Connell and Sousa 1983), so it requires explicit specification of (1) an abundance threshold below which the population will be considered extinct or extirpated; (2) a time interval, usually in years from present; and (3) a probability of remaining extant or, conversely, going extinct during the interval (Table 1-1).

Secondary viability.— Secondary viability, in addition to primary viability, is the resilience of a population (i.e., the probability of returning to a desired level after a change). The idea that populations may or may not return to a potential equilibrium state after a perturbation of a given magnitude has a long history of its own (Holling 1973). Dodson et al. (1998) listed resilience as one of many factors by which to assess population viability. In pragmatic terms, viable populations are resilient to fluctuations in abundance, where fluctuations may be due to deterministic threats or stochasticity (e.g., catastrophes). We propose quantifying secondary viability using a more conservative application of criteria for primary viability. Therefore, we must explicitly specify (1) the expected reduction in abundance or extension of the time interval over which viability is evaluated, and (2) an acceptable reduction in probability of remaining extant (or, conversely, increase in probability of extinction). For example, if a population of 10,000 individuals has an 80% chance of persistence for 100 years, it might satisfy criteria for secondary viability if its predicted probability of persistence is reduced by <50% for a period of 200 years or for an initial population size of only 5,000. Dennis et al. (1991) suggested that the conservation status of a population would change if its abundance declined by an order of magnitude, which is a possible rule of thumb for evaluating secondary viability. Our definition of secondary viability includes the ideas of genetic diversity and adaptability mentioned in traditional, generic definitions of viability. For example, a population that satisfies criteria for primary viability (i.e., genetic stochasticity is not a threat over a short time period) may not satisfy criteria for secondary viability because global climate change is shifting the distribution of appropriate environmental conditions faster than the population can adapt or individuals can disperse.

Tertiary viability.— Tertiary viability is the ability of a population to provide desired benefits, in addition to remaining extant and resilient. This third facet is the catch-all that makes our definition comprehensive and equally applicable to rare and common species and declining, stable, and increasing populations. Examples of desired benefits are a harvestable surplus, recreation, aesthetics, or an ecosystem function. All these benefits can be quantified and evaluated, and might be addressed by planning for a target population size that is in excess of what is required for primary or secondary viability. In general, (1) the relationship between direct human uses and their effects on the wildlife population must be formalized in a model, and (2) the maximum level of human use that still maintains tertiary viability must be quantified. The concept of maximum sustained yield (MSY, Hjort et al. 1933) is one example of a quantitative criterion for establishing a level of harvest by humans that maintains tertiary viability. Certainly, a population sustaining exploitation by humans (i.e., satisfies criteria for tertiary viability) should satisfy criteria for primary and secondary viability. We propose that tertiary viability also include the maintenance of primary and secondary viability without direct human intervention. Decisions regarding the degree of human intervention will necessarily be based on subjective, normative judgments, but they may still be quantitatively explicit.

Suggestions for Modeling Viability in Large Landscapes

The benefits of using "viability" as a general framework management is that it helps us focus on defining quantitative management objectives and evaluation criteria for comparing models and management scenarios. This is a necessary step in using models in an adaptive management framework. In focusing on viability, managers and modelers should consider the following suggestions:

1. Organize viability problems in a risk assessment framework (Harwood 2000). We propose that acknowledgment and rigorous, quantitative comparisons of risks associated with management alternatives should not be restricted to conservation of endangered species. Given a pragmatic concept of viability that includes exploited populations, managers should consider a decision analysis and risk assessment framework for all their decisions (Maguire 1986, 1991). For example, Nicholls et al. (1996) applied risk assessment to populations facing mostly deterministic rather than stochastic threats. Hatter (1998) and Tyutyunov et al. (2002) applied risk assessment to decisions about harvested populations.

2. State explicitly what is and is not known (i.e., based on sound empirical data) about the population and factors limiting or regulating it.

3. When assessing population viability at the landscape level, a metapopulation structure may not be appropriate. Although the theory and applications related to metapopulation dynamics are well developed, managers must realize that most populations are not structured as true metapopulations (Harrison and Taylor 1997, Elmhagen and Angerbjörn 2001). Nonetheless, it remains useful to recognize interactions between somewhat local populations of management interest and populations of the same species in a much larger landscape.

4. Several methods exist for evaluating viability; population viability analysis (PVA; Reed et al. 2002) is only one. In many situations PVA is not appropriate because the methods were developed for specific purposes related

to small, declining, relatively well-studied populations. Several habitat-based approaches were outlined by Andelman et al. (2001).

5. An ideal performance measure for assessing viability should integrate all aspects of viability. It must balance realism with generality and understandability. Generally, managers will have to select several measures (e.g., population size, growth rate, age structure, genetic diversity) to fully assess viability.

