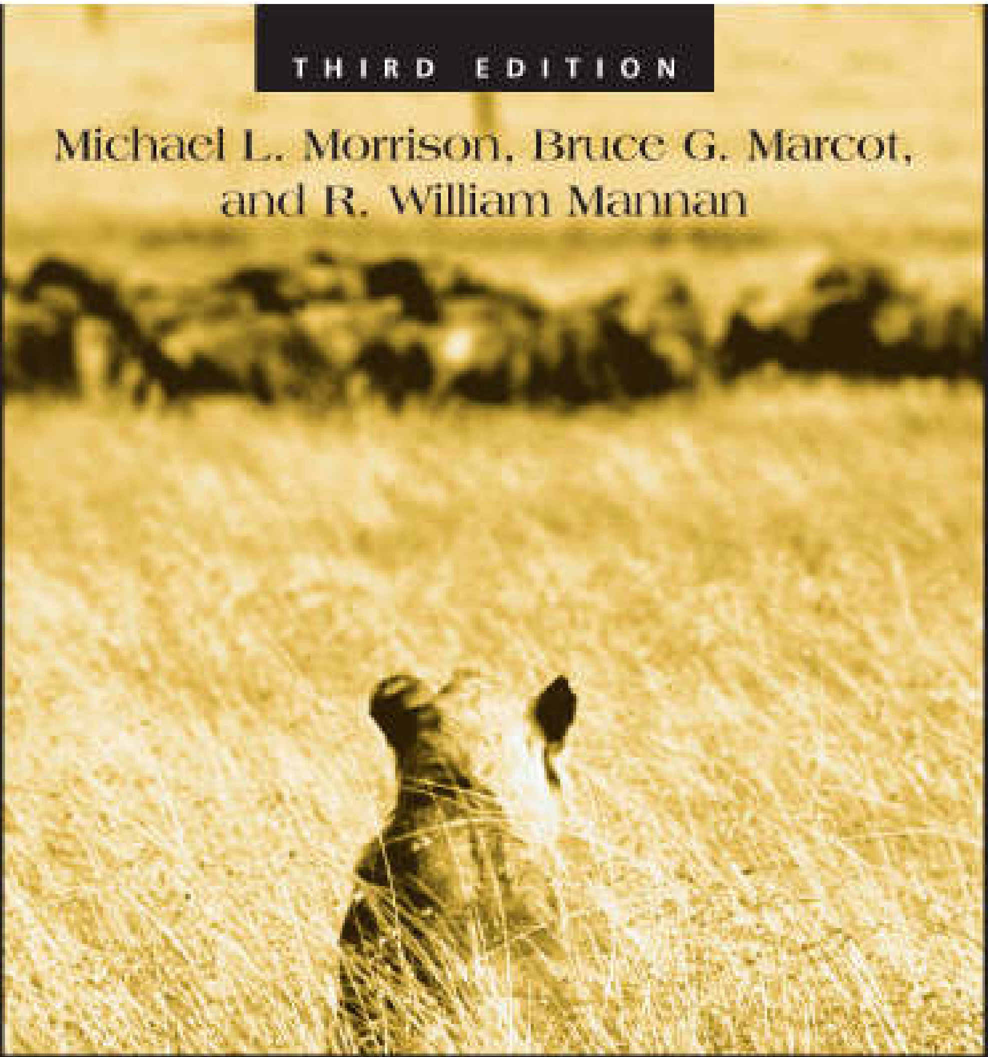

THIRD EDITION

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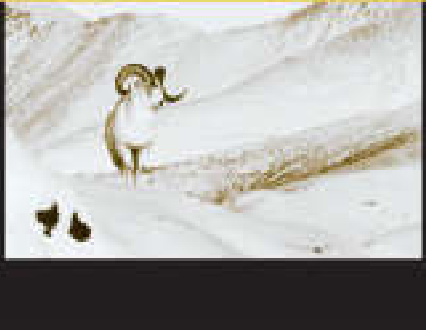
Wildlife-Habitat Relationships

Concepts and Applications



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Modeling Wildlife–Habitat Relationships

> *Models are not like religion. You can have more than one . . . and you don't have to believe them.*
>
> Daniel Pauly and Villy Christensen*

In this chapter we explore the basis and use of models of wildlife–habitat relationships. First, we discuss the use, types, and objectives for modeling wildlife–habitat relationships. Then, we discuss how scientific uncertainty affects wildlife modeling and management, and how models should be used in light of uncertainties. We then review general types of model structures; traditional and new model forms used in research and management of wildlife–habitat relationships; and how models can be used in habitat planning and conservation. We end with a discussion of model validation.

Use and Types of Models

In this section we define models and discuss objectives for modeling types of predictions, model selection, and accounting for correlation and causation.

What Is a Model?

In its broadest sense, a model—from the Latin *modus,* meaning mode or measure—is any formal representation of some part of the real world. Hall and Day (1977) suggested that a model can be conceptual, diagrammatic, mathematical, or computational. These forms can also be viewed as stages in a logical model-building process.

Developing a *conceptual model* may entail synthesizing current scientific understanding, field observations, and professional judgment of a particular species or habitat, and proposing a few hypotheses to explain the species' distribution and abundance. Even (especially) at the conceptual stage, it is vital to explicitly state assumptions and simplifications necessary for the model to be true or useful. The *diagrammatic stage* takes a conceptual model one step further by explicitly showing interrelationships among various environmental parameters and species' behaviors. The *mathematical stage* quantifies these relationships by applying coefficients of change and formulae of correlation or causality. Finally, the *computational stage* aids in exploring or solving the mathematical relationships by analyzing the behavior of formulae on computers.

The conceptual and diagrammatic stages of modeling are often the most difficult, and the most revealing, stages of building ecological theories and enhancing understanding. They must derive from a well-shaped statement of modeling goals and objectives and from basic understanding and articulation of the system being represented.

Objectives for Modeling

The main objectives for developing models of wildlife–habitat relationships are (1) to *formalize* or describe our current understanding about a species or an ecological system; (2) to *understand* which environmental factors affect distribution and abundance of a species; (3) to *predict* future distribution and abundance of a species; (4) to *identify* weaknesses in and improve our understanding; and (5) to *generate testable hypotheses* about the species or system of interest.

Not all of these goals are mutually reachable. For example, many observational field studies may result in statistical descriptions of wildlife-habitat relationships. Such observational descriptions are pertinent to specific locations, environmental conditions, and time periods, and help to explain observed patterns. They should not be assumed to necessarily also provide much power to predict conditions beyond those contexts with any reliability, but such studies are often used this way. At best, they can be used to generate hypotheses. Typically, though, most interest in modeling wildlife–habitat relationships does deal with prediction. In this book, *predictive modeling* refers to estimating the historic, future, or potential presence, distribution, or abundance of a wildlife species or group of species, given information on actual or possible environmental and habitat conditions. We include historic conditions under prediction because retrospective studies are so important.

Types of Predictions

There are two main types of predictions that may be made from models. One is *hindcasting,* which identifies key environmental variables, typically those of vegetation structure or environmental attributes, that account for observed variation in species variables such as abundance. Hindcasting is used to explain historic patterns observed in species occurrence and abundance and is pertinent, strictly speaking, only to the time and place at which the original data were gathered. Hindcasting is typically done from retrospective studies that try to tease out main correlations or causes from conditions or changes that have already occurred. Retrospective studies are vitally helpful in many fields—for example, as used by Louda et al. (2003) to reduce risks in biocontrol programs. Retrospective approaches have also been used to reconstruct historic vegetation (Schulte and Mladenoff 2001), to study the effects of habitat fragmentation on birds (Manolis et al. 2001), and in many other areas.

The other class of prediction is *forecasting.* Forecasting is an explicit attempt to predict future or potential species conditions, given environmental conditions at a time or place not represented by the field data used to generate the model in the first place. Many workers use results of hindcasting, such as obtained with use of correlation, regression, or multivariate statistics, to predict future species conditions, typically under alternative habitat management scenarios (e.g., McCune et al. 2003). However, without proper description of the initial investigation and without validation studies, predictions from hindcasting may be quite unreliable because environmental, demographic, and ecological conditions may vary significantly among locations or over time. At best, using hindcasting models for prediction in new situations entails the assumption that factors not accounted for in the prediction model are insignificant or are unchanged. This assumption should be explicitly stated.

What is the best means of predicting species responses to environmental conditions? Proper forecasting techniques account for autocorrelation of a variable over some time series or over spatial (such as environmental) gradients (Lichstein et al. 2002, Diniz-Filho and Telles 2002). More fundamentally, forecasting should be based on an understanding of the causes of the distribution and abundance of a species, rather than simply correlations as with hindcasting.

Types of predictions can be *deterministic,* as with point estimates of some future or expected population density; *statistical,* as with estimates of central tendency values and some measure of variation of a parameter, such as a mean population density plus or minus some standard deviation or tolerance interval; or purely *probabilistic,* as with estimates of the likelihoods of population persistence to future time periods.

Selecting Models

The manager should be wary of models that produce purely deterministic predictions because there is no measure of uncertainty of the prediction or variation around the outcome. Without knowledge of uncertainty and variation, the manager has no way to judge the relative risk associated with alternative courses of action. As we will suggest below, one of the best uses of wildlife–habitat relationships models is to aid risk analysis in decision making.

If the purpose of modeling is to assist management, one might consider a multiscale approach to model development and selection. A first step might be to clearly identify the management scales (see Table 8.1) in terms of geographic extent, map scale, spatial resolution, time period, administrative hierarchy, and levels of biological organization for which the management activity or plan is directed. Next, one might identify the key areas of scientific inquiry (fig. 8.1) and management issues (fig. 8.2) that pertain to a particular management activity or plan, along with the expected duration of the activity or plan and the need for assessing prehistoric or historic conditions and cumulative effects. Finally, one might consider models by their purpose and function and select the kinds of models most pertinent to the questions, issues, and scales. Of course, other factors will guide model selection as well, such as availability and the need to integrate with other management activities or plans.

Of Correlates and Causes

When we build a model, including a statistical evaluation (hindcast) based on empirical observations, it is not always evident which factors are correlates and which are true causes. This is an old problem (Wright 1921). Often it is important to identify true causes in order to know which management activities to change or reaffirm to better meet objectives. But, frequently, teasing apart the "causal web" of wildlife–habitat relationships with any degree of predictive confidence is immensely difficult.

Consider four progressively more complex situations, as depicted in figure 10.1. In the first instance (fig. 10.1A), some species response, S, such as population presence or abundance, is assumed to be directly caused and explained by some environmental variable, E. There may also be some degree of unexplained variation in species response (shown as *?* in the figure). The unexplained variation (*?*) is due to measurement error, experimental error, or the effect of other environmental factors not included in the study. It can be quantified by such means as calculating residuals in a regression analysis or partitioning error terms in an analysis of variance.

However, as depicted in figure 10.1B, in the real world we may be measuring one environ-

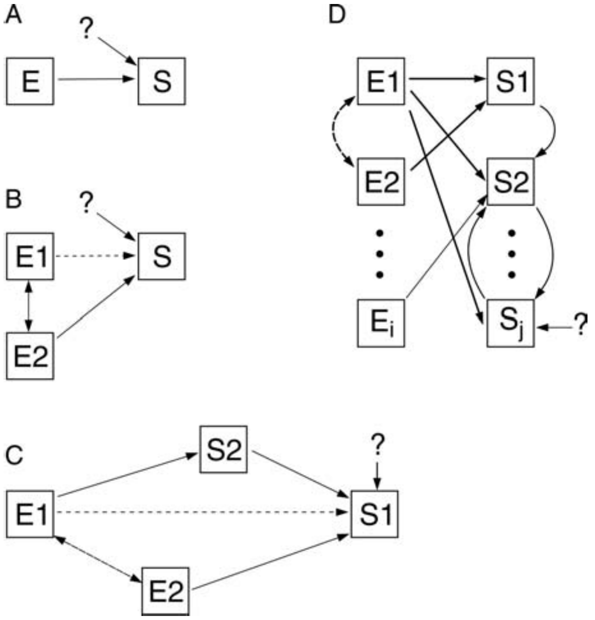


Figure 10.1. Causes and correlates: four increasingly complex and realistic scenarios of wildlife–habitat relationships. S = wildlife species response; E = environmental factors; ? = unexplained variation; solid arrows = causal relations; dashed-line arrows = correlational relations that may or may not be causal; large dots = a sequence of other E and S variables. See text for explanation. (From Marcot 1998, 137.)

mental variable, E1, when the real causal factor is another, unmeasured environmental variable, E2. In this case, the two environmental variables are themselves correlated and there may or may not be a causal relation between them. E1 and E2 may be vastly different kinds of environmental factors and may operate at different spatial or temporal scales as well. We think we have explained the biological response of the species S by the observed correlation with E1, and we may even be able to predict S from E1 to a limited degree (in which case E1 is termed the "latent variable"), but we may be greatly mistaken to presume that management of E1 will necessarily affect the species as we wish. Further, the unexplained variation (*?*) in S is then due to the less than perfect correlation between E1 and E2 as well as to measurement and experimental error, and to influential environmental factors beyond E1 and E2 not addressed in the study. Such a situation may be analyzed using univariate multiple regression techniques.

As an example, we may find that mean fecundity rates (S) in a population of Townsend's vole (*Microtus townsendii*) are negatively correlated with food abundance during the previous season (E1), and thereby infer that high food abundance leads to high population density, which in turn suppresses mean fecundity levels as a population regulation mechanism. However, on closer inspection, it may turn out that the real culprit, E2, causing lower mean fecundity of voles is parasitism by botflies (*Cuterebra grisea*) (e.g., Boonstra et al. 1980). It may turn out that both food resources and botfly incidence are affected by weather, so that environmental factors

E1 and E2 are correlated, but there is no direct causal link between them. If our study focused only on food resources and vole fecundity, we would conclude that food abundance is the cause and that managing for higher vole densities could be afforded by managing for more consistent food resource levels. This conclusion would be in error. Also, the unexplained variation in vole fecundity would be caused by the less than perfect correlation between food resources and botfly incidence, as well as by additional factors beyond food or botflies not addressed in the study.

However, the real world is often even more complicated. As shown in figure 10.1c, another species, S2—potentially a competitor, predator, or symbiont—may also play a role in affecting the species of interest, S1. (We included the parasite as an environmental factor in the last example.) Following our example above, mean vole fecundity might be influenced by some (hypothetical) predator, S2, that selectively removes high-fecundity individuals from the vole population. S2 itself may share some environmental factor, E1, that correlates with (but does not cause) S1. In an even more complicated but increasingly realistic schematic, as in figure10.1d, S2 may also be influenced by other environmental factors beyond E1. And so the causal web expands.

It is important to recognize such *causal webs* of organisms and environmental factors, and to focus attention on the main influences (instead of the entire possible causal web). We should at least challenge ourselves to draw a causal diagram (the diagrammatic phase of modeling as outlined above)—often called an influence diagram—so that we can hypothesize which are major causal factors, which are minor causal factors, and which are merely correlative. Differentiating between causes and correlates is critical for guiding costly habitat management activities to respond to complex environmental issues such as changes in air quality or regional climate, and for establishing an appropriate monitoring scheme, including identifying and tracking key indicators.

Path regression analysis is a statistical technique that can aid in quantifying the relative contribution of causal factors (Shipley 2002). Path regression is used to determine and display the partial correlation coefficients of individual factors that can influence a species population or, in some instances, a management objective, such as used by Howe and Brown (2000) to model effects of rodent foraging on vegetation communities, and by Johnson et al. (2001) to model foraging behavior of woodland caribou (*Rangifer tarandus caribou*). An example of a path regression analysis is shown in figure 10.2. Other techniques useful for teasing out the relative contributions of environmental factors, species factors, and uncertainty are those of multivariate multiple regression and two-stage regression.

Uncertainty and Unknowns in Wildlife–Habitat Relationship Models

Biological models do not predict species distribution and abundance without error. Rather, modeling wildlife–habitat relationships, like managing species habitats, typically entails dealing with the following kinds of obstacles:

- Imprecise data
- Uncertain inferences
- Limiting and fallacious assumptions
- Unforeseen environmental, administrative, and social circumstances
- Risks of failure

Imperfections are often present in habitat analyses and management decisions but are especially

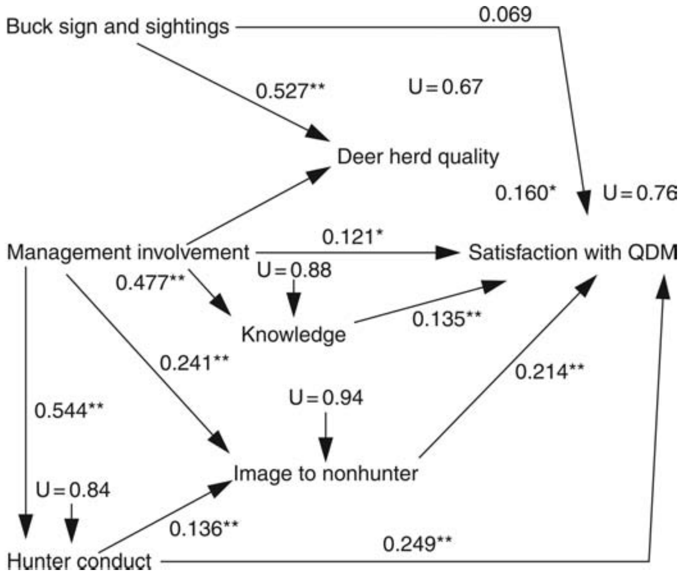


Figure 10.2. Example of a path analysis that partitions the various factors accounting for variation in public satisfaction with quality deer management (QDM). The values are partial correlations (i.e., the correlation of each factor once the contribution of all other factors is accounted for). U = unexplained variance, calculated as $(1 - R^2)^{1/2}$; * $P = < 0.05$, ** $P = < 0.0001$. (Reproduced from Woods et al. 1996 [fig. 1], by permission of the Wildlife Society.)

important when there is risk of reducing a wildlife population or eliminating a species. Uncertainty may be encountered when analyzing biological data, when making inferences about species' responses to environmental conditions, and when selecting and instituting a management plan.

