



ELSEVIER

Forest Ecology and Management 153 (2001) 29–42

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement

Bruce G. Marcot^{a,*}, Richard S. Holthausen^b, Martin G. Raphael^c,
Mary M. Rowland^d, Michael J. Wisdom^e

^aUS Forest Service, Pacific Northwest Research Station, Portland Forest Science Laboratory, 1221 S.W. Yamhill St., Portland, OR 97224, USA

^bUS Forest Service, Forestry Sciences Laboratory, 2500 South Pine Knoll, Flagstaff, AZ 86001, USA

^cUS Forest Service, Pacific Northwest Research Station, Olympia Forest Science Laboratory, 3625 93rd Avenue, Olympia, WA 98512, USA

^dUS Bureau of Land Management, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA

^eUS Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory,
1401 Gekeler Lane, La Grande, OR 97850, USA

Abstract

We developed procedures for using Bayesian belief networks (BBNs) to model habitat and population viability of selected at-risk fish and wildlife species. The BBN models represent the ecological causal web of key environmental correlates (KECs) that most influence habitat capability, potential population response for each species, and influence of habitat planning alternatives. BBN models represent site-specific KECs, habitat capability at the subwatershed level, and pattern of habitat capability across all subwatersheds. BBNs use Dirichlet prior probability distributions and standard Bayesian updating of posterior probabilities. We derived estimates of prior and conditional probabilities from a mix of empirical data and expert judgment, mostly the latter. Sensitivity analyses identified planning decisions and KECs that most influence species outcomes, and can help prioritize monitoring activities. BBN models, however, substitute for neither field studies nor empirical, quantitative population viability analyses of population demography and genetics. Published by Elsevier Science B.V.

Keywords: Bayesian belief networks; Bayesian statistics; Wildlife modeling; Fish modeling; Population viability; Columbia River; Interior Columbia basin

1. Introduction

Fish and wildlife experts are often faced with the daunting task of analyzing effects on species from land management activities when only scant scientific data are available. Only under special circumstances, such as with federally listed threatened or endangered species, can management halt activities until studies

are conducted. Much more commonly, the experts must provide their best professional evaluation or step aside and let activities proceed without their input. One method for combining available scientific data with expert knowledge and experience is the use of Bayesian statistics and, more specifically, Bayesian belief networks (BBNs).

Despite some controversy (Dennis, 1996), Bayesian statistics have proven useful in ecology for evaluating and managing wildlife species (Cohen, 1988) and forests (Crome et al., 1996), and for other areas of

* Corresponding author.

E-mail address: bmarcot@fs.fed.us (B.G. Marcot).

environmental research and management (Dixon and Ellison, 1996; Ellison, 1996; Wolfson et al., 1996). BBNs provide a means of modeling likelihoods of management effects (Oliver and Smith, 1990). A BBN is a form of influence diagram which, as applied in ecology, depicts the logical or causal relations among ecological factors that influence the likelihood of outcome states of some parameter(s) of interest, such as forest condition or wildlife species viability. BBNs have been used in ecology and forest management to evaluate regeneration of aspen forests (Haas, 1991; Haas et al., 1994), to depict and help frame resource decision-making (Haas, 1992), to manage fisheries resources (Lee and Rieman, 1997), and for other uses (Olson et al., 1990).

The purpose of this paper is to present our methods of using BBN models and to suggest cautions in their application to conservation problems. Specific results of analyzing planning alternatives are presented by Rieman et al. (2001) on fish and by Raphael et al. (2001) on wildlife. We describe the general framework we devised for developing BBN models to evaluate viability of fish and wildlife species for the Interior Columbia Basin Ecosystem Management Project (ICBEMP) of US Department of Agriculture (USDA) Forest Service and US Department of the Interior (USDI) Bureau of Land Management. We also direct the reader to existing primers on BBN structure (Charniak, 1991; Jensen, 1996; Morawski, 1989) and Bayesian statistics (Press, 1989).

2. Methods

We selected a BBN approach to modeling species viability after a broad review of numerous approaches including data mining, rule induction, network induction, neural network, fuzzy logic, expert system, traditional statistics, simulation modeling, and other modeling algorithms. BBNs best met our modeling needs, particularly by providing a useful communications medium that (1) clearly displays major influences on wildlife population viability or quality of fish habitat and their values and interactions; (2) combines categorical and continuous variables; (3) combines empirical data with expert judgment (Heckerman et al., 1994), often from multiple experts; and (4) expresses predicted outcomes as likelihoods as a basis

for risk analysis and risk management (Marcot, 1998). Our BBN models of wildlife population response, however, do not substitute for empirically based, quantitative, stochastic analyses of population demography, genetics, and persistence such as those used in population viability analysis (PVA; Boyce, 1992). Rather, our BBNs complement such PVA models, and are most useful when empirical data on population trends, demography, and genetics are unavailable.