6. Viability assessment should be spatially explicit when possible (c.f., Hof and Raphael 1993). In fact, managers can learn more about the system and be more confident in subsequent management actions if viability is assessed at multiple scales (Marcot et al. 2001, Mitchell et al. 2001). The extent and resolution of spatial and temporal dimensions can be varied (Probst and Gustafson, this volume), as can levels of biological organization (e.g., population versus multispecies versus community).

7. Focus on relative differences in viability instead of trying to establish a single quantitative measure of viability for a population (Reed et al. 2002). Pragmatically, many management decisions lend themselves to relative comparisons between populations, land units, or management alternatives anyway. Furthermore, estimates of viability are based on many simplifying assumptions and, when considered in isolation, cannot usually be trusted to provide robust recommendations (c.f., Brook et al. 2000). Qualitative comparisons of viability estimates over space or time, however, are considered more informative because biases due to the model are consistent for all scenarios under consideration.

VISUALIZATION

Communicating the modeling process and results to stakeholders is a critical step in conservation planning, and visualization is an important tool for this purpose. Visualization is an important and often misunderstood part of analyzing data and assessing model output. Visualization and visualization tools are analogous to well formulated figures (Day and Gastel 2006). In the case of landscape modeling, the purpose of visualization is not simply to produce a photorealistic picture of the simulation. The role of visualization in science and resource management is to effectively convey complex information and relationships about the state and change of the resource, in a clear and unambiguous way. Whether or not a realistic picture is necessary depends on the objectives and use of the output.

Several methods of visualizing data in natural resources contexts have been used, and each has strengths and weaknesses because of the way an image is perceived by the human brain (e.g., Orland 1992; McGaughey 1997, 1999, 2000; Brabyn 2003; Lang and Langanke 2005). The human brain processes visual data quickly. While generally quite accurate, the observer makes a number of assumptions about what is expected in a particular environment. However, if the environment is unfamiliar or assumptions change, observer perception might be incorrect. The effect of this biological legacy is that when observing data, humans often perceive patterns that are difficult to confirm statistically and that are highly dependent on the context and assumptions of the observer. This inherent human tendency toward subjective visual interpretation plays a role in how people interpret visual data.

To illustrate this point, consider three classic optical illusions (Figs. 1-2, 1-3, and 1-4). In Fig. 1-2, the observer often has difficulty determining the correct extension of the line that passes underneath the rectangle (Poggendorff 1863). In Fig. 1-3, the parallel lines appear to be curved because of the visual distraction of the background lines (Hering 1861). Last, Fig. 1-4 illustrates the effect of local context on the perception of size, where the center dots are the same size, but do not appear so at first glance. These figures highlight the point that while people trust visual images as a realistic portrayal of a situation, a person's assumptions and the context of the image affect perception. When presenting the results of landscape models, we must be careful to provide an appropriate context for accurate transmission of results and implications.

Most people are familiar with traditional data visualization techniques such as graphs, maps, and photographs. These tools can be of limited value in

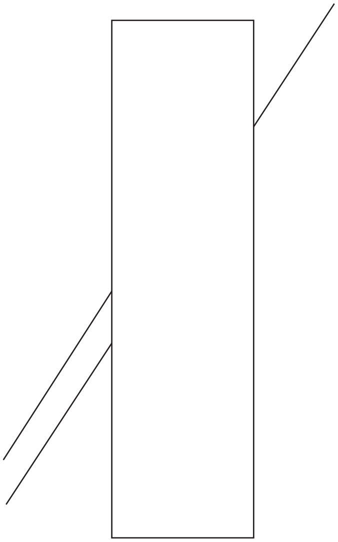


FIG. 1-2

The Poggendorff illusion (1863) in which one can easily misinterpret the association of lines passing underneath the rectangle.

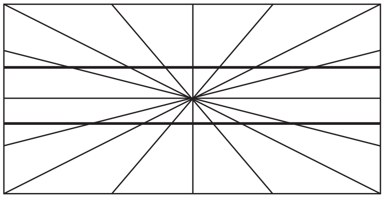


FIG. 1-3

The Hering illusion (1861) illustrates parallel straight lines that are perceived as curved.