Types of uncertainty may be classified as scientific uncertainty and decision-making uncertainty. Just as analyzing species and habitats entails a different process from that used to make decisions on resource management, so too are the kinds and implications of uncertainties from the analysis process distinct from those in a decision-making process. Results of a technical study, such as a risk analysis of population viability, may be part (but only part) of the information used by a decision maker in developing a habitat management plan.

Types of Uncertainty

Scientific uncertainty in habitat modeling refers to the nature of the data and the ways in which information on species and habitats is represented and applied. Scientific uncertainty essentially means that our predictions of how species respond to environmental conditions are not perfect. Uncertainty may occur because (1) the system itself is naturally variable and very complex, and thus difficult to predict; (2) the process of estimating values of parameters in the habitat model entails a degree of error; (3) models used to generate predictions are in some sense invalid;

or (4) the scientific question being asked is ambiguous or incorrect.

VARIABILITY OF NATURAL SYSTEMS—NOISE IN THE MESSAGE

Many aspects of natural systems vary over time. Predicting attributes of the system—the "message" we are trying to interpret—may often involve observing and modeling traits that are influenced from outside factors (fig. 10.1); that is, "noise" inherent in the message. Such noise introduces variation in measurements and uncertainty in estimating and predicting attributes of the system. In statistical models of habitat relationships, noise is typically depicted as unexplained variation in the occurrence or abundance of a species. One kind of unexplained statistical variation is the value of "residuals" in regression models. Sometimes this kind of noise in the system can be a useful source of information itself (e.g., Motta 2003).

In a most revealing review of models in ecology and evolution, Moller and Jennions (2002) determined that the mean amount of variance (r^2) explained was a dismal 2.51 to 5.42%, and that the mean effect size reported was between Pearson $r = 0.180$ and 0.193. They concluded that, because of so much noise in the data, most studies had inadequate sample sizes to determine the absence of a particular relationship with a power of 80% and $\alpha = 0.05$. This conclusion is not encouraging and suggests the need to conduct initial pilot studies to estimate the degree of variation in parameters so sample sizes can be adjusted accordingly (see chapter 4). However, Peek et al. (2003) viewed this same study from the perspective that about *half* of the variation in statistical models is *not* explained (the unexplained residual or random error), suggesting a far higher success rate in ecological modeling. They concluded that the success of ecological models should be judged not by single-factor relationships, but by overall model performance. Still, in a risk management framework, and to set realistic expectations for results of their actions, decision makers should know that such models may explain or predict only half the variation in whatever conditions they wish to manage.

De Valpine and Hastings (2002) suggested a numerical method for incorporating noise and observation error when fitting population models, and their tests of fit suggested that such an approach works best with stable-point Ricker recruitment models and worst with Beverton-Holt models. Hewitt et al. (2001) suggested treating temporal variability as a parameter instead of as noise, thereby increasing the detection of treatment effects in before–after/control–impact (BACI) studies.

UNCERTAINTY OF EMPIRICAL INFORMATION—ERRORS OF ESTIMATION

Values of environmental parameters are typically estimated from a sample set of observations. A parameter, for example, may be the mean number of tree stems per hectare or the variance of litter sizes of black-footed ferrets (*Mustela nigripes*) to the extent that these can be attributed to individual and environmental variation. When a parameter is estimated from a sample set of observations, from a statistical viewpoint, uncertainty or errors in estimation occur. The estimations are *biased* if each of the values of the observations are consistently lesser or greater than actual (unknown) values; *inaccurate* if the estimated value of the parameter of interest (such as a mean or a variance) is substantially different from the true value; or *imprecise* if values of individual observations vary widely among each other.

Each of these errors in estimating the value of a parameter constitutes a different kind of scientific or statistical uncertainty. Bias is estimated by the difference between the mean of observed values and the true parameter value; accuracy is measured by mean square error of observed values; and precision is estimated by variance in the observed values. Statistical estimators always have these properties of bias, accuracy, and precision, as well as others, particularly *consistency.* Bias tells you how far you missed the bull's-eye on average; accuracy tells you the spread of misses among individual trials; and precision tells you how tightly grouped your trials are, whether they missed the bull's-eye or not. Then, *consistency* tells you if you're even shooting at the right target. An estimator can be consistent, but biased, and adjusting the sampling methodology can reduce bias; likewise, an estimator can be consistent, but imprecise or inaccurate, and increasing sample size can increase precision and accuracy.

Such errors of estimation can arise from a number of sampling problems, including inadequate sample size, observations taken from disparate times or places, and samples taken nonrandomly or nonsystematically, depending on the assumptions of the estimator being used. Errors of estimating the value of parameters may also arise from applying the wrong kind of estimator, such as in applying a formula for calculating variance. If correct use of the formula assumes that observations were made independently and randomly—when they were actually made over a time series or systematically, such as at even intervals over a transect—then an error of applying the wrong kind of estimator has been made. (With systematic samples, the appropriate variance estimator should instead use the mean square of *successive differences* in values measured along the time or spatial series of samples.)

MODEL VALIDITY AND UNCERTAINTY OF MODEL STRUCTURE

Model validity refers to a broad spectrum of performance standards and criteria. Examples are model credibility, realism, generality, precision, breadth, and depth (Marcot et al. 1983). The various criteria refer to such attributes of models as the number of parameters in a model and their interactions, the context within which a model was developed or should be used, and the underlying and simplifying assumptions of the model structure (see table 10.1 for definitions of model validation criteria).

A parameter that is estimated precisely, accurately, and without bias may still be used inappropriately, as in a model that is applied to the wrong environment, location, season, or species.

APPROPRIATENESS OF THE PROBLEM—ASKING THE RIGHT QUESTION

The context in which a theory is applied or a model is used may introduce yet another source of uncertainty. Even given that a model has been validated—that is, shown to be a useful tool and to generate acceptable predictions according to particular criteria—it still may be applied to the wrong problem. (This conclusion is analogous to the property of consistency in statistical estimation.) In some cases, this problem of inappropriate application may be unavoidable if no other models are available.

For example, a life table model that assumes equal sex ratios and that adults breed each year may generate acceptable predictions for use with Dall sheep (*Ovis dalli*) but may generate grossly inaccurate predictions when used for species with variable or quite different social breeding organizations, such as pronghorn (*Antilocapra americana*). This application would call into question the reliability of the model when used with some species or under some circumstances.

Further, the hypothesis or problem being addressed by using a particular model may be ambiguous or even unanswerable. For example, a model of species–habitat relationships that describes vegetation types may not provide a particularly useful foundation for answering questions about landscape dynamics necessary for maintaining viable populations of the species.

Table 10.1. Criteria useful for validating wildlife–habitat relationship models

Criterion	Explanation
Precision	The capability of the model to replicate particular system parameters
Generality	The capability of the model to represent a broad range of similar systems
Realism	The capability of the model for relevant variables and relations
Precision	The number of significant figures in a prediction or simulation
Accuracy	The degree to which a simulation reflects reality
Robustness	Conclusions that are not particularly sensitive to model structure
Validity	The capability of the model to produce all empirically correct models.
Usefulness	The existence of some empirically correct model.
Reliability	The fraction of models that are empirically correct
Adequacy	The fraction of pertinent empirical observations that can be simulated
Resolution	The number of parameters of a system that the model attempts to mimic
Wholeness	The number of biological processes and interactions reflected in the model
Heurism	The degree to which the model usefully furthers empirical and theoretical investigations
Adaptability	The future development and application
Availability	The existence of other, simpler, validated models that perform the same function
Appeal	The degree to which model results match our intuition and stimulating thought, and practicable.
Breadth, Depth	The number and kinds of variables chosen to describe each (habitat) component
Face validity	The credibility of the model
Sensitivity	The match of model variables and parameters with real-world counterparts, and their variation causing outputs that match historical data; also, the dependence of model output on specific variations of variables
Hypothesis validity	The realism with which subsystem models interact
Technical and operational validity	The identification and importance of all divergence in model assumptions from reality, as well as the identification and importance of the validity of the data
Dynamic validity	The analysis of provisions for application to be modified in light of new circumstances

Source: Based on Marcot et al. 1983; reproduced by permission of the Wildlife Management Institute.

Accounting for Error in Modeling

One of the major problems in using models of wildlife–habitat relationships is that of *propagation of error.* Error can arise from model structure, missing data, mismatched scales of geographic extent and spatial resolution, and other systematic sources, as well as from measurement error and the stochastic nature of biological systems. How do all such errors compound in a particular model? The problem of error propagation has been poorly addressed in the statistical and modeling literature and needs much work. One approach to depicting the compounding of error is to partition the variance associated with model output into additive factors, each representing the major sources of error. This method is analogous to methods used in analysis of variance, in which mean square errors are partitioned into sampling error and experimental error. This approach may entail an analytic formulation for summing variance and covariance terms (box 10.1). Other approaches may invite use of model sensitivity analysis. We also further discuss errors in modeling below under "Validating Wildlife–Habitat Relationship Models."

Box 10.1 Propagation of error in modeling wildlife–habitat relationships

How does error compound in wildlife–habitat models, and why should we worry about it?

Every variable and function in a wildlife–habitat model can have several kinds of associated error, including measurement error, experimental error, and random error. Although it may be feasible to estimate such error for each variable or simple relation in a univariate sense, it is the compounding of error among variables and in complex functions that combine variables that may seriously affect final model output. The result of such *error propagation* may be model output that is significantly biased, imprecise, or inaccurate. Thus it may be critical to understand how error terms compound.

The biostatistical literature continues to poorly address or even to ignore the estimation of error propagation, in large part because it is such a wicked analytic problem. The classic approach to the problem is to dissect the variance of some variable y into its Taylor series expansion terms of component measured quantities $F(x_1, x_2, x_3, \ldots)$ (Kotz et al. 1982):

$$\mathrm{var}(y) = \sum \left(\frac{\partial F}{\partial x_i}\right)^2 \mathrm{var}(x_i) + 2 \sum_{ij} \left(\frac{\partial F}{\partial x_j}\right) \left(\frac{\partial F}{\partial x_j}\right) \mathrm{cov}(x_i,x_j).$$

The wicked part of this problem is not in estimating the first variance term, but in the covariance terms $\mathrm{cov}(x_i,x_j)$. In the simplest case, if x_i and x_j are uncorrelated, then $\mathrm{cov}(x_i,x_j) = 0$, and the entire second term for var(y) drops out. Ecological variables are quite often at least partially correlated (figs. 10.1, 10.2), so that $\mathrm{cov}(x_i,x_j) > 0$ and the second term in the above equation is nonzero and needs to be calculated.

In the case of estimating covariance among means, the parent covariance term $\mathrm{cov}(x_i,x_j)$, or $\sigma^2_{\mu\upsilon}$, can be calculated as (Eadie 1983):

$$\sigma^2_{\mu\upsilon} = \lim_{N\to} \frac{1}{N} \sum [(\mu_i - \bar{\mu})(\upsilon_i - \bar{\upsilon})].$$

This covariance term may be extremely difficult to impossible to measure from empirical data. This difficulty is especially true with real-world studies of landscapes, ecosystems, and populations in conditions that are poorly, or not, replicable, and for which control conditions are not feasible.

However, it is the covariance between ecological variables that may often be a major source of variation and error in model output. Even in the simple case of two interacting variables, x and y, the appropriate variance estimator involves the wicked covariance term: for the interaction term xy, variance is calculated as $y^2\,\mathrm{var}(x) + x^2\,\mathrm{var}(y) + 2xy\,\mathrm{cov}(x,y)$ (Kotz et al. 1982, 549). Empirically, covariance among all such key variables in a wildlife–habitat model may be impossible to estimate empirically and to calculate analytically.

Propagation of error also means that initial errors may have a fatal effect on the final results—that is, that small changes in initial data may produce large changes in final results. Such problems are called *ill-conditioned* and may include population models that exhibit chaotic or initially unpredictable behavior (Morris 1990; Hassell et al. 1991). Additional sources of error, particularly in computer models and that can propagate across functions, include rounding errors and truncation errors.

What is a modeler to do? One tractable approach to evaluating error propagation is to conduct sensitivity analyses of the model, whereby changes in outputs are plotted as a function of incremental changes in input variables (Nelson 2003). This approach can help identify the domains over which models exhibit chaotic behavior, such as when populations exhibit irregular cycles or suddenly crash or expand with only minor changes in the input variables. Sensitivity analysis can be one phase of model validation, discussed further in the text. Another analytic approach to dissecting propagated errors is forward and backward analysis (see Fröberg 1969, 3–9).

Decision Making under Uncertainty and What to Do about It

Probably all management decisions dealing with wildlife habitat are made under some uncertainty of current conditions or future effects. Decision-making uncertainty can arise from imprecise data, uncertain inferences, limiting and fallacious assumptions, and unforeseen environmental, administrative, and social circumstances. Each of these factors can contribute to risks of failure in meeting desired management goals.

How might the manager or decision maker proceed under such uncertainties? A host of decision-analysis techniques are available that aid in assessing the value of perfect information, the value of sample information, the credibility of information, and quantitative measures of the state of knowledge (e.g., Clemen and Reilly 2001; McDonald and McDonald 2003; Pielke and Conant 2003). We review some decision-aiding approaches and models below. Using these approaches to identify areas and degrees of decision-making uncertainty may also be useful for establishing management activities as adaptive management experiments. In a sense, uncertainty is an opportunity for testing management hypotheses about outcomes of actions, as long as basic tenets of adaptive management are not violated (see chapter 11).

Balancing Theory with Empiricism

We have dedicated several chapters in this book to reviewing study design and measures of habitat and wildlife behavior. Empirical field studies—whether observational descriptions or experimental tests—can be used to develop models of wildlife–habitat relationships. Theory, however, often plays an important role in model development. Theoretical models may tend to be more robust and general, whereas empirical models may be more locally accurate and precise. Each complements the other. Ultimately, empirical models can be used to induce more general theoretical ones, and theoretical models can help guide the specific development of empirical models.

Using Models to Generate Research Hypotheses

The modeling process should be a means by which we challenge ourselves to explicitly articulate what we think we know about some system. This challenge occurs in the conceptual and diagrammatic phases of model development as discussed previously. To this end, model output can be used to generate research hypotheses. In an adaptive management context, management activities can be crafted to test the more important assumptions or provide information on the key unknowns. When management activities are applied on the ground, these assumptions and unknowns may be termed *management hypotheses.*

To scientifically test management hypotheses, management activities should be crafted to follow the guidelines for correct study design, including evaluation of baseline conditions, provision of controls, adequate study and treatment duration, appropriate spatial scale, and adequate replication of controls and treatments. Such considerations pertain to ensuring consistency, reducing bias, and providing for appropriate levels of accuracy and precision of estimates. Then, effects of the management activities can be analyzed to validate the original assumptions and provide new information to revise or reaffirm the management hypotheses and guidelines. In turn, the models used to suggest the original management activities would be updated and new activities suggested, if warranted by the findings. Thus the ideal adaptive management process is cyclic, not linear, and entails strict adherence to correct experimental design. That is, management trials on the ground are crafted as scientific experiments, and their results are used to pose new management hypotheses and to further craft and test new management trials.

As models become more complex, and as management objectives broaden to include landscapes and ecosystems, use of models for generating research hypotheses should become more salient in the decision-making process. Real-world constraints of uncertain future research budgets, changing management goals, and balancing the need for short-term publications and long-term studies must be addressed in this use of models.

Types of Model Structures

The array of models in wildlife ecology and conservation is bewildering. There has been an exponential increase in the number of publications on modeling in the ecological and wildlife literature since the middle of the last century (fig. 10.3), with no asymptote in sight. Clearly, modeling continues to play central roles in many facets of wildlife–habitat relationships (WHR) research and management.

In this section we briefly review some general types of WHR model structures as a way to provide a classification of types of models. In the next section we discuss specific models that are directly or potentially useful to WHR research and management.