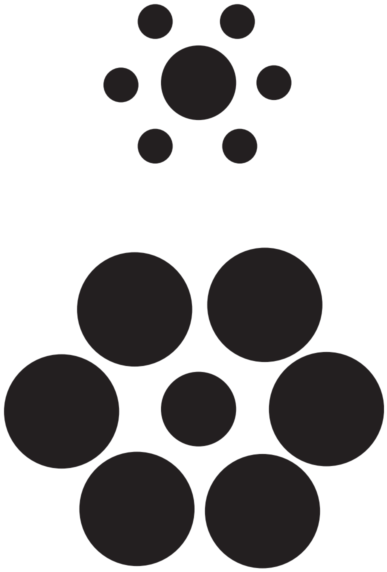


FIG. 1-4

In this illusion the center dots are the same size but can be easily interpreted as differing because of the context of the neighboring dots.

relaying complex situations because they allow only two or sometimes three dimensions of data to be displayed in a two-dimensional context. In complex situations, these tools can easily oversimplify the relationships of the data. However, a tool that helps the user understand complex relationships is more useful than one that creates a pleasing image (Tufte 1986, 1990). Sometimes, realistic detail that does not inherently convey important information can simply be distracting. For example, in some large-scale modeling activities, we can produce images of woody vegetation on a landscape surface (Oliver et al., this volume). In this context, the adage "one cannot see the forest through the trees" is true. Trees that make up the forest image can distract from our understanding of the relationship of the trees that create the forest structure. Given these issues, how do we create visualization output that facilitates our understanding of important principles?

Issues, Solutions, and Examples

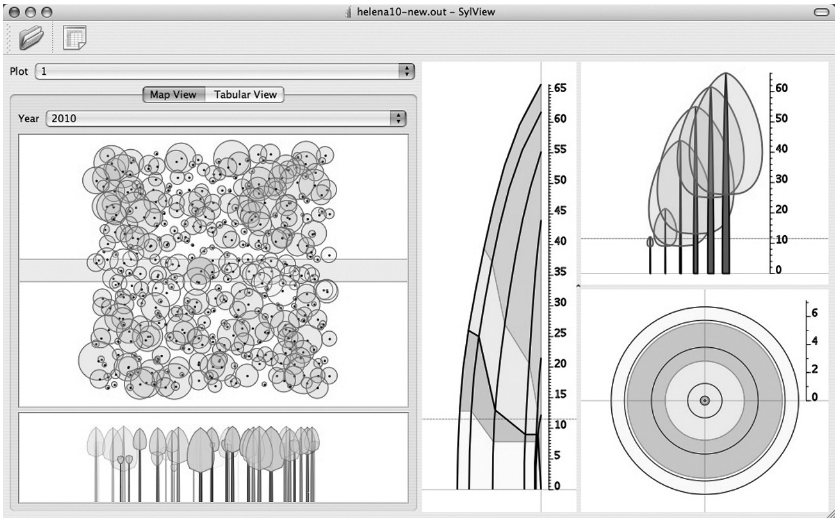
Motion.— One helpful tool in visualization that is not available in traditional printed images is motion. In some cases an interactive two-dimensional image might allow for better interpretation of the relationships than a rotated three-dimensional view. The reason is that many of the objects of interest are hidden in the three-dimensional view but can be easily singled out in the two-dimensional view. In this context, we use motion for interpretation the same way we use motion in a real landscape. Moving objects (e.g., wildlife) are much easier to see than the same objects remaining motionless in the same landscape. Additionally, for objects that do not move, such as trees, we often change our point of view to more fully comprehend the shape and size of the object. Motion allows users to move among the visualized objects, which enables a better understanding of their relationship in the landscape.

When one is using motion to visualize output, it is important that interactive opportunities take place at a reasonable speed so the user can adequately experience the visualized objects. An older tool in this area of visualization is called a "Flyby" and is available in many GIS software packages. These packages allow one to create a landscape with a digital elevation model (DEM) and other coded data and pass over the landscape on a predefined path, creating a feeling of flying over the landscape. These techniques have been used to effectively convey aspects of a landscape through the use of motion.

The software in Google Earth™ (<http://earth.google.com/>) is another example of observer perspective motion that is widely available. Using this software, the observer can alter his or her perspective from a vertical map (i.e., looking straight down on the earth) to a low oblique (i.e., looking at the earth at an angle with no horizon) to a high oblique (i.e., looking at the earth at an angle with the horizon visible) or even a sky view from the specified location. With these various perspectives, the observer can move around the space. At the present time, man-made objects such as buildings are the only available objects that can stand above the landscape surface. However, the Google Earth™ KML Gallery contains many useful examples relevant to conservation at large scales (e.g., forest logging in southeastern Australia; nature preserves at the Cornwall Wildlife Trust in England; conservation work by the African Wildlife Foundation; the migratory patterns of different bird species across Europe and Asia). This tool is relatively simple to use and very accessible to a wide variety of people over the Internet.

At a tree stand level, software often illustrates a representative plot (e.g., 1 ha) of the forest that displays the trees of interest (McGaughey 1997, 1999; Davidson 1995). In many currently available software packages for visualizing trees, objects of interest are presented in a three-dimensional cube that can be rotated. Again, motion aids in understanding the relationships between trees displayed in the image. However, this view might not be helpful in understanding the objects. New software developments (Scott 2006) allow not only map and profile views, but also allow interactive selection of the objects of interest. This allows one to observe the object in context and quickly move to the neighbors to understand the relationships between the objects (see Fig. 1-5).

Larger Context.— An important aspect of visualization software is the ability to place objects in a larger context. With vegetation, this allows one to quickly access several aesthetic qualities affected by proposed resource management. Envision, a product of the U.S. Forest Service, was one of the first software



Plot 1

Year 2010

FIG. 1-5

Example of plot and tree level visualization illustrating a plot in the forest and the wood character produced in one of the trees in the plot.

packages to allow such actions (McGaughey 2000). Using Envision, a collection of forest stands is processed to determine stand average characteristics. When one combines the model with a stand map and a digital terrain model, it is possible to display the size and status of many stands on a forested landscape. DeGraaf et al. (2005) offers an alternative to this same problem; their approach models the landscape using traditional forest growth models to determine stand characteristics.

Issues of Human Perceptions.— Forest scientists have studied human perceptions of visualized forests versus photographs (Stewart et al. 1984, Kellomäki and Pukkala 1989, Pukkala 1998, Tyrväinen and Tahvanainen 1999, Lange 2001, Karjalainen and Tyrväinen 2002). Stewart et al. (1984) compared field observations with photographs taken at field sites (Fig. 1-6). They found that photographs provided a good analog to the field visit. In the other cited studies, people's perception of the aesthetic beauty of forests was compared between visualizations prepared from data collected from a forest landscape and photographs taken in the same landscape. These studies collectively demonstrate that in terms of aesthetic perceptions, visualizations are a good analog for photographs.

Issues of Misrepresentation.— With the development of new technology, software exists that can create visually believable landscapes that are not physically or biologically possible (Fig. 1-7). Sheppard (2001) argued for a code of ethics for those developing resource visualizations to avoid the creation of unrealistic but believable landscapes. Visualization should reflect as honestly as

FIG. 1-6

The image on the left is a photorealistic image created from data from 1998. The image on the right is a photograph taken in 1998 (Wilson and McGaughey 2000).

FIG. 1-7

The image is from a New England hardwood stand generated using NE-twigs for the stand conditions and Visual Nature Studio 2 (<http://3dnature.com/>) for the image. This image is the work of Anna Lester (DeGraaf et al. 2005).

possible the data or analyses. However, how are users of visualization to know if the images portray a viable future reality or a fiction? These constraints are not that different from those placed on other forms of data. Sheppard (1989) suggested that all visualizations adhere to the following principles: accuracy, representativeness, visual clarity, interest, legitimacy, and access. Additionally the person preparing the visualizations should provide the source data in other formats to the readers when requested. Wilson and McGaughey (2000) also explored the issue of representing a landscape in a way that presents useful information that accurately summarizes the model and its output. Thus, visualization tools can be helpful and powerful to illustrating alternatives; however, they can also be misleading and confusing in presenting conditions that cannot possibly exist or by making certain conditions appear different than the data would indicate.

SUMMARY

Models have become a necessary tool for the land manager, particularly when large landscapes are considered. Models are formal frameworks for organizing and synthesizing existing knowledge of an ecological system. We reviewed principles underlying the construction and use of models, with an emphasis on habitat suitability modeling. We believe most landscape models are best viewed within an adaptive management framework because such an approach inherently acknowledges uncertainty in our knowledge of the system to be managed while recognizing that management decisions must be made. We discussed the attributes of effective models and believe that "good" models are those that promote a better decision than could be made without them (see Starfield 1997, Johnson 2001). Ineffective or unreliable models account for processes that are not relevant or well understood, depend on parameters that cannot be estimated precisely, or are dependent on too many parameters. We discussed the basic issues and approaches for addressing uncertainty in landscape models.

Population viability is an increasingly important concept in wildlife conservation, and it is useful because it focuses attention on values and risk. Several definitions of population viability are commonly used in biology; most relate to small or declining populations. We argued that the concept of viability and the quantitative risk assessment tools associated with it should be applied to the management of all wildlife populations, including potentially stable populations of abundant species, many of which are exploited by humans. We provided a definition of viability that incorporates the wide variety of current uses of the term and described a broader concept of viability that places the term in the pragmatic context of resource management. Our comprehensive, hierarchical, quantitatively explicit definition consists of persistence (i.e., primary viability), resilience (i.e., secondary viability), and the ability to provide desired services (i.e., tertiary viability).

Visualization technology has progressed with the rapid advancement of computer technology. We presented the topic of data visualization in a number of forms to help the reader understand the differing motives for creating visualization and the role of the various techniques in producing these images. Visualization software can be a powerful tool to illustrate alternative management options presented by landscape models. A major issue in the current field is the need to use advanced visualization technology in a way that accurately represents conditions being portrayed, including uncertainty in the model structure or output. When one supplies the underlying information in other forms, visualization can be evaluated for the adherence to Sheppard's (2001) principles.

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