Statistical Empirical Models

Statistical empirical models provide statistical analyses or summaries of empirical data. These models are usually based on statistical correlations among variables. They include many kinds of bivariate and multivariate analyses that describe relations among variables (see chapter 6). Recently, meta-analysis methods have come into vogue that provide a means of combining information, and making inference across, multiple studies (Pena 1997; Gurevitch et al. 2001). Meta-analysis has been used in a variety of research questions, including understanding the effects of

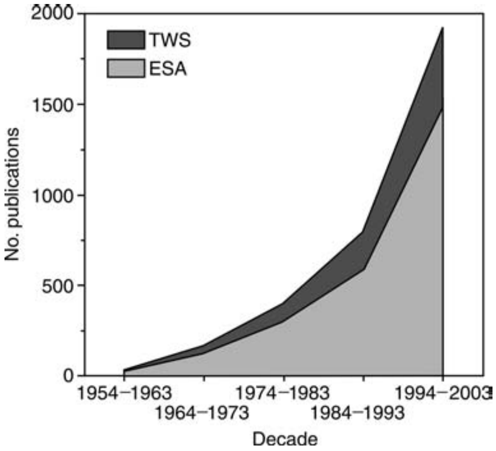


Figure 10.3. Number of articles on models or modeling published in all journals by The Wildlife Society (TWS) and the Ecological Society of America (ESA), by decade, 1954–2003.

competition on predator–prey interactions (Bolnick and Preisser 2005), determining the influence of organic agriculture on biodiversity (Bengtsson et al. 2005), and estimating vital rates of raptors (Boyce et al. 2005).

Statistical empirical models also include statistical approaches that derive relations among variables in a post hoc manner. Some of these newer approaches are termed *knowledge discovery, data mining,* and *rule induction* (Jeffers 1991; Hastie et al. 2001). These approaches entail discovering relations among variables in typically large data sets or from a series of examples. These newer approaches deviate significantly from the traditional "frequentist" statistical methods. Some entail use of Bayesian statistics, and others depart entirely from statistical considerations of hypothesis-driven analyses altogether. Some classical, frequentist statisticians despair of such post hoc approaches as "fishing expeditions" that may yield spurious results with unknown degrees of confidence (Anderson et al. 2001). However, the methods seem to be here to stay, and when used judiciously and thoughtfully, they can be very helpful in further hypothesis creation. We discuss some tools under these new approaches below.

Habitat Relationship Models

A variety of traditional WHR models have been used for many years. These include wildlife-habitat matrix models, gap analysis models, habitat suitability index (HSI) models, habitat effectiveness (HE) models, habitat evaluation procedures (HEP), and others. The basis for these models can be a combination of expert opinion, literature, and field data. These models may be structured as simple look-up tables (WHR matrix models), as geometric mean equations incorporating key or limiting factors (HSI, HE models), or as hybrids of equation-based analysis within additional assessment procedures (HEP models). They may also predict wildlife species presence and distribution based on vegetation and land cover conditions (WHR matrix models, gap analysis models).

Analytic and Numerical Population Models

Analytic and numerical population models include more traditional population demographic and genetic models, such as Leslie matrix life tables (e.g., Henny et al. 1970; Taylor and Carley 1988; Miller et al. 2002) and calculations of rates of inbreeding and genetic drift (e.g., Perrin and Mazalov 1999; Edmands and Timmerman 2003).

Simulation Models

Simulation models include traditional dynamic models that simulate time-based interactions of variables of populations and ecosystems. Most simulation models are discrete and based on difference equations or other representations of time-step functions, and as such derive largely from "queueing theory" (Gordon 1978). A queue is a sequence of events waiting to happen (for example, dispersal of an organism from a particular habitat patch); how they happen is determined by the structure of the model (such as equations that describe the direction and distance of dispersal), and when they happen is usually based on a probability distribution of event frequency (such as the probability of dispersal events per time increment). Time-dynamic simulation models are used widely in ecology (e.g., Bolliger et al. 2005).

Geographic Information System–Based Models

Simulation models also include, more recently, geographic information system (GIS)–based, geographically referenced ("spatially explicit") models of landscape patterns and disturbance events (see chapter 8) and simulations of individual-based movement throughout a landscape and use of habitat patches (see chapter 9). GIS models can be very flexible and incorporate other modeling constructs, such as population viability analysis. For example, Zhu et al. (1998) integrated GIS with a decision support structure using a knowledge-based information system, and illustrated its utility for strategic planning for development of the island of Islay off Scotland. Reynolds et al. (2000) used the Ecosystem Management Development System (EMDS) model (Reynolds et al. 1997), which integrates a fuzzy logic modeling framework within a GIS system, to evaluate watershed conditions. Raphael et al. (2001), Wisdom et al. (2002), and Rowland et al. (2003) integrated Bayesian belief networks with GIS to evaluate broad-scale management effects on terrestrial wildlife in the interior western United States. Zhang et al. (1997) integrated a neural network model (see below) into GIS to classify vegetation types from remote sensing imagery. Many other examples of GIS modeling, including hybrid models of GIS with other modeling constructs, are available (O'Neil et al. 2005).

Knowledge-Based (Expert) Models

Knowledge-based (expert) models represent the experience and judgment of human experts rather than being based strictly on empirical data, simulations, or theoretical constructs. These models include expert systems of various types, as well as models in which the state variables and relations are determined by expert judgment. Knowledge-based models are often devised by use of an intermediary "knowledge engineer" or someone who quizzes the expert and puts the gained expertise into formulae, functions, and computer code. Such expert-based models can pose particular challenges for verification and validation.

A Review of Specific Types of Wildlife–Habitat Models

In this section we will review specific examples of various types of models that are useful for assessing wildlife–habitat relationships. We split our review here into traditional WHR models and a set of newer, more avant-garde types of models.

Traditional Models of Wildlife–Habitat Relationships

In this section we review types of wildlife-habitat relationship models that have been commonly used in many studies of management situations.

MODELS OF VEGETATION COMPOSITION AND STRUCTURE

A number of models have been developed that display current and future composition and structure of vegetation stands. These models include *forest stand growth and yield models* of many kinds, which are typically based on growth and yield information generally available for a variety of commercial forest types.

It is common practice to use forest growth models designed for silviculture to infer amount of wildlife habitat (e.g., Thompson et al. 2003). However, this use assumes that the vegetation variables output by the model are directly pertinent to wildlife—that is, that they are the vegetation conditions selected by specific wildlife species (see fig. 10.1). In many cases, however, the representation of habitat for specific wildlife species may be uncertain, at best. Thus the user should interpret actual wildlife response with a fair degree of caution and skepticism. In other words, a portion of the uncertainty (variation) in species' response may be due to simply not tracking the most appropriate habitat variables. This uncertainty also means that if successful wildlife management is dependent on models built for other purposes, the models should be evaluated for how precisely and fully they represent key habitat attributes for specific species of interest.

Models of ecological succession are useful for predicting changes in vegetation composition and structure over time. Such models are used in conjunction with WHR matrix models to depict changes in macrohabitat for wildlife species. As a systems model, a model of successional changes can also incorporate the ecological functions of wildlife as influencing vegetation. For example, the models of Lesica and Cooper (1999) of shrub vegetation succession in the Centennial Sandhills of southwest Montana incorporated the salient effects of pocket gopher (*Thomomys talpoides*) burrowing and ungulate browsing, as well as fire, on maintaining early seral vegetation.

DISTURBANCE MODELS

Disturbance models can include a variety of process, simulation, or even analytic models to determine how environmental conditions, especially vegetation and river systems, are affected by intermittent disturbance events such as fire, radical climate change, drought, and floods. Disturbances are being considered more frequently in models used to assess wildlife–habitat relationships and other kinds of land use (Schelhaas et al. 2002). Some disturbance models pertain to fine-grain features of environments, such as simulating forest canopy gaps (Lundquist and Beatty 2002). Other disturbance models address broad geographic areas, such as the effects of fires on the amount and distribution of old-growth forests across a broad area—for example, the Pacific Northwest of the United States (Wimberly 2002).

Disturbance models can be immensely useful for conservation of rare species or recovery of threatened species, by understanding the roles—negative and positive—played by disturbance events. For example, Root (1998) determined that the long-term viability of the threatened Florida scrub jay (*Aphelocoma coerulescens*) requires fires at least every 30 years—fires serving to maintain a diversity of habitat patches used by the species. Probst and Weinrich (1993) found a similar, positive relation between the endangered Kirtland's warbler (*Dendroica kirtlandii*) and frequent fires in its jack pine (*Pinus banksiana*) forest habitat in Michigan.

Recently, there has been a return to modeling disturbances by using *stable-state analysis* (Beisner et al. 2003; Didham and Watts 2005). Popular in the 1960s, this modeling approach views specific patterns of composition and structure of ecosystems and ecological communities as semistable conditions that can be perturbed to varying degrees by disturbance events. If the perturbation is sufficiently strong, the system may enter a new configuration and a different stable state. Examples include repeated fires, livestock grazing, and agricultural development in native grasslands that allow invasive species to gain an irreversible foothold and basically destroy native grass and forb communities (Harrison et al. 2003); the creation of new stable states in forests of the eastern United States under immense herbivory pressure from overabundant deer herds (Stromayer and Warren 1997); grasslands maintained by herbivore foraging (Seabloom and Richards 2003); and, in a case of the *absence* of a natural disturbance event, the exclusion of wildfire in sagebrush-steppe or arid savanna communities that leads to invasion ("encroachment") by conifer trees or other woody plants (e.g., Skarpe 1991).

The degree to which systems, including wildlife species, can rebound following a disturbance event is a measure of their *resilience* (Gunderson et al. 2002), and the degree to which systems do not change is their *resistance* (Knapp et al. 2001; Byers and Noonburg 2003). One implication of this rebounding for managing resource production, including wildlife habitat, is that more resilient and resistant systems are better able to withstand the onslaught of disturbance events. And by implication, more resilient and resistant systems can produce more predictable and sustainable levels of renewable natural resources. Another implication of multistate modeling is that some systems can attain several stable states, or may take a long time to recover to original or desired states (Ludwig et al. 1997), or, if pushed too far, may never be able to be restored to a previous state. These outcomes can have important implications for guiding conservation and restoration actions, particularly if recovery times following disturbances do not match expectations (Paine et al. 1998).

Another type of disturbance model pertains to *climate change.* Much work is being done to understand climate trends as disturbance events themselves; the influence of climate shifts on other disturbances, such as fire frequency (Whitlock et al. 2003) and pests and parasites (Jaenike 2002; Logan et al. 2003); and the implications of these influences overall changes in ecosystems (Beckage et al. 2005), ecological communities (Weltzin et al. 2003), and individual wildlife taxa (Torti and Dunn 2005). For example, analyzing data on temperature and precipitation trends in Europe, Lemoine and Bohning-Gaese (2003) predicted that climate change would result in a decrease in the proportion of long-distance migratory birds and an increase in the proportion and number of short-distance migrants and residents. They concluded, with some empirical corroboration, that increasingly warm winters will disproportionately threaten long-distance migrants (also see Jonzen et al. 2002).

WHR MATRIX MODELS

WHR matrix models have been around since the 1970s—and probably far earlier in more primitive forms. They are essentially static tables that relate wildlife species to habitat types and components (Verner and Boss 1980) and that depict other features of their life history (Johnson and O'Neil 2001). Often the data are categorical and qualitative, and are derived from a combination of field studies and (largely) professional judgment. Such matrices or information bases may be useful for predicting the potential presence of wildlife species associated with specific environmental conditions, although they tend to err on the side of commission (predicting more species to be present than actually are). This error is because factors not specified in a query of WHR matrix databases are tacitly presumed to be optimal or do not affect species absence. Still, such matrices are of great value to explore general trends and patterns of potential species presence and community composition.

GAP ANALYSIS MODELS

Gap analysis is a method of identifying "gaps" in conservation area networks in which high species richness or locations of particular species or taxa of interest are unprotected. Gap analysis maps are typically produced in GIS by overlaying land ownership and management categories with species' range maps or distribution maps of vegetation and land cover categories that represent species' habitats. Then, "hot spots" of high species richness, centers of endemism or rarity, or other such features of conservation interest are delineated, and it is then determined if such sites are unprotected (Jennings 2000).

Gap analysis has been used widely as part of reserve design tools (also see discussion below on other methods of reserve design). As examples, Clark and Slusher (2000) used gap analysis to design a national wildlife refuge in the Kankakee River/Grand Marsh area in Indiana and Illinois. Caicco et al. (1995) used gap analysis to determine the conservation and management status of vegetation communities in Idaho. Allen et al. (2001) used gap analysis to model viable mammal populations, and suggested that defining minimum critical areas via gap analysis was a useful way to produce better maps of critical unprotected areas for mammal species.

Several cautions pertain to gap analysis. Hot spots of high species richness may represent disturbed or ecotonal environments rather than cores of species' ranges and optimal habitat conditions, so some care needs to be taken in interpreting results and in understanding the underlying distributional data. Church et al. (2000) suggested a method to balance species richness objectives with assessment of habitat quality. Flather et al. (1997) suggested that several key assumptions of gap analysis should bear critical evaluation, including (1) that a subset of taxa can represent overall diversity patterns, and (2) that accurate reserve design can be affected by data uncertainty and error propagation in the underlying distributional data. Other concerns for accuracy of mapping gaps and species richness hot spots were expressed by Dean et al. (1997) and NCASI (1996), who found that boundaries of species-rich areas vary greatly depending on the accuracy of the underlying habitat and species distribution maps.

HABITAT SUITABILITY AND EFFECTIVENESS MODELS

One of the more popular and simpler approaches to modeling WHR has been the use of *habitat suitability index (HSI) models.* HSI models are used extensively by USDI Fish and Wildlife Service (Schamberger et al. 1982) and other federal resource management agencies. These models typically denote habitat suitability of a species as the geometric mean of n environmental variables deemed to most affect species presence, distribution, or abundance. The general model form is: $HSI = (V_1 \cdot V_2 \cdot \ldots V_n)^{1/n}$, where the V's represent n key environmental variables. Each variable and the resulting HSI values are scaled from 0 to 1. The overall HSI value assumedly represents the final response of the species to the combination of the values of the environmental parameters. A geometric mean is used so that when one variable goes to zero, HSI = 0.

For example, the three environmental variables denoted in an HSI model for yellow warbler (*Dendroica petechia*) are percentage of deciduous shrub crown cover, average height of deciduous shrub canopy, and percentage of shrub canopy consisting of hydrophytic shrubs (Schroeder 1983). The resulting suitability index in the yellow warbler model represents relative habitat values for reproduction. HSI models have been constructed for a wide variety of species in the United States.

HSI models are useful for representing in a simple and understandable form the major environmental factors thought to most influence occurrence and abundance of a wildlife species. However, HSI models are best viewed as hypotheses of species–habitat relationships rather than as causal functions (Schamberger et al. 1982). Their value lies in documenting a repeatable assessment procedure and in providing an index to a very few, and easily evaluated, environmental characteristics that can be compared among alternative management plans.

However, HSI models do not provide information on population size, trend, or behavioral response by individuals to shifts in resource conditions, and seldom include interaction or error terms. In fact, Bart et al. (1984) found that HSI models performed poorly because they were not based on field data and did not sufficiently account for interactions between the predictor (habitat) variables. Cole and Smith (1983) voiced similar concerns. Also, as we have discussed elsewhere, users should be wary of models that provide purely deterministic predictions with no statements of uncertainty or variability. At best, such models should be viewed as providing potentially testable hypotheses (although the 0–1 indices of HSI models are not particularly interpretable as empirical parameters) and interpreted as average conditions at a relatively broad geographic extent.

Comparable to habitat suitability index models are habitat capability and habitat effectiveness models. These models essentially perform the same function as HSI models but may vary slightly in structure. *Habitat capability (HC) models* typically provide an estimate of the total area within which resources for a particular species can be found, or rank a given area for the relative capability of supporting a species, given a few key environmental factors. *Habitat effectiveness (HE) models* rank resources in an area according to the degree to which maximum use or carrying capacity can be met.

An HE model was constructed for assessing habitat effectiveness for Rocky Mountain elk (*Cervus elaphus nelsonii*) winter range in the Blue Mountains of eastern Oregon and Washington (Wisdom et al. 1986). This model calculates an elk habitat effectiveness index as the geometric mean of four environmental variables, including distance from cover-forage edge, miles of road open to motorized traffic per square mile of habitat, habitat types and successional stage, and type of management treatment. The model was evaluated by Holthausen et al. (1994) by use of expert opinion.

With HSI, HC, and HE models, it is difficult to interpret if the resulting index value is intended to represent environmental conditions or population response. Also, the sensitivity of the resulting habitat index values to any one environmental variable is diminished as more variables are added to the model. This behavior is a function of the mathematics of a geometric mean model, and may not accurately reflect actual habitat use or population response. Finally, as with HSI models, HC and HE models should be used to represent relative environmental conditions and as a means of generating hypotheses about species–habitat relationships rather than as evidence of causal relations or as reliable predictions of actual species response. Bender et al. (1996) provided a procedure for evaluating confidence intervals for HSI models; this approach may be extended to HC and HE models as well.

A related modeling approach is *habitat evaluation procedures (HEP).* The USDI Fish and Wildlife Service has used HEP models extensively to assess environmental conditions at the species level (Flood et al. 1977). The procedure is based on *habitat units (HUs),* which are defined as the product of habitat quality (on a 0–1 index, as from a habitat suitability index) and habitat quantity. HEP models have typically been based on HSI models that serve to estimate habitat unit scores (e.g., Cole and Smith 1983). HEP models may require much field data on specific environmental attributes, such as forage quality or quantity. However, the procedure provides a structured way to document a repeatable assessment of environmental conditions. HEP is often used to evaluate impacts of, and mitigations for, proposed projects on environmental conditions for species of special interest. Roberts and O'Neil (1985) provided a procedure for selecting species for HEP assessments. Rewa and Michael (1984) provided a way of evaluating environmental quality for ecological guilds by using a HEP approach.

Wakeley and O'Neil (1988) presented methods to increase efficiency in applying HEP. Their suggestions included delineating cover types by using remote imagery and combining types; choosing wildlife species to model for which there is available inventory information; choosing model forms that make best use of available inventory data and that focus on the most important life history components; designing field sampling for environmental conditions to be cost-effective and tailored to the range of modeled conditions; and using computers to aid in collecting and analyzing field inventory data and conducting model analysis.

POPULATION AND METAPOPULATION DEMOGRAPHY AND SIMULATION MODELS

A rather vast literature has developed in the past two decades on population viability concepts, models, and conservation (for entry, see McCullough 1996; Morris et al. 1999; Beissinger and McCullough 2002; see also chapter 3). *Population viability analysis (PVA)* usually entails using stochastic models of population demography and perhaps population genetics (usually for analyzing effects of inbreeding and genetic drift in small or isolated populations). Some popular PVA modeling packages include the RAMAS series (Ferson 2002) and VORTEX (Lacy and Kreeger 1992).

PVA can also entail individual-based, geographically referenced simulation models designed to analyze habitat patch occupancy by organisms and effects of environmental changes and disturbances on habitat patterns. In these models, individual demography is linked to location-specific environmental conditions, including quality and extent of habitat (Kareiva and Wennergren 1995; Mooij and DeAngelis 2003). Spatially explicit models predict occupancy of habitat patches in heterogeneous landscapes by breeding individuals, as well as various population and metapopulation trends. As examples, Akçakaya et al. (1995) assessed the effect of spatial patterns of habitats on viability of populations of helmeted honeyeaters (*Lichenostomus melanops cassidix*), and Raphael and Holthausen (2002) analyzed effects of habitat management alternatives on populations of northern spotted owls (*Strix occidentalis caurina*). It should be remembered, however, that such models usually do not explicitly include factors that can have strong influences on population dynamics in patchy environments, such as density-dependent survival, fecundity, and dispersal.

Brook et al. (1999) evaluated four PVA modeling packages and concluded that subtle differences among the models can affect results and conclusions. This outcome is not unexpected but is a wake-up call to those who use only one model or who rely heavily on models for decision making. It suggests that model users should fully understand their models—the state variables, functions, and especially the implications of what real-world attributes are *not* represented well or at all. Reviews of spatially explicit population models were provided by Dunning et al. (1995), Holt et al. (1995), Turner et al. (1995), and Seppelt (2005). Their general conclusions were that such models can fundamentally aid basic ecological knowledge of landscape phenomena and the application of landscape ecology to conservation and management. However, one caveat worth remembering when using spatially explicit population models is that many factors usually not explicitly included in the model—such as density-dependent demographic effects, competitors, predators, and effects of harvest—often have strong influences on population dynamics.

A number of models are available for analyzing data on population demography and census results. Examples include several models for analyzing the Breeding Bird Survey (BBS) data (Sauer et al. 2003), such as COMDYN (Hines et al. 1999).

LANDSCAPE MODELS

Landscape models include a wide variety of tools to help depict and predict habitat patch patterns across watersheds, basins, and beyond. For example, Westphal et al. (2003) used stochastic dynamic programming to design optimal landscape patterns for persistence of metapopulations of the Mount Lofty Ranges southern emuwren (*Stipiturus malachurus intermedius*), a critically endangered bird of Australia. Knapp et al. (2003) used semiparametric logistic regression and spatial autocorrelation to estimate likelihoods that mountain yellow-legged frogs

(*Rana muscosa*) would occupy habitat patches across a landscape. Many other modeling techniques have been devised, including a wide array of metrics of habitat patch patterns used in GIS (see table 8.3; O'Neill et al. 1988; McGarigal and Marks 1995).

As with using forest stand growth and yield models to infer wildlife habitat, models designed to guide spatial scheduling of activities at the landscape scale for forest harvest, transportation infrastructures, and related pursuits are sometimes used to interpret wildlife habitat at the landscape scale. Their use carries the same caution—that is, that landscape-scale scheduling models may not produce the most useful or pertinent variables for predicting wildlife species' response with relative certainty. Examples include using models of timber harvest scheduling across multiple stands of varying ages to infer extent and connectivity of wildlife habitat (Rempel and Kaufmann 2003; Taylor et al. 2003).

A number of algorithms have been devised by which optimal or satisfactory scheduling of resource-use activities at the landscape scale are calculated. An example is from Falcão and Borghes (2002) who combined three random and systematic search heuristic algorithms to calculate the best forest management schedule under spatial constraints (also see Boston and Bettinger 2002). Again, the pertinence of such models, if used to design and evaluate landscape characteristics for wildlife presumed to be associated with represented forest conditions, needs to be evaluated with caution.

COMMUNITY STRUCTURE AND ECOSYSTEM PROCESS MODELS

Of increasing pertinence to modeling and managing wildlife and its habitat are ecosystem process models. These models can be quite valuable for understanding the ecological roles of wildlife in structuring their communities and food webs, and in regulating flow of energy and cycling of nutrients and substances within their ecosystems.

Systems modeling was developed in the 1950s under the field of operations research and was adopted by ecologists in succeeding decades (e.g., Holling 1966; Patten 1971; Grant et al. 1997). A vast literature is available on modeling food webs and trophic dynamics of ecological communities and ecosystems (e.g., Montoya and Sole 2003), with current debates in ecology focused on relations between ecosystem complexity and stability (e.g., Wardle and Grime 2003) and such dynamics of ecosystems as resilience, resistance, elasticity, and restoration (Brang 2001; Redman and Kinzig 2003). Such models are useful for managing wildlife when they reveal the specific dynamic roles played by wildlife species and diverse communities in regulating community and ecosystem function and structure (Kinzig et al. 2001). For example, Eichner and Pethig (2003) found that modeled population dynamics varied according to food chain equilibria far more than would be predicted from traditional Lotka-Volterra equations or predator–prey relations.

The ECOPATH, ECOSIM, and ECOSPACE modeling shells (Christensen and Pauly 1992; Walters et al. 1999; Pauly et al. 2000) have been used to study equilibrium conditions and trophic networks in aquatic systems. ECOPATH has been used to model ecosystem dynamics of a coral reef in French Frigate Shoals (Polovina 1984), a sandy barrier lagoon in Taiwan (Lin et al. 1999), the Newfoundland–Labrador continental shelf (Bundy et al. 2000), and other aquatic ecosystems. It may also be useful if adapted for terrestrial wildlife community and ecosystem analysis.

Other modeling tools useful for simulating time-dynamics relations of predator–prey relations, energy flow, and other aspects of community and ecosystem functioning include use of discrete difference equations in computer simulation programs such as STELLA (High

Performance Systems, Inc., Lebanon, New Hampshire). STELLA was used by Costanza et al. (1990) to model dynamics of coastal landscapes, and by Hudson (1995) to depict relations of people and wildlife (fig. 10.4).

A major manifestation of ecosystem modeling in wildlife management appears in the guise of so-called ecosystem management, which essentially is the management of selected components of a system, such as specific species and their habitats, under the assumption of benefits for the entire ecosystem (see chapter 11).

Decision Support and Knowledge-Based Models of Wildlife–Habitat Relationships

In this section we review a host of model types that deviate from the traditional population, habitat, landscape, and WHR approaches surveyed above. Decision support and knowledge-based models include decision modeling approaches used for some time now in wildlife habitat management, as well as a number of new approaches just being applied to WHR assessment and management. This field is developing remarkably fast.

DECISION SUPPORT MODELS

A major challenge in conservation is managing species and ecosystems when scientific knowledge is scant and uncertainty is great. Decision support models (DSMs) can aid this challenge by (1) evaluating the implications of uncertainty in meeting management goals, (2) combining empirical data with expert judgment, and (3) identifying key habitat elements, through sensitivity testing and validation, as a basis for prioritizing inventory and monitoring. DSMs are tools to aid decision makers; they should *not* be used as a blanket final decision, as a replacement for unclear thinking, or as an unexplainable black box.

DSMs include a wide range of tools, such as Bayesian analyses and belief networks, data and text mining, decision modeling such as decision tree analysis, expert systems, fuzzy logic and fuzzy set theory models, genetic algorithms, rule and network induction, neural networks, reliability analyses, quantitative (environmental) risk analysis, simulation and scenario modeling, and other approaches.

Successful use of DSMs in risk analysis and risk management for plant and animal conservation depends largely on the availability of data or experts, and the willingness of decision makers to articulate their risk attitudes and decision criteria. These are no small hurdles. Many DSMs can aid in merging scientific data with expert knowledge, although no model can replace empirical field studies in basic zoology, taxonomy, demography, and population genetics. DSMs can neither substitute for such work nor create knowledge and understanding where such information is initially lacking.

The appropriate role of DSMs is as a support structure. DSMs can be used to test the value and cost of additional information, the importance and influence of missing data, and the potential utility of alternative management activities. They can help evaluate the likelihood of various outcomes and the social and ecological costs and values of those outcomes. They can also provide a framework for combining information from multiple, disparate sources, including expert judgment. They can provide a structure—call it a working hypothesis—for depicting environmental correlates of species in a "causal web" of factors that affect species' distribution, abundance, and persistence.

SELECTING DSMS

Selecting decision support models for use in species-environment planning and management should follow several criteria. A good decision model should be able to combine disparate data

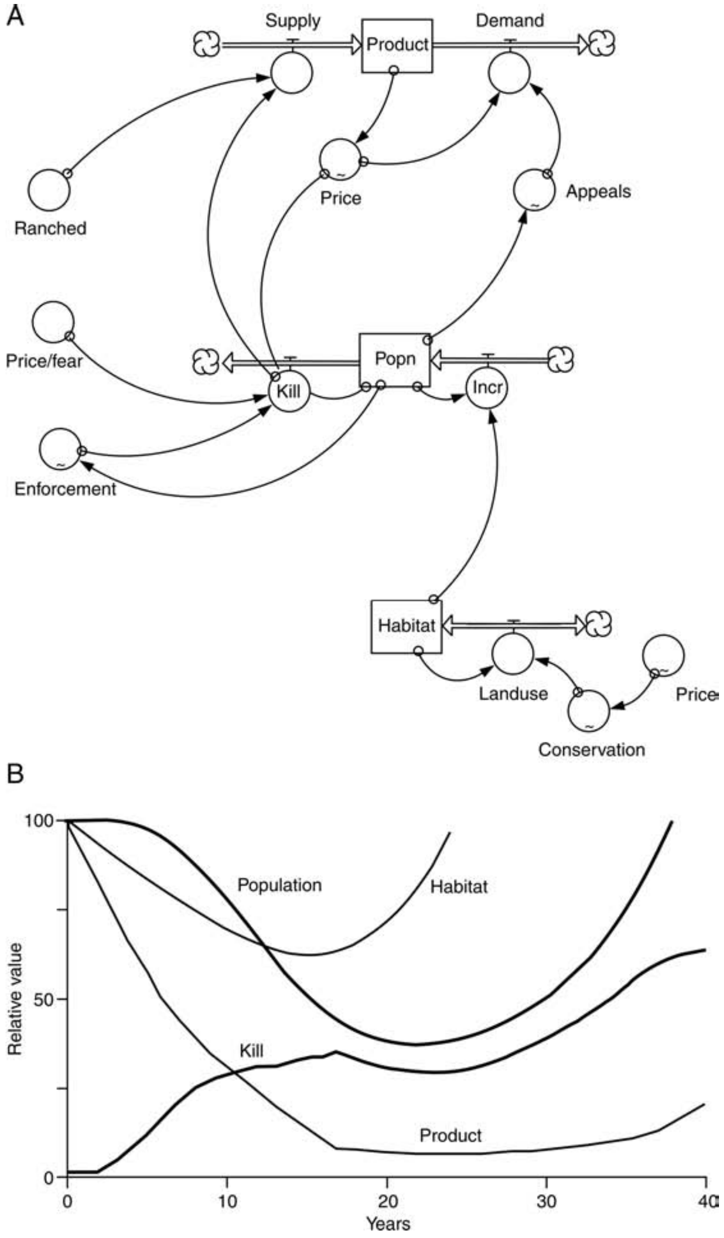


Figure 10.4. Example of a STELLA model. (A) Relations among factors influencing the dynamics of a commercially exploited wildlife population (boxes = stocks; arrows = flows; valves = rates; circles = auxiliary variables). (B) Model run illustrating recovery after an initial phase of overexploitation. (Based on Hudson 1995, 320–21.)

sources and handle missing data, combine different kinds of variables, clearly display influences, handle uncertainties and represent outcomes as probabilities, and identify major factors that can be influenced by management. A number of DSMs, such as Bayesian belief networks, provide for combining empirical data with expert judgment (Heckerman et al. 1994), often from multiple experts.

DSMs should be able to clearly display major influences on (the "causal web" of) wildlife population viability or quality of habitat, including the values and interactions of such key environmental correlates. In this way, DSMs should provide a lucid communication medium to clearly show the intuitive effects of management activities, and to express predicted outcomes as likelihoods as a basis for risk analysis and risk management. And, lastly, DSMs should be able to provide a means to test the sensitivity of management activities and to determine which key environmental correlates have the greatest influence on the organism to help prioritize inventory, monitoring, or restoration and conservation actions.

BUILDING DSMS

Part or all of most DSMs are based on expert judgment. There are specific methods for extracting and representing knowledge from experts, and this procedure has been called "knowledge engineering" in the artificial intelligence literature. It entails the process of interviewing experts, extracting their expert knowledge, quizzing them on their degree of certainty, and accurately representing that knowledge in computer models, such as in expert system control rules (Hink and Woods 1987).

The acceptability of using expert opinion for analyzing WHR has been established in a number of modeling efforts and the ecological literature. Examples include using expert opinion to interpret or supplement empirical evidence of population trends or habitat effectiveness (e.g., Cohen 1988; Blaustein et al. 1994; Holthausen et al. 1994); to evaluate effects of environmental pollution on forest systems (de Steiguer 1990); to determine species richness of Diptera (Petersen and Meier 2003); to model vegetation and faunal distribution (Pearce et al. 2001); and to evaluate population viability of a broad array of wildlife species and taxa under alternative forest management plans (FEMAT 1993). However, use of expert judgment should be approached with due caution (Kahneman et al. 1985; Seoane et al. 2005), as it may be broader in scope but more biased and less accurate than empirical data. Using expert opinion needs an established methodology to ensure credibility and avoid bias, such as the guidelines suggested by Meyer and Booker (1990) and Cleaves (1994). When used correctly, however, expert knowledge can provide a cost-effective means of providing predictions on effects of management on biodiversity and wildlife (Martin et al. 2005).

Review of New Approaches in the DSM Arena

Following is a brief review of a number of new or more resent approaches in the DSM arena.

BAYESIAN ANALYSES AND BELIEF NETWORK MODELING

Once the poor stepchild of traditional "frequentist" statistics, Bayesian statistical approaches to modeling WHR have been used widely to evaluate wildlife populations, effects of habitat management, and other aspects of wildlife ecology and management (Dorazio and Johnson 2003). A straightforward application of Bayes' theorem was used in the PATREC, or pattern recognition, WHR models of the 1970s, which still provide a valuable structure for analyzing species–habitat relations (see box 10.2). For example, Grubb et al. (2003) used the PATREC approach of Bayesian inference to assess nesting habitat suitability for

Box 10.2 Bayesian modeling and wildlife habitat

What to do when sample sizes are few—as with unreplicable landscapes or with threatened species with tiny populations? What to do when controls do not exist, when baseline conditions cannot be established, and when unforeseen disturbances wreck the experiment? These and other nightmares haunt many real-world wildlife studies, in which funding levels and the pace of human activities and natural perturbations seldom allow for perfect experimental designs.

One answer may lie in the use of Bayesian statistics, which provide a useful complement to other traditional approaches.

Bayesian approaches entail first describing a priori probabilities of outcomes given specific conditions, such as the specific environmental states E present with populations of specific sizes S. Priors are thus denoted as the conditional probability of the environmental condition given a specific population size, or P (E|S). For various population sizes, S, a *likelihood function* of priors can then be plotted. We will return to likelihood functions in a moment.

For a particular study area, the unconditional probabilities (overall frequency distribution) of population sizes P (S) and of environmental conditions P(E) are additional factors. Then, the posterior probability P(S|E) of predicting a population size given an environmental state can be calculated by using Bayes' theorem: P(S|E) = [P(E|S) P(S)] / P(E). A graph can then be plotted showing posterior probabilities of population size for various environmental states.

Another way of expressing Bayes' theorem (Reckhow 1990, 2056) more explicitly displays the role of null hypotheses H_O and competing alternative hypotheses H_A in relation to data *x:*

$$P(H_o \mid x_1, \ldots, x_n) = \frac{P(x_1, \ldots, x_n \mid H_o) \cdot P(H_o)}{P(x_1, \ldots, x_n) \cdot [P(H_o) + P(x_1, \ldots, x_n \mid H_A) \cdot P(H_A)]} .$$

In this formulation, the odds for H_o against H_A can be calculated as the ratio of the likelihood function of conditions *x* given the null hypothesis, to the likelihood function of conditions *x* given the alternative hypothesis. This odds ratio is roughly analogous to the *P* value in classical statistics. The basic formula can also be extended to accommodate more than one alternative hypothesis.

Major advantages of the Bayesian approach are (1) it makes use of existing knowledge or expert judgment in the estimation of the prior probabilities, and (2) it produces a useful formula that predicts outcomes in terms of likelihoods or odds.

Major complaints against the Bayesian approach are (1) prior probabilities can be biased when based on best guesses rather than on empirical research; (2) prior probability values often greatly influence the posterior probabilities, so that even minor bias or inaccuracy will change outcomes; and (3) the environmental states must be depicted in only a few, oversimplified categories.

In more complex Bayesian approaches, the "independent variable" E can be partitioned into multiple components and the unconditional and conditional likelihoods for each component evaluated separately. Other variants to the approach provide for sequential estimation of the posteriors so that biases can be reduced by successive approximations or by continuous data collection. Some authors have revised the formulae for calculating posterior probabilities under various assumptions of statistical distributions of the prior probabilities.

bald eagles (*Haliaeetus leucocephalus*) in the western United States. Wikle (2003) demonstrated use of a Bayesian approach to assess the probability of spread of invasive species in an analytic diffusion model of house sparrows (*Carpodacus mexicanus*) in the eastern United States. Bayesian approaches to analyzing metapopulations have been used by Goodman (2002), O'Hara et al. (2002), Wade (2002), ter Braak and Etienne (2003), and others. Jonsen et al. (2003) used meta-analysis to combine data on animal movement from several sources in a Bayesian statistical framework.

Other uses of Bayesian statistics include sequential and hierarchical empirical Bayesian approaches (Gazey and Staley 1986; Ver Hoef 1996; Oman 2000), which incrementally incorporate new data to refine estimates of population response or other prediction variables and probabilistic relations. Empirical Bayesian approaches to learning may be useful for studying landscapes or ecosystems, which tend to be unique, meaning there is only a sample size of one (Schindler 1998), and also for studying populations of threatened or endangered species that cannot be subjected to experimental treatments and replication. Such dynamic approaches differ fundamentally from more traditional statistical correlation models that produce fixed results and that avoid use of prior information.

In fact, one of the hallmarks of Bayesian approaches in general is the use of prior knowledge to structure probabilistic relations among variables for predicting outcomes. That is, a Bayesian approach incorporates prior knowledge such as by setting *a priori probabilities* that in turn influence the calculation of new states and outcomes as *posterior probabilities.* In wildlife and environmental management, this Bayesian approach means that outcomes are represented as likelihoods, which in turn are statements of uncertainty (Toivonen et al. 2001) and which can feed directly into risk analyses. Bayesian models, however, can be rather arbitrary, in that values of priors can greatly affect posteriors, which means that unless the prior probabilities are sound and unless the model structure itself is in some way validated, the analysis can lead to faulty predictions with unknown accuracy and bias.

One aspect of Bayesian modeling that has become popular is *Bayesian belief networks (BBNs).* In its best form, a BBN is essentially a causal model representing the major factors of some system (Marcot et al. 2001). Such causal models are also called *dependency networks* or *influence diagrams,* and they display probabilistic relations among stressor and wildlife variables (e.g., fig. 10.5). BBNs have been used for a wide variety of ecological problems, including aspen management (Haas 1991), wildlife assessment in the interior western United States (Raphael et al. 2001), and participatory resource management (Cain et al. 1999).

DATA AND TEXT MINING

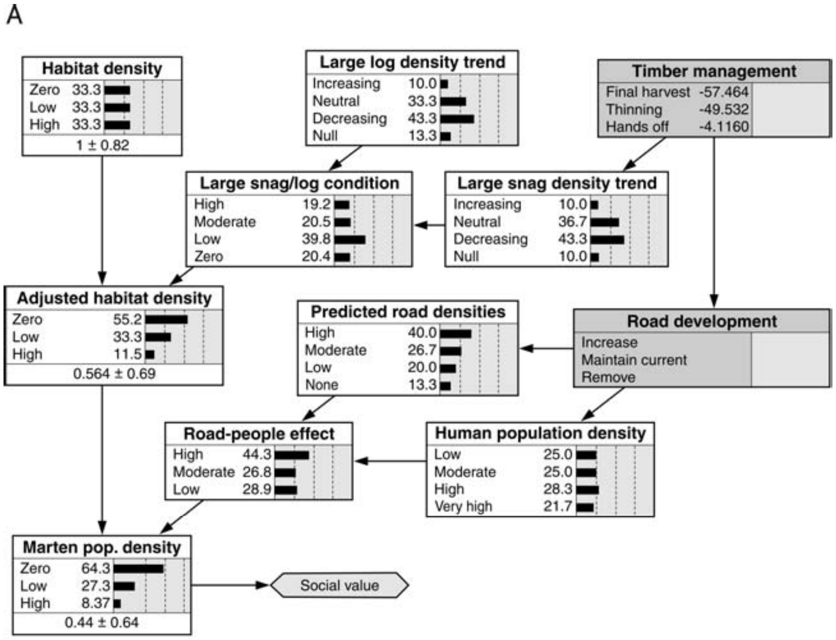
Data and text mining constitute one form of "knowledge discovery," or statistical learning approaches in which systematic patterns and correlations among variables are discerned from large data bases or documents (Hastie et al. 2001). The objective is to produce predictions. The main techniques of data and text mining are *bagging* (in which alternative data classification and regression analyses are considered); *boosting* (in which multiple models or classifiers are generated and weighted for prediction or classification); and *stacking* and *metalearning* (in which predictions from multiple models that may be very different in structure are combined).

Whereas data mining is used on numeric data, text mining is based on analysis of multiple text documents by extracting and analyzing cooccurrence of key phrases, words, and concepts. Text mining may have great utility in wildlife management for analyzing anecdotal written descriptions of historic habitat conditions, stories of wildlife encounters, and other nonquantitative information sources. We know of no such use to date.

Examples of data and text mining modeling tools are CBA (classification based on association, developed by the School of Computing at the National University of Singapore) and Weka (a collection of machine learning algorithms written as open-source software in Java code developed by the University of Waikato).

DECISION TREE ANALYSIS

Decision tree analysis is a more traditional approach than most of the other techniques discussed in this section. Decision trees typically depict a series of decisions with various chance outcomes denoted by probabilities. Fully speci-



B

Adjusted habitat density	Road-people effect	Zero	Low	High
Zero	High	100.00	0.000	0.000
Zero	Moderate	100.00	0.000	0.000
Zero	Low	100.00	0.000	0.000
Low	High	50.000	50.000	0.000
Low	Moderate	20.000	80.000	0.000
Low	Low	0.000	100.00	0.000
High	High	0.000	50.000	50.000
High	Moderate	0.000	20.000	80.000
High	High	0.000	0.000	100.00

Figure 10.5. Hypothetical example of a Bayesian belief network model. (A) The model includes alternative management decisions (nodes "Timber management" and "Road development"); the intermediate habitat attributes they would affect; the final influence on a wildlife species of interest; and utilities ("social value," incorporating social benefits and economic costs) of wildlife outcomes. The numbers in the timber management node reflect overall costs of each decision, given the probability structure of the model, and the costs and benefits associated with each outcome. (B) The conditional probability table (CPT) underlying the node "Marten pop. density," illustrating the combined effects of adjusted habitat density, which accounts for management influence on snags and down logs (denning habitat for marten) and road-people effects (representing disturbance of marten). For example, if adjusted habitat density is high but road-people effects are also high, there is only a 50% likelihood of marten populations being high. Numbers in CPTs can be derived from empirical data, best professional estimates, or a combination of the two. (Model constructed by B. Marcot using the program Netica, by Norsys, Inc.)

fied decision trees also show costs or benefits of each decision, effects of chance outcomes on those values, overall utilities of final outcomes, and expected values of each decision pathway. The best decision is the one with the lowest expected cost or highest benefit. Expected values are calculated as the sum of the products of probabilities and values along a given decision pathway. An example of a hypothetical decision pathway is shown in figure 10.6 and discussed in box 10.3.

Decision trees can be crafted from expert opinion (Failing et al. 2004) or induced from data analysis (Kampichler and Platen 2004). They can be a very useful way to explore potential costs and benefits of alternative conservation actions, such as explored by Maguire et al. (1988) for conservation of black-footed ferrets (*Mustela nigripes*) in Montana. New uses of decision tree modeling include induction of decision structures from empirical data. An example is from Stockwell et al. (1990), who induced decision trees to predict density of greater gliders (*Petauroides volans*) in Australia. However, various problems with decision tree analysis include the difficulty of representing a full decision pathway, identifying all major chance responses, estimating probabilities of outcomes, and estimating future costs and benefits of current and future decision actions.

CLASSIFICATION AND REGRESSION TREES

Classification and regression trees (CARTs) are diagrams that depict prediction variables found to have the greatest explanatory power for some response variable (Breiman et al. 1984). Classification trees are based on categorical response variables (such as categories of pelage color), whereas regression trees are based on continuous response variables (such as body length).

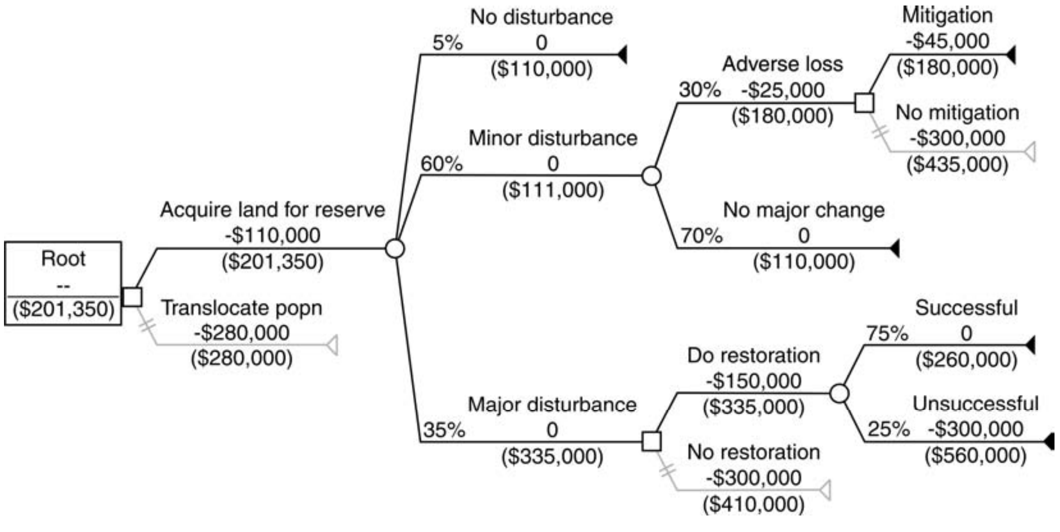


Figure 10.6. Hypothetical example of a decision tree designed to evaluate whether to translocate a threatened wildlife population or acquire land for a reserve. Boxes = decision nodes, circles = response nodes, with probabilities of various chance outcomes. Values above the lines are (hypothetical) dollar costs for each activity; and values below the lines are dollar expected values, given probabilities of chance outcomes. (Model constructed by B. Marcot by using the program DecisionPro, by Vanguard Software Corporation.)

Box 10.3 Using decision trees for conservation planning

Decision trees are used widely in many kinds of decision making. In decision tress, decision points are shown as boxes and responses are shown as circles. To illustrate, the hypothetical scenario shown in figure 10.6 is explained as follows. You have the option of translocating a threatened population for $280,000 or acquiring the land for establishing a reserve for only $110,000. If you acquire the reserve, management of the land will change to allow natural disturbance regimes to resume. You estimate the chance of no disturbance events in the near term to be low, about 5%; the chance of a minor disturbance in the near term to be about 60%; and the chance of a major disturbance to be 35%. If there is a minor disturbance, there is a further 30% chance of significant adverse loss of habitat and a 70% chance of no significant loss. The adverse loss will cost $25,000 to curtail (e.g., fighting a fire, stopping flooding), and then you will be faced with a decision of mitigating the loss for $45,000, or not mitigating it and thereby losing the population. In the case of a major disturbance event, restoration will cost $150,000 and has a 75% chance of being successful, but if you choose not to conduct restoration, it will be an unrecoverable loss, and further mitigation will cost $300,000. If you choose to do restoration and it is unsuccessful, then the population is lost and further mitigation will also cost $300,000.

The question in this scenario is, What to do?

The central initial question is, Should you purchase the land for the reserve or translocate the population? Which decision has the lowest expected cost? Which has the highest probability of population persistence regardless of the cost? and what is that associated cost?

These questions are answered by solving the decision tree, which means calculating expected values for each decision node. This solution is done by backwards calculation—that is, starting at the end of each branch of the tree and working backwards. Expected values are the running sum of the products of probabilities of chance outcomes times the cost (or benefit, if so displayed) of each event or decision. For example, in figure 10.6, on the bottom outcome of "major disturbance," the expected value (cost) of doing restoration, not knowing initially if it will be successful, is $335,000, which is (75%)($260,000) + (25%)($560,000). Note that the values $260,000 (successful outcome) and $560,000 (unsuccessful outcome) are the sums of expected values for each respective pathway through the decision tree. The best decision to be made at any given decision node in the tree (the boxes in fig. 10.6) would be the one that has the lower expected value of cost. So if there is a major disturbance, you should do restoration (expected cost = $335,000) rather than not (expected cost = $410,000).

Calculating backwards through the rest of the tree, it turns out that the expected value of acquiring the land for a reserve, given all the probabilities and costs of subsequent disturbances, losses, and mitigation, is about $201,000, whereas the expected value of translocating the population is a significantly higher $280,000 (again, this is purely a hypothetical example). So the prudent—less expensive—decision is to purchase the land.

However, the expected values can be sensitive to the accuracy of the future cost estimates, accuracy of the probabilities of outcomes, how the tree is structured in the first place, and the difference in risk among alternative decision pathways. On this last point, one should consider a decision's risk in addition to its expected value. This is told by assessing all possible outcomes that could result from an initial decision—that is, the range of expected values shown along each decision pathway in the decision tree. One aspect of risk is denoted by the joint probability of outcomes. For example, the probability of a minor disturbance *and* an adverse loss is (60%)(30%) = 18%, and the probability of a major disturbance and an unsuccessful mitigation is (35%)(25%) = 9%. These may be low-enough odds to risk the land acquisition decision if cost is less of a factor.

Another systematic way to account for risk is to incorporate a risk attitude in calculations of the expected values. The *risk attitude* of the decision maker—that is, whether the decision maker is risk-averse, risk-neutral, or risk seeking—can greatly alter expected values and best-decision pathways. Risk attitude can be determined by posing hypothetical betting scenarios to the decision maker—for example, asking how much the decision maker would be willing to receive for certain as an equivalent to a 50% chance of receiving $100,000. In our example, if the decision maker says a sure receipt of $40,000 is just as good as a 50% chance of receiving $100,000, this response defines the decision maker's risk attitude for the project. Depicting such trade-offs in a utility function can be used to modify the expected values in the decision tree. In such an example, the new expected values are now approximately $302,000 to acquire the land and $280,000 to translocate the population; clearly, translocation now costs less, so translocation is the preferred decision if cost is the main factor. If absolute numbers are hard to come by, one can also simply determine what risk attitude would be needed to equalize the expected values of both decisions and then determine if one's attitude is more or less risk seeking than that; this determination would tip the balance in favor of one decision over another.

Much has been written on variations and statistical methods and considerations in CART modeling, and CART has been used rather extensively in ecological modeling (De'ath and Fabricius 2000). As examples, Lehmkuhl et al. (2001) used a regression tree to determine which life history attributes best predict level of viability risk for a sample set of 60 wildlife species in the Pacific Northwest of the United States (fig. 10.7). Munger et al. (1998) used CART modeling to predict occurrence of Columbia spotted frogs (*Rana luteiventris*) and Pacific treefrogs (*Hyla* [=*Pseudacris*] *regilla*) from U.S. National Wetland Inventory data. Grubb and King (1991) predicted effects of human disturbance on bald eagles using classification trees. Andersen et al. (2000) used regression trees to model desert tortoise (*Gopherus agassizii*) habitat in the Mojave Desert. Kintsch and Urban (2002) used classification and regression trees to determine the degree to which biotic communities could be predicted by parameters

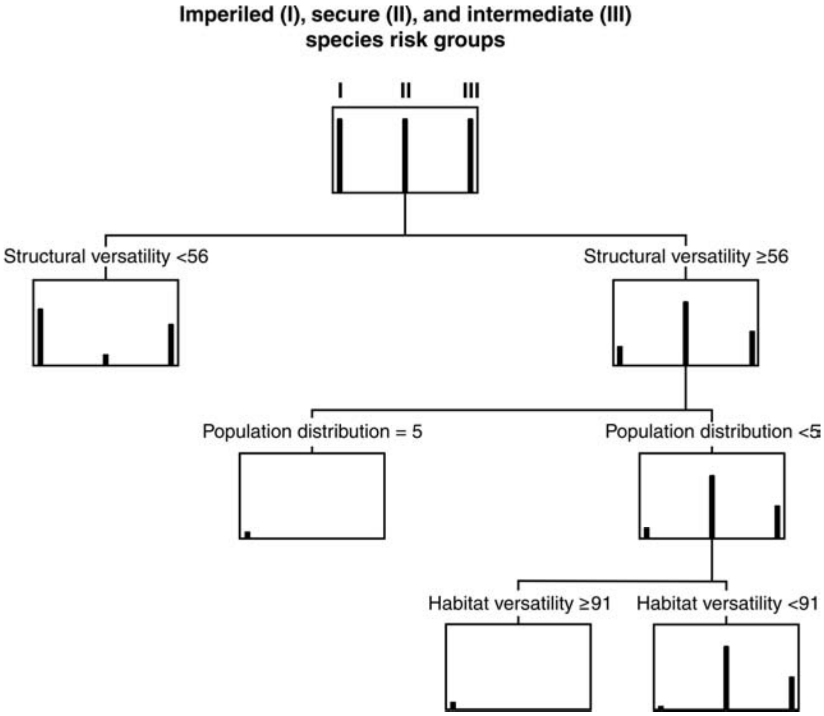


Figure 10.7. Example of regression tree modeling of three categories of species viability risk levels predicted from life history and habitat use attributes, based on 60 wildlife species in the Pacific Northwest of the United States. Structural versatility is an index of the percentage of structural condition classes of vegetation types used by each species; population distribution is an index of the geographic range of each species; and habitat versatility is an index of the percentage of vegetation types used by each species. In this model, none of the life history attributes of species, including reproductive rate, mean number of progeny, and other factors, were statistically significant predictors. (From Lehmkuhl et al. 2001, 484 [fig. 4] reprinted with permission of Oregon State University Press Copyright 2001.)

of their physical environment, and to identify focal indicator species.

De'ath (2002) proposed a method of devising multivariate regression trees to model species–environment relations, which may hold promise in much WHR work. CART analyses can be done in many general statistical software packages, although there are also specific programs developed for this purpose, such as CART and MARS (Salford Systems) and SIPINA (D. A. Zighed and R. Rakotomalala, University of Lyon).

EXPERT SYSTEMS

Once the shining future of artificial intelligence research, the use of expert systems seems to have faded in recent years. The classic framework of expert systems is in the form of if-then-else control rules that guide classification, diagnosis, or other evaluation of some condition. Control rules are based on a human expert's understanding in some narrowly defined field, are typically couched in terms of degrees of confidence or probabilities, and when chained together form an interactive system by which some problem can be solved by querying the expert's knowledge. Classic expert systems suffered from the difficulty of combining opinions from multiple experts (although procedures were eventually developed for this purpose; e.g., Clarke et al. 1990) but excelled in combining qualitative and quantitative information, in handling unknowns, and in explaining reasoning behind queries. Some early examples of the use of expert systems in WHR include Marcot (1986) and Robertson et al. (1991).

Current forms of expert systems have deviated from the classic control rule format, where expertise is now integrated into other model structures. While these are not true expert systems in the classic sense, they have advanced the field by incorporating expert knowledge into other modeling approaches, such as GIS, fuzzy logic models, and decision analysis. Such hybrid models—perhaps now call them "expert-based systems"—have been devised for such problems as conservation of rivers (Pedroli et al. 2002) and coral reefs (O'Connor 2000). Commercially available hybrid expert system shells include DXpress (Knowledge Industries), which is used in a Bayesian-based modeling shell; CORVID (EXSYS Inc.), for building online expert advisory systems; and others.

FUZZY LOGIC AND FUZZY SET MODELS

Fuzzy logic or fuzzy set models describe the logical relations among factors that affect the degree to which some entity (such as a species) belongs to a particular set or outcome (such as having a particular level of viability). Confusing to many users, a fuzzy logic value is not the same as a probability. Values in fuzzy logic (often expressed between 0 and 1 or between –1 and +1) refer to the strength of evidence that would put some entity into some set (McNeill and Freiberger 1993)—for example, evidence that a particular wildlife population belongs to the set of threatened species (Regan and Colyvan 2000). A popular fuzzy logic modeling shell is NetWeaver (M. C. Saunders and B. J. Miller, Pennsylvania State University).

Fuzzy logic models have been devised for a variety of classification and evaluation problems, such as mapping historic forests in Michigan (Brown 1998), predicting coral reef development (Meesters et al. 1998), and prioritizing habitat management for a salamander (Pyke 2005). Fuzzy logic models have also been used in procedures for evaluating suitability of lands for conservation (Stoms et al. 2002) and have been integrated with GIS in risk assessment tools (Reynolds et al. 1997; Bojorquez-Tapia et al. 2002) (also see fig. 10.8). Advantages of a fuzzy logic model are that it is relatively easy to build; the relation between some environmental factor and a species response, for example, can be easily

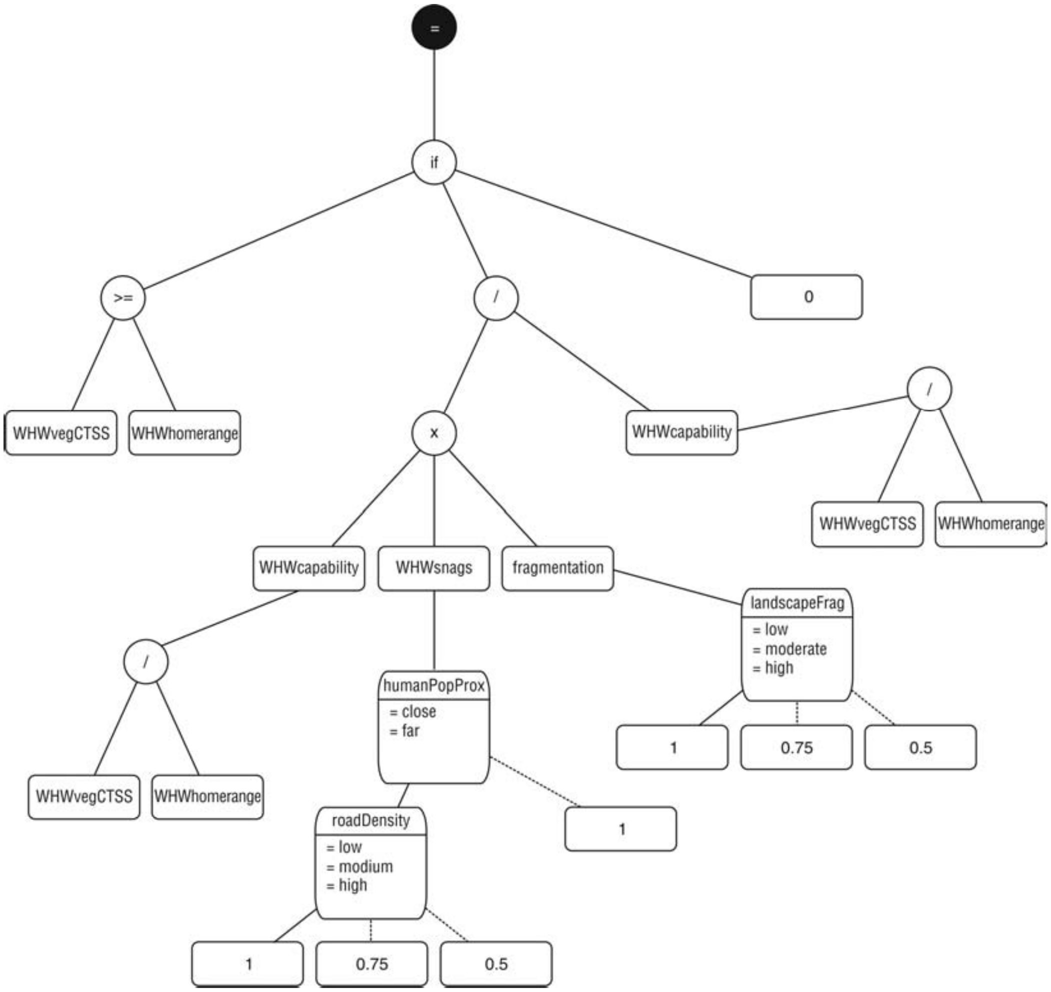


Figure 10.8. Example of the structure of a fuzzy logic model predicting density of white-headed woodpecker (WHW; *Picoides albolarvatus*) territories, using the NetWeaver fuzzy logic modeling shell (Reynolds et al. 1997). WHWvegCTSS = total area of vegetation cover types and seral stages usable by WHWs; WHWhomerange = mean home range size of a WHW territorial pair; WHWcapability = effective area of habitat divided by home range size; WHWsnags = influence of snag density on WHWcapability; humanPopProx = relative proximity of human habitats to WHW habitat; roadDensity = relative density of roads within WHW habitat; fragmentation = influence of WHW habitat fragmentation on WHWcapability; landscapeFrag = relative degree of fragmentation of WHW vegetation conditions. The functions refer to fuzzy arithmetic. (Model constructed by B. Marcot by using the program NetWeaver, by Penn State University.)

depicted in user-defined curves expressing strength of evidence. Fuzzy models are useful for quickly building knowledge-based systems to compare relative outcomes among alternative conditions. A disadvantage of fuzzy models is that it is unclear how to interpret and, especially, validate the final results, such as total strength of all evidence for some outcome, as a fuzzy value is neither a statement of probability nor a directly measurable empirical variable.

GENETIC ALGORITHMS

Genetic algorithms are computer programs designed to mimic the evolution and adaptation of genetically based populations by retaining characteristics denoted as having "adaptive advantage" and discarding maladaptive behaviors. Genetic programs include the "game of life" (also called artificial life; Stein 1991), cellular automata, and related programs (Goldberg 1988). As examples, genetic modeling has been used successfully to solve problems of scheduling optimal spatial forest harvest (Boston and Bettinger 2002), to model site selection by species (Moilanen and Cabeza 2002), and to test models that use indicator species to predict species richness (Thomson et al. 2005).

RULE AND NETWORK INDUCTION MODELS

These modeling techniques take a fully or partially specified database and induce an expert rule set that optimally (or otherwise) describes the (known) outcomes based on the descriptor variables in the examples (Jeffers 1991). For instance, a database might consist of a series of observations where a species is present or absent, along with variables representing the environmental conditions at each site. A rule induction model would produce a "key" of sorts that identifies which environmental variables best account for presence and absence of the species. In this way, rule induction models are similar to classification and regression tree models but can handle more kinds of data (categorical, continuous, binary, and ordinal) and, most usefully, missing data. A variation of the rule induction approach is used to induce a network of factors that can then be developed into an influence diagram, Bayesian belief network, loop model, decision tree, or other tools. An example of a rule induction modeling shell is See5/C5 from Rulequest Research (Australia), and a network induction modeling shell is BKD (Bayesian Knowledge Discovery) from The Open University, United Kingdom.

Rule and network induction models are very powerful for helping to make sense of a database of known examples. In this way, they are similar to data mining models but produce specific tools for prediction as well as hindcasting (explanation). A common method used in rule and network induction models is the ID3 algorithm (Quinlan 1986; also see Shapiro 1987). More recently developed is the EM algorithm used in Bayesian networks, which is applied to learning from new data to update model probabilities and to induce network structures (Lauritzen 1995; Bauer et al. 1997). As an example, Uhrmacher et al. (1997) used a fuzzy-based rule induction approach to analyze the dynamic behavior of an ecological system by generalizing system behavior and dynamics from specific cases. Lehmkuhl et al. (2001) presented an optimally generated rule to predict level of viability risk based on species' life history characteristics, induced from 60 examples species in the Pacific Northwest of the United States by using the ID3 rule induction algorithm (fig. 10.9). The rule induction approach tends to include predictor variables that best match given examples even if the correlation among variables is not statistically significant (as with regression trees). Thus the user needs to evaluate whether results are still biologically meaningful and useful, even if they are not statistically significant in the classic parametric sense.

- A. Population is contiguous.
  - B. The organism forages underwater or aerially, or foraging substrate is unknown.
    - C. The upper elevation range of typical or regular occurrence is up to 1000 ft. (no identification)
    - CC. The upper elevation range of typical or regular occurrence is up to 3000 ft. (no identification)
    - CCC. The upper elevation of typical or regular occurrence is up to 5000 ft. Group III
    - CCCC. The upper elevation range of typical or regular occurrence is >5000 ft. Group I
  - BB. The organism does not forage underwater or aerially, and foraging substrate is not unknown.
    - C. The average age at first breeding (females) is <6 months. (no identification)
    - CC. The average age at first breeding (females) is 1 year. Group II
    - CCC. The average age at first breeding (females) is 2 years.
      - D. The structural versatility of the species is <99. Group II
      - DD. The structural versatility of the species is >=99. Group III
    - CCCC. The average age at first breeding (females) is 3 years. Group III
    - CCCCC. The average age at first breeding (females) is 4+ years. Group II

- AA. Population distribution consists of gaps.
  - B. The taxonomic order is Caudata.
    - C. The structural versatility of the species is <90.50. Group II
    - CC. The structural versatility of the species is >90.50. Group III
  - BB. The taxonomic order is Anura. (no identification)
  - BBB. The taxonomic order is Squamata. Group III
  - BBBB. The taxonomic order is Falconiformes.
    - C. The average age at first breeding (females) is <6 months. (no identification)
    - CC. The average age at first breeding (females) is 1 year. Group II
    - CCC. The average age at first breeding (females) is 2 years. Group III
    - CCCC. The average age at first breeding (females) is 3 years. Group I
    - CCCCC. The average age at first breeding (females) is 4+ years. (no identification)
  - BBBBB. The taxonomic order is Charadriiformes. Group II
  - BBBBBB. The taxonomic order is Strigiformes.
    - C. The habitat versatility of the species is <34.50. Group I
    - CC. The habitat versatility of the species is >=34.50. and <50.00. Group III
    - CC. The habitat versatility of the species is >=50.00. Group II
  - BBBBBBB. The taxonomic order is Apodiformes.
    - C. The habitat versatility of the species is <53.50. Group II
    - CC. The habitat versatility of the species is >=53.50. Group III

Figure 10.9. Example of a rule induction model called SARA (Species at Risk Advisor), using the ID3 rule induction algorithm (see text for explanation), of species viability risk levels predicted from life history and habitat use attributes. This model was derived from the same data set used in figure 10.7. (From Lehmkuhl et al. 2001, 486–87 [fig 6]; reprinted with permission of Oregon State University Press Copyright 2001.)

NEURAL NETWORKS

Neural networks are models that predict the value of some response variable (such as population density of some wildlife species) from a set of predictor variables (such as habitat attributes) by generating intermediate dummy variables and juggling their weights and relationships. Neural networks are constructed from a set of examples and are "trained" by iteratively readjusting weights and functions among the variables to produce a set of equations that best fit the examples. The dummy variables ("perceptrons" in neural networking parlance), created by training and solving a neural network, are intermediate combinations of the predictor variables (Kosko 1990).

Overall, neural network models do not produce explainable networks, particularly the intermediate network strata (the dummy variables), which are the critical parts of the networks that most influence the predicted outcomes. Instead, these models result in a "black

BBBBBBBB. The taxonomic order is Piciformes.
  C. The habitat versatility of the species is <50.00. Group III
  CC. The habitat versatility of the species is >+50.00. Group II
BBBBBBBBB. The taxonomic order is Passeriformes.
  C. It is a “patch” species, likely using only 1 homogenous habitat patch during the life cycle. Group III
  CC. It is a “mosaic” species, likely using an aggregate of habitat patches but 1 structural stage.
    D. The migration or seasonal movement is <100 km. (no identification)
    DD. The migration or seasonal movement is 100 – 100 km. Group II
    DDD. The migration or seasonal movement is >1000 km. Group II
    DDDD. The species is non-migratory. Group II
  CCC. It is a “generalist” species, likely using all or many patch types, & >1 structural stage. Group III
  CCCC. It is a “contrast” species, likely requiring contrast between 2 structural stages in close proximity.
  (no identification)
BBBBBBBBBB. The taxonomic order is Rodentia.
  C. The structural versatility of the species is <28.50. Group I
  CC. The structural versatility of the species is >=28.50. Group II
BBBBBBBBBBB. The taxonomic order is Carnivora. Group II

AAA. Population distribution consists of patchily distributed populations.
  B. The average age at first breeding (females) is <6 months. Group II
  BB. The average age at first breeding (females) is 1 year. Group I
  BBB. The average age at first breeding (females) is 2 years. Group III
  BBBB. The average age at first breeding (females) is 3 years.
    C. The habitat versatility of the species is <34.50. Group I
    CC. The habitat versatility of the species is >=34.50. Group II
  BBBBB. The average age at first breeding (females) is 4+ years. Group III

AAAA. Population distribution consists of isolated population(s).
  B. The migration or seasonal movement is <100 km. Group III
  BB. The migration or seasonal movement is 100 – 100 km. Group II
  BBB. The migration or seasonal movement is >1000 km. Group I
  BBBB. The species is nonmigratory. Group I

AAAAA. Population distribution is scarce.
  B. The habitat versatility of the species is <16.00. Group III
  BB. The habitat versatility of the species is >16.00. Group I

Figure 10.9. Continued

box” that may nonetheless be useful as a tool to calculate outcomes for some tasks. Neural networks are more useful for interpolating values of some continuous variables, such as topographic relief or some climate variable (Cook and Wolfe 1991; Derr and Slutz 1994; Christopherson 1997), than for extrapolating values beyond the domain of the predictor variables. They are not particularly useful for aiding understanding of the underlying ecological causal web.

Neural networks have been used in natural resource and wildlife management in a variety of problems, such as developing vegetation management plans (Deadman and Gimblett 1997), monitoring and simulating changes in forest resources (Gimblett and Ball 1995), forecasting recreational use of wilderness areas (Pattie 1992), classifying land cover types from Landsat imagery (Skirvin and Dryden 1997), and other areas. Yeh and Li (2003) devised interesting models of urban planning by integrating GIS, cellular automata, and neural networks. Monteil et al. (2005) used neural networks to determine correlates to bird species richness in forest patches. Olden (2003) used a neural network model to predict species composition of temperate lake fish communities from habitat attributes, and suggested that such predictive models are powerful ways for explicitly considering and conserving species membership and their functional roles in the community (fig. 10.10).

Liu et al. (2003) compared two neural network modeling approaches and three traditional statistical methods for classifying forest inventory data into ecological types. They reported that accuracy of the neural network models was at least 90% and did as well as the kth-nearest-neighbor statistical classification method. However, as with all neural network models, theirs failed to explain the underlying causal web structure that accounted for the accurate results. Still, neural networks can be rather flexible and can be combined with other modeling approaches (such as GIS; see "GIS-Based Models" section above). Ejrnaes et al. (2002) combined ordination techniques with neural network modeling to successfully predict habitat quality (in terms of species richness, nativeness, rarity, and beta diversity) of vascular plant species.

Examples of commercially available neural network modeling shells include the NeuralWorks series (NeuralWare Inc., Carnegie Pennsylvania) and SNNS (Stuttgart Neural Network Simulator, University of Stuttgart).

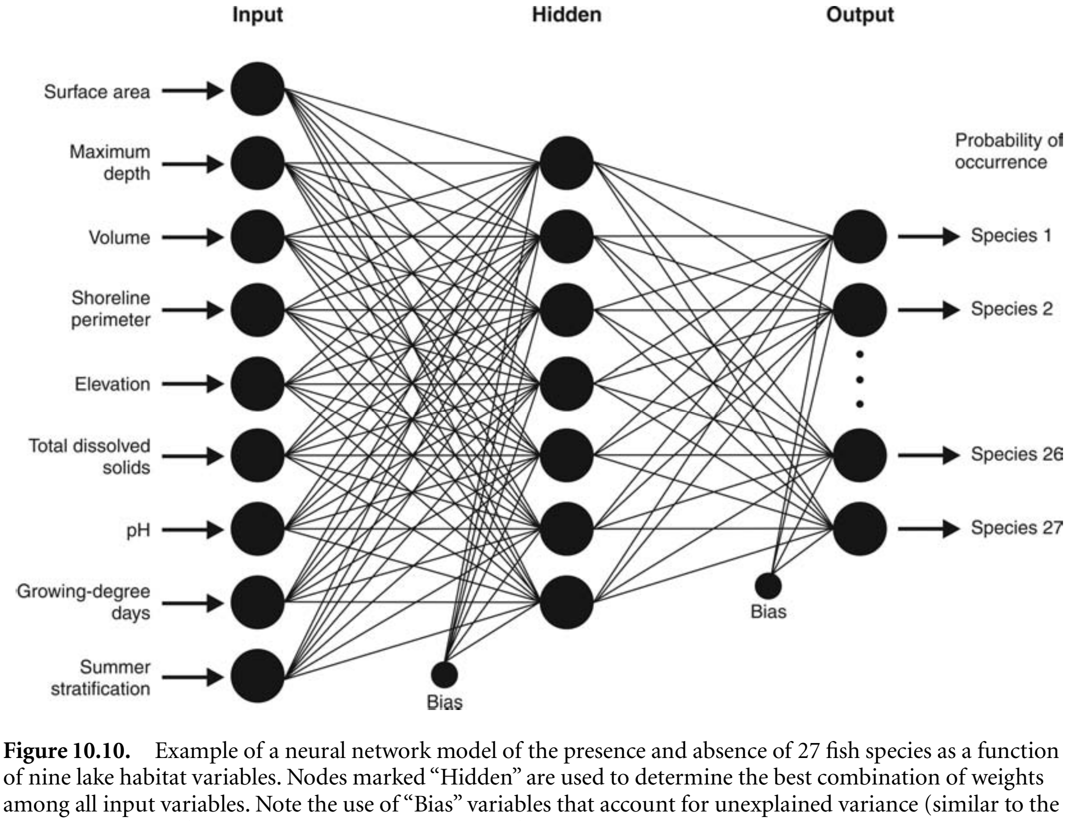


Figure 10.10. Example of a neural network model of the presence and absence of 27 fish species as a function of nine lake habitat variables. Nodes marked "Hidden" are used to determine the best combination of weights among all input variables. Note the use of "Bias" variables that account for unexplained variance (similar to the nodes marked *?* in fig. 10.1). (From Olden 2003, 857 [fig. 1].)

RELIABILITY MODELS

Reliability analysis refers to equations that depict the probability of failure of a system component (such as a species within an ecosystem) over time. Also called survival analysis and failure time analysis, reliability modeling describes and depicts system trends and patterns more than it represents and explains the underlying influences. As used in reliability engineering, failure models are typically based on negative exponential or other probabilistic distributions of MTBF (mean time between failures) of some element (such as an electronic component; Barlow 1998). Reliability analysis is inherently probabilistically based, and in that sense corresponds well with how population viability is viewed as a probabilistic phenomenon. However, reliability models have not been used much in WHR modeling, although the probability distributions may be useful for calculating expected persistence of species or habitat conditions, given effects of stressors.

QUANTITATIVE (ENVIRONMENTAL) RISK ANALYSIS

Quantitative or environmental risk analysis, as a general topic, includes a very wide variety of models and tools used to estimate likelihoods of outcomes, given alternative management actions and subsequent environmental conditions, and to clearly display and interpret uncertainty in such decisions (Morgan and Henrion 1990). Quantitative environmental or ecological risk assessment is generally used to collect, organize, analyze, and present scientific information to improve decision making (Serveiss 2002). Tools used in risk analysis can include all of the models discussed in this chapter. Additionally, the RAMAS Risk Calc modeling shell (Ferson 2002) was specifically designed to help analyze species viability in a risk assessment framework.

There is also a formal quantitative risk analysis (QRA) methodology developed by the U.S. Environmental Protection Agency (EPA 1996). QRA has been used mostly to evaluate toxicological human health risks. QRA has also been used successfully with laboratory toxicity tests on single species to help predict impacts on aquatic ecological communities (de Vlaming and Norberg-King 1999).

LOOP ANALYSIS MODELS

Loop analysis models are used to represent the patterns of relationships among variables. Loop analysis draws from graph theory, in which variables are shown as nodes and their relations as paths or arcs between the nodes (Puccia and Levins 1985). A loop diagram can be a useful starting point to depict a causal web, as in the diagrammatic phase of modeling. A simple loop diagram can be evaluated for its qualitative patterns (Dambacher et al. 2003a, 2003b), such as degree of connectivity and stability of food webs. More sophisticated loop diagrams can also include quantitative causal modeling or path analysis. The patterns of loop diagrams can be evaluated using what is called structural equation modeling, which has been used in ecology (Iriondo et al. 2003; Pugesek et al. 2003).

An early application of loop analysis was demonstrated by Marcot and Chinn (1982), who devised graph theory measures of habitat connectivity. Examples of habitat maps represented as graphs and nearest-neighbor adjacency matrices are shown in figure 10.11. The adjacency matrix of a "habitat graph" can be mathematically analyzed for various connectivity features, such as the average juxtaposition of each habitat patch; presence of habitat patch "cut points" whose disturbance might disconnect the graph (e.g., node 5 in fig. 10.11C); overall connectivity of the graph (e.g., mean number of arcs per node); and distance (number of intervening habitat patches) between any two nodes (patches). Their analysis demonstrated that linear features such as roads and riparian areas

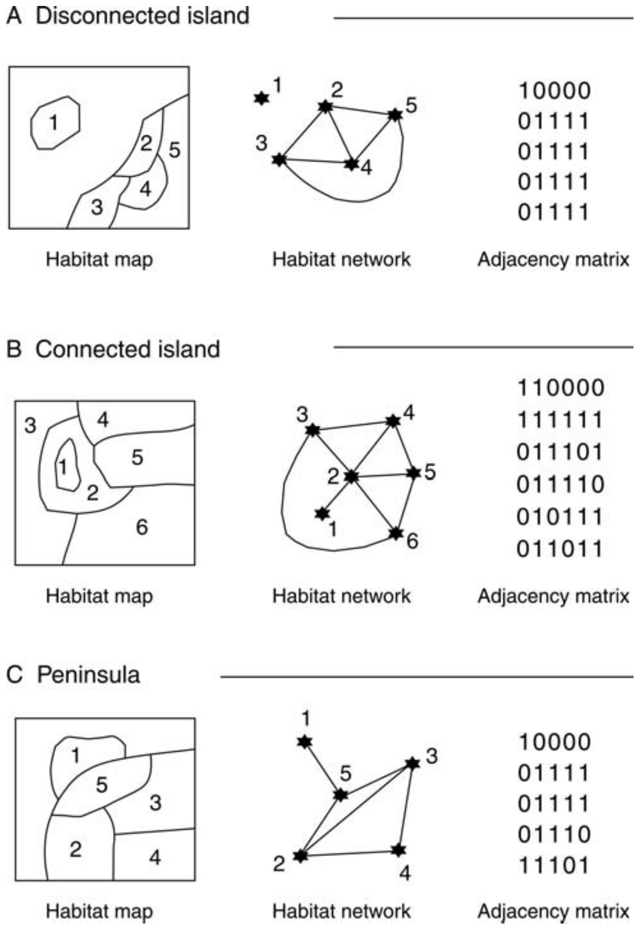


Figure 10.11. Example of a habitat map and its graph theory analog. Note how each patch on the habitat map is represented by a node on the habitat network, and patches that share a common edge are shown by a *1* in the adjacency matrix. Matrix algebra calculations can reveal further information about connectivity of individual nodes and of the overall map.

usually create cut points in a graph and serve as nodes with the highest local connectivity to other nodes. This condition may help explain the high species richness of native linear features, such as riparian areas, and the potential for disproportionately disrupting a landscape from anthropogenic linear features, such as roads and transmission line corridors.

Other authors later suggested various graph theory measures of habitat patch patterns across a landscape (e.g., Cantwell and Forman 1993; Ricotta et al. 2000; Urban and Keitt 2001). Bunn et al. (2000) demonstrated the use of graph theory to analyze the very different degrees of connectivity of a given landscape for American mink (*Mustela vison*) and prothonotary warblers (*Protonotaria citrea*). They analyzed, for each species, the functional distance between reachable habitat patches by using least-cost path modeling and discovered that habitats within their test landscape were fundamentally connected for mink and unconnected for warblers. In general, a graph theory and loop analysis approach to assessing habitat patch patterns and connectivity may have advantages over more complicated mathematical spatial indexes (see table 8.3; O'Neill et al. 1988; McGarigal and Marks 1995) by being simpler to explain and calculate, and by having more direct pertinence to movement patterns of animals.

This overview of various traditional and newer model constructs does not include a number of other approaches with potential for WHR analysis and management, such as rough set theory, a mathematical tool similar to fuzzy set theory to manage uncertainty and vagueness in data sets (Berger 2004, Tan 2005). Doubtless, many new modeling concepts and tools will continue to be developed that push the envelope of traditional statistical analysis and that may find utility for WHR assessment and management. This is an exciting time for wildlife modelers.

Models for Habitat Conservation

In this section, we briefly review two topics related to modeling habitat conservation for wildlife: models that aid optimal allocation of lands for designating conservation areas, and scenario models that aid overall wildlife habitat and land use planning.

Models for Optimizing Land Allocations

A host of modeling approaches has appeared in the past decade to aid optimal design of conservation areas. Kingsland (2002) suggested that the science of nature reserve design has benefited from optimality modeling derived from operations research from the 1970s and 1980s, in a decision analysis framework. More recently, use of simulation modeling of vegetation growth and use of new optimization algorithms have provided the field of reserve design with many practical tools.

Many tools used for design of reserves and conservation areas draw from some of the modeling approaches discussed above. For example, the approach used by Strange et al. (2002) uses genetic algorithms of "evolutionary self-organization" to find the optimal solution. Guisse and Gimblett (1997) used neural networks to help map conflicting recreational impacts on state parks. Other hybrid design models were suggested by Nalle et al. (2002).

A popular model for weighing costs and values of land areas for conservation area planning is SITES, which produces alternative maps of boundaries of potential reserves to meet stated conservation objectives, such as protection of undisturbed ecosystems. SITES is complicated to run and understand, but it has utility in designing reserves and regional conservation plans (Carroll et al. 2002). An advantage of SITES is that one can specify some selected land allocation boundaries to be inviolate so as to aid conservation planning within a landscape already partitioned under existing land use plans.

Many other models of conservation area planning have been proposed, such as using a focal species (e.g., moose, *Alces alces*) to design reserves in Nova Scotia, Canada (Snaith and Beazley 2002). Rothley (2002) proposed a method of applying multiobjective integer programming (MOIP) to surrogate design criteria, such as reserve size or connectedness. McDonnell et al. (2002) used nonlinear integer programming in their algorithm to design reserves in Northern Territory, Australia. Cumming (2002) used habitat shape geometry to design reserves for staving off invasive species. Many other examples and approaches based on concepts of reserve complementarity (Williams et al. 2000), redundancy (ReVelle et al. 2002), representativeness (Powell et al. 2000), and other criteria are available in the literature.

The lessons to be drawn from such a variety of approaches are that (1) there is no one single approach to reserve design that meets all conservation area planning objectives; (2) thus it is critical to articulate those planning objectives first and not let the design model dictate them; and (3) a combination of models or trying alternative design algorithms may be a useful way to test the practicality and utility of their results.

Scenario Modeling

In one sense, most wildlife habitat planning involves exploring alternative scenarios for land allocation, habitat modification, and natural resource use. There are also more formal approaches to scenario planning useful for natural resource and wildlife conservation (Bennett et al. 2003). In this sense, a "scenario" can be a specific level of expected use of a resource or land area, and even a worldview of how resources ought to be used or conserved, such as under utilitarian, humanistic, ecological, or other ethical stances (Callicott et al. 1999). In fact, scenario modeling can even test implications of alternative worldviews (Marcot et al. 2002).

A scenario model is a type of systems model designed to understand social and ecological systems (Bennett et al. 2003). In this sense, scenario modeling of social-economic-ecological systems has been around since the 1970s (e.g., Jantsch 1972). In scenario modeling, wildlife management is viewed as part of a broader social, economic, and ecological system (Walker et al. 2002). Scenario planning can use specific kinds of models discussed above to assess effects of alternative social direction and resource use interests on wildlife conservation, ecosystem services, and human communities. Irwin and Freeman (2002) used such an approach to evaluate social and ecological implications of conservation options for the Tallapoosa River in Alabama under various adaptive management scenarios. Sheppard and Meitner (2005) evaluated forest planning scenarios with stakeholder groups by using multicriteria analysis and visualization methods.

Validating Wildlife–Habitat Relationship Models

Most of the types of models discussed in this chapter are difficult to validate. In part, this difficulty exists because the models consist of many relations and entities that confound simple prediction (Gentiol and Blake 1981). Many also represent outcomes in abstruse terms, such as unitless indexes, fuzzy set membership, Bayesian posterior likelihoods, or influence webs, which sometimes defy simple interpretation and easy comparison with empirical observation. The problem of validation of the more avant-garde modeling approaches discussed above has received limited attention in the wildlife literature.

The concept of model validation should be addressed in any modeling exercise. Analyses that cannot be falsified or otherwise rigorously tested are essentially little more than belief systems and have little to no value in science. It is therefore essential in the model-building process to represent variables and their relations as empirically quantifiable entities. For example, it is easy to build an expert system, a Bayesian belief network, or an influence diagram with vaguely worded variables such as "habitat quality" and "species response." It is more difficult, but essential, to craft such models using empirically verifiable variables, such as area of a specific vegetation condition or density of reproductive individuals.

Species-habitat models built using various kinds of complicated DSM tools often approximate habitat evaluation or suitability models (e.g., Adamus 1996) and could be evaluated by validating their specific ecological predictions. Other approaches may include using Bayesian statistics to use new information to test, calibrate, and refine certain kinds of network models. Also see Reinhardt et al. (1992), Preece (1994), and Sequeira et al. (1996) for other examples of validating decision support- and knowledge-based models.

Purposes of Validation

Validating wildlife-habitat models should be part of each step in building and using such tools (Marcot et al. 1983). Model validation is best viewed as a general approach to developing, calibrating, and testing models, and should be conducted in a variety of ways throughout the model development and application process.

Aspects of validating a model (see table 10.1) include:

1. *Verifying the model*—verifying that mathematical equations are correct or that the computer program code has been written without bugs
2. *Testing the audience*—ensuring that the audience for whom the model is intended will accept and use the tool
3. *Running the model*—confirming that the model can be run with available or obtainable data
4. *Assessing purpose and context*—ensuring that the purpose of the model and the conditions in which it is to be used have been clearly stated and adhered to in its use
5. *Testing the output*—assessing whether the output of the model matches real-world biological conditions

Model validation is typically associated with just the first and final items on this list. Each item, however, contributes to successful development and application of a wildlife–habitat model.

VERIFYING THE MODEL

Ensuring that formulae and computer code are written correctly is a simple but important aspect of model validation. A similar task is documentation. *Documentation* refers to explicitly explaining the development procedure used to create the model; writing down major assumptions and uncertainties inherent in the model; disclosing sources of information and analyses used to develop variables and their relationships in the model; and annotating any computer code. The more a model is verified, the more open it is to understanding—and critique.

Verification is an important aspect of modeling where meeting legal mandates is a concern, as in developing models for use in National Environmental Policy Act (NEPA) documents, such as environmental impact statements. In this case, keeping careful records in process documents is paramount.

TESTING THE AUDIENCE

The best model in the world may fail to be used if it is too complex or too esoteric. It will also be ignored if existing administrative organizations or policies do not provide for its use, or if it is, for some reason, not credible. In an operational sense, a model is valid, in part, if it is accepted (has face validity) and is usable in the intended work setting. Thus developing models with teams combining managers and researchers helps enhance the utility of such tools (Bunnell 1989). A team approach would help ensure that the model addresses the correct question, is based on data available from existing databases, is credible, and can be used in the everyday course of work.

RUNNING THE MODEL

In a typical management situation, a wildlife-habitat model is used to predict response of wildlife species to potential environmental conditions created from alternative management activities. For such a model to be used, it must run from information available from existing or easily obtainable inventories of vegetation and environments. This requirement may limit accuracy of model predictions, however, if inventories are dated or incomplete, or fail to include pertinent variables. In such a case, the models may be more useful for suggesting changes to inventory procedures.

At best, proxy variables might be used to represent the missing variables (Marcot et al. 2001), such as using size of a forest opening to represent a more complex representation of habitat patch juxtaposition, or using road density available as a GIS data layer to represent hunter access. When proxy variables are used, their degree of correlation with the intended predictor variable should be evaluated.

ASSESSING PURPOSE AND CONTEXT

The purpose of a model is often incompletely stated, and clarifying the intended purpose should guide how the model is used. If a model is truly intended to predict real-world environments and populations, it should be evaluated using a different set of criteria than if its purpose is to formalize our knowledge and understanding.

Also, the context of a model should be specified by the model builder. Context includes the range of environmental conditions (e.g., weather), types of environments, and seasons in which the model was built and tested. It is the onus of the model builder to document these conditions, and of the model user to adhere to those conditions. When a model is used outside its intended context, its accuracy and reliability are essentially unknown unless they have been formally evaluated.

TESTING THE OUTPUT

Too often, models created for prediction are untested against real-world situations. This problem occurs for a variety of reasons. Models are often developed without regard to validation until after they are built, and postconstruction validation costs too much time and money. Or, models are built mostly from theory and are difficult or impossible to test, even if they are used for prediction. Or, it is unclear or unspecified what the model output represents, such as with models that calculate some relative index of habitat value.

Depending on the purpose, not all models require rigorous field testing. However, the validity (and uncertainty) of models used for helping make decisions about irreversible or expensive losses of environments and populations should be known. In this case, the accuracy, bias, precision, and reliability of the model should be evaluated (e.g., see guidelines by Golbeck 1987).

A Type I error in prediction occurs when a model predicts species presence (or some other measure) and the species is actually absent. This error could occur because of inadequate or incorrect sampling for the species, because the field study was conducted during the wrong season, because the species is inherently rare and does not maximally occupy all suitable environments, or because the model was wrong and overstated the value of environmental parameters or failed to account for an environmental condition that deducts the presence of the species. The degree to which a model avoids Type I errors is given by the confidence coefficient P (where $P = 1 - \alpha$, where α is the significance level).

Contrariwise, a Type II error in prediction occurs at rate β when the model predicts absence and the species is actually present. This error could occur because the animals detected were wandering or their presence is not indicative of actual environmental quality; because of sampling design; or because the model is wrong and does not include a vital parameter that affects presence of the species. The degree to which a model avoids Type II errors is given by the power of the model, $1 - \beta$ (Steidl et al. 1997). Power provides a means for selecting models for trend analysis (Gerrodette 1987), detecting environmental impacts (Osenberg et al. 1994), and determining population declines (Strayer 1999). Tyre et al. (2003) suggested an extension of logistic modeling using a zero-inflated binomial model to better estimate Type II error rates.

Typically, the modeler must make a trade-off between reducing Type I errors and Type II errors (Roback and Askins 2005; Verhoeven et al. 2005). The ramifications of each type of error of model prediction depend on how the model is to be used. If the objective is to identify needs for mitigation, such as with purchasing or trading habitats with high opportunity costs, or by restoring or enhancing environmental conditions, then the model must accurately predict species presence. That is, frequencies of Type I errors should be minimized because costs of actions based on model predictions are high. On the other hand, if the model is to be used for predicting impacts, especially on rare or vulnerable species, then errors in predicting species presence or positive responses may be tolerable, but false predictions of species absence or negative responses might be of greater concern than in the case of mitigation. In this case, the power of a model and its ability to avoid Type II errors is critical.

In general, most habitat models can be expected to account for less than half the variation in species density or abundance. On-site environmental conditions generally account for even less variation in population density when considering migratory species, especially migratory birds. At first it might seem that low correlations in a habitat model are not very useful, but considering the large array of other factors that affect populations, even relatively low correlations may provide useful insights.

This characteristic of low correlation is also a lesson for the manager who will use the model for maintaining environmental conditions. The manager must understand that most models that predict species presence, population density, or species richness from environmental characteristics are likely to capture only a portion, typically half or less, of the variation in those species' parameters. This low explanatory power does not mean that habitat is unimportant; it is usually critical. It means that one cannot manage for environmental conditions alone and expect with high confidence that the population will show a direct response. Another way of interpreting this low explanatory power is that by managing for (readily measurable) environmental conditions, we control only a portion of the factors that affect the occurrence and abundance of species.

Given these validation results, the appropriate use of habitat models then appears to be to help us recognize the degree (correlation) to which we can provide for species presence and abundance, and thus which environmental parameters under consideration are the more critical. Such models can also be used to assess potential (hypothetical) effects on species from alternative management scenarios. However, if such models are used specifically to predict population size, the predictions should be treated as hypotheses. Such predictions would assume that all factors not considered by the model—that is, the 50% or more of unexplained variation in occurrence or abundance—are unimportant or are at optimal values. This assumption is invariably false.

Overall, validating models is a many-faceted problem and should be done routinely as models are built and used. Validation should address the appropriateness of objectives and structure of the model; the utility, reliability, accuracy, and completeness of the model; and its credibility.

Some Methods of Model Validation

We have given some tips above about model validation. Specific methods used to test the performance of models are many, and the modeling literature about testing and validation is rich and deep. In brief, methods of model validation can be categorized as (1) those that empirically test specific model predictions, (2) those that evaluate the appropriateness of the underlying model structure, and (3) those that assess the usability of the model for its intended audience and purpose.

Empirical tests of model predictions can use various statistical methods, such as cross-validation of a data set (building the model with a randomly chosen portion of the data set, and testing it against the other half) using techniques of data bootstrapping (with replacement of the data after random selection) or jackknifing (without replacement) (see Meyer et al. 1986, Lillegard et al. 2005). Recently, use of the Akaike's information criterion (AIC) (Anderson et al. 1994) has come into favor. AIC is used to guide selection of best-fitting statistical model structures (e.g., Spendelow et al. 1995; Halley and Inchausti 2002; Rushton et al. 2004).

Evaluating the underlying model structure can be notoriously difficult, particularly if the model hides its structure well, such as with neural networks. The state variables and relations, however, should be articulated through the model verification and documentation phase. The veracity of how they are represented in the model, and how well they in turn represent accepted ecological theory, can then be evaluated through peer review. Lastly, assessing the usability of a model for its intended purpose and audience can be done by use of questionnaires and interviews.

Another method of model validation is use of sensitivity testing, particularly for the model-building stage. By evaluating the degree of sensitivity of model output to its structure and underlying state relations (e.g., Pacala et al. 1996), one can determine whether the model is performing as expected and desired. Further validation may be necessary once the model is built and performing to specifications, however, or else the model is simply a representation of one's understanding and biases. For some modeling exercises, such as evaluating the performance of a model, this level of variation may be enough. But for use in real-world conservation, further validation may be needed to ensure that the model is calibrated correctly and is adequately representing reality. Other validation methods suggested in the literature include use of diffusion approximation to validate time series data on population counts to validate population viability models (Holmes and Fagan 2002) and use of logistic regression to analyze sensitivity of population viability analysis models (Cross and Beissinger 2001).

Examples of Validation

The past decade has seen a number of studies aimed at validating various kinds of WHR models. This increase in validation studies is most encouraging, because validation is difficult but often essential. In each of these tests, different criteria were used to test various aspects of model prediction, including the robustness of the models to being used in various ways, sensitivity of predictions to precision of input variables, and accuracy of predictions of species' abundances as compared among different seral stages. Following are examples of recent or important validation studies.

VALIDATION OF WHR MATRIX AND MULTISPECIES MODELS

Raphael and Marcot (1986) validated for errors of omission and commission a WHR model of amphibians, reptiles, birds, and mammals in a Douglas-fir sere in California. Results suggested that, because of errors of commission (predicting more species than actually occur), WHR matrix models are probably best used to predict the occurrence of species in general vegetation types and environmental conditions across broad regions rather than at the individual-stand scale. A shortcoming of such models is that they do not quantify population response. Thus such models cannot be used to gauge population density or to quantify population trend.

Edwards et al. (1996) tested predictions from a gap analysis of terrestrial vertebrate species in national parks in Utah using long-term species lists and found error rates of omission of species to range from 0% to 25%, and those of commission to range from 4% to 33%; error rates were highest with amphibians and reptiles, lowest with birds and mammals, and lower with larger-sized parks. They concluded that the gap analysis WHR models were adequate for aiding conservation planning at the ecoregional level. Overall, errors of commission in WHR matrix models can be explained, in part, by the fact that fine-scale environmental data are typically lacking with which to "trim" predicted lists of species, which also causes errors when predicting spatial distributions of species at levels of fine-scale resolution and small geographic areas (Mackey and Lindenmayer 2001).

Stephens et al. (2002) compared a simple species matrix model of alpine marmot (*Marmota marmota*) in southern Germany with detailed empirical data from 13 years' study on behavior and demography and found that the simplest matrix model adequately predicted population size and density under equilibrium conditions, but not under dynamically changing conditions. For the latter, it was necessary to have data on behavior—in particular, Allee effects on population dynamics.

Dettmers et al. (2002) tested the predictions of presence of forest bird species by habitats in the southern United States as modeled by a combination of published census and natural history data, field experience, and expert opinion. Using point-count survey data from three states, they found that 23% to 52% of the models correctly predicted ranks of positive associations between predictions and observation data. The models performed better in predicting species restricted to mid-aged to mature deciduous forests or to high elevations, and poorer for species in mature deciduous forests because those species were also observed to use some early-aged deciduous forest sites.

A study by Fleishman et al. (2001) of 10 data sets revealed that umbrella species (selected a priori using a recently developed index) were no more effective than randomly selected species in protecting unrelated species. Such use of umbrella species may be useful, but their work suggests caution in unbridled use of the concept without testing.

VALIDATION OF POPULATION VIABILITY ANALYSIS MODELS

Several recent studies have focused on comparing and testing models used in population demography and viability analysis. Mills et al. (1996) evaluated four population viability analysis programs and found that idiosyncrasies among the programs of their input format, and whether and how the models handled density dependence, led to great differences in estimates of extinction rates and expected population size.

They concluded that PVAs should include at least one scenario run without density dependence and to exercise caution when interpreting PVA modeling results.

Likewise, Lindenmayer et al. (2000) tested VORTEX to predict abundance of three species of arboreal marsupials in southeastern Australia and found that model runs based only on patch area and home range size overpredicted number of occupied patches and total abundance of animals. These authors also suggested caution when using such tools to predict dynamics and response of populations in fragmented environments.

Coulson et al. (2001) cautioned that PVA models are generally unable to perform well because of the inability of precisely predicting catastrophic disturbances. However, despite their conclusion that PVA models have limited utility as absolute predictors, it is our experience that PVAs can be useful for comparing relative effects of alternative habitat management scenarios.

VALIDATION OF SINGLE-SPECIES MODELS

Fielding and Haworth (1995) tested predictions from a range of models developed using discriminant analysis and logistic regression of nest location and occupancy of golden eagles (*Aquila chrysaetos*), ravens (*Corvus corax*), and buzzards (*Buteo buteo*) in northwest Scotland. They found that the models' predictions were correct 6% to 100% of the time. They attributed this widely variable outcome in prediction success to methodological and ecological processes and cautioned that great care must be taken about making predictions from such studies and that such systems may be inherently *unpredictable.*

Cross and Beissinger (2001) compared logistic regression of demographic data with results of stochastic and deterministic demographic models of African wild dogs (*Lycaon pictus*). The logistic model results suggested that pup survival explained the most variation in the probability of extinction regardless of density dependence, whereas the standard demographic models suggested that adult survival was more important. The authors concluded that logistic regression is a useful tool for exploring sensitivity of extinction probability from vital rate parameters, although it is clear that model structure, analysis methods, and variance of the vital rate parameters all affected results.

Fecske et al. (2002) reported on a test of a habitat-relation model for American marten (*Martes americana*) in the Black Hills of South Dakota. They used stepwise logistic regression to test their model predictions of presence of the species, and found that their model correctly predicted presence in 60% of the 46 10.2-km^2 quadrats surveyed. Roloff et al. (2001) tested a spatially explicit habitat effectiveness model of Rocky Mountain elk, using two-way ANOVA to compare observed use with predicted habitat quality. They found that the elk model performed more consistently during fall than other seasons, and for subherds unaffected by recent fire. Their results suggested the need to model elk herds by season and disturbance influences, as affecting forage dynamics, topographic usage, and road effects.

Other validation studies include tests of three habitat suitability models for Kirtland's warbler in Michigan (Nelson and Buech 1996).

Conclusions

WHR models are essential partners on our journey to better understand, manage, and monitor wildlife species and communities and their environments. As natural environments on this globe become increasingly stressed and scarce under bourgeoning human populations and natural resource use, we are coming to rely more on technologies such as remote sensing imagery, on expert judgment, and on the various kinds of

WHR models to help us find acceptable balances between conservation and exploitation.

No single model is fully general, completely accurate and precise, and completely devoid of bias. As with human understanding, models will always be wrong—perhaps a better term is "not useful"—in some context. This does not invalidate models, and we should avoid the urge to cry "fatal flaw" and engage in a "battle of the models" when a prediction goes awry or when personal interests contrast with model results. Instead, we should strive to understand in which contexts a model may be most useful and the degree of that utility, and then view with due caution any application of the model outside those circumstances. Only then can managers best understand when to use a model and what confidence to place in it.

Models based on expert judgment can provide valuable information, but they should be peer reviewed and, where possible, empirically validated or at least calibrated, else they constitute little more than belief systems. We also advocate use of multiple models because models tell us as much about the modeler's biases and knowledge and the specific structure of the model as they do about the real world.

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