We selected the BBN modeling shell Netica (Norsys) for its ability to incorporate case files, provide sensitivity analysis, operate in batch mode, and other functions (USDA Forest Service does not necessarily promote any particular software product, including this one). Netica performs standard belief updating which solves the network by finding the marginal posterior probability for each node. In BBN analysis, a *prior (unconditional) probability* is the likelihood that some input parameter will be in a particular state, such as some habitat substrate being present; a *conditional probability* is the likelihood of the state of a parameter given the states of input parameters affecting it, such as how presence of several habitat substrates affect overall habitat suitability; and a *posterior probability* is the likelihood that some parameter will be in particular state, such as population size being high, given the input parameters, the conditional probabilities, and the rules governing how the probabilities combine. A network is solved when Bayesian belief updating has been done on the nodes. As is mostly standard with BBN models, Netica assumes that conditional probabilities are independent and that prior probabilities are Dirichlet functions (Spiegelhalter et al., 1993) meaning that probabilities are continuous and bounded between 0 and 1 (Castillo et al., 1997) and are a multi-state extension of the beta distribution.

We developed BBNs for selected aquatic and terrestrial vertebrate species found on federal lands within the interior Columbia River basin in the United States (hereafter, "Basin"). The Basin encompasses 58.5 million hectares east of the Cascade Mountains crest in Washington and Oregon and also includes most of Idaho, western Montana, and parts of Wyoming, Utah, and Nevada. The Basin has a wide array of conifer and hardwood forests, shrublands, grasslands, alpine, agriculture, urban, aquatic, and other environments.

The fish and wildlife BBN models were intended to represent influences of the “causal web” of key environmental correlates (KECs) on populations. The fish BBN models were constructed based on the expected influence of habitat and biotic conditions on fish populations (see Rieman et al., 2001 for further methods). For the wildlife BBNs, we first listed KECs for each species from three sources: the species–environment relations (SER) database that was previously developed for ICBEMP, published databases of associations of species with suitable cover types and seral stages (Wisdom et al., 2000), and additional expert review. The SER database lists qualitative and, where known, quantitative ecological factors most influencing the distribution and abundance of each wildlife species, and was developed from published literature, theses and research reports, and knowledge and judgment from panels of species experts (Marcot et al., 1997). The SER database was developed using a formal Delphi process to elicit knowledge from species experts (Marcot et al., 1997). We followed a similar method when querying species experts for parameterizing the BBN model probabilities.

The fish BBN models were developed at two scales, one representing the influence of habitat, existing biotic conditions, and ocean and migratory conditions (for two anadromous fish species); and one representing landscape characteristics and the expected influence of management activities. The wildlife BBN models were developed at three scales: site-specific, subwatershed, and Basin. BBN models for fish and wildlife were peer reviewed for each species.

The site-specific wildlife BBNs represented conditions that would be determined on the ground from a field-based inventory of resources, such as from a watershed analysis. Subwatershed wildlife BBNs represented use of habitats and resources as mapped in geographic information systems (GIS) by ICBEMP at 1 km² pixel resolution. For site-specific and subwatershed wildlife BBNs, we arrayed the appropriate KECs for each species into influence diagrams representing ecological causal webs that depict how ecological factors influence wildlife habitat and population density.

The Basin wildlife BBNs represented potential population response at the scale of the entire distribution of each wildlife species within the Basin. The

Basin BBN depicted the distributional pattern of habitats within the Basin and predicted the probability of each wildlife species occurring in five outcome states ranging from populations being widely distributed and interconnected to isolated and disjunct (Raphael et al., 2001). We revised these five population outcome states from those used in Lehmkuhl et al. (1997) and FEMAT (1993).

We structured the site-specific and subwatershed BBN models as six shells of nodes representing: (1) decisions, (2) GIS proxy variables that best represent KECs, (3) KECs, (4) summary habitat nodes representing combinations of KECs, (5) population response, and (6) utility or value of the population outcome (Fig. 1). In practice, we did not include decision and utility nodes, but we show here how they can be made explicit and used in making decisions for wildlife resources. The ecological “causal web” mentioned above is represented by shells 3–5. Summary habitat nodes can be used to help clarify and simplify relations in the model by combining effects of KECs into themes of influence of habitat, other species, endogenous population characteristics, and human activities. Proxy variable nodes depict the closest approximation to the KEC nodes based on available resource inventories and GIS data.

In BBN parlance, node shells 2–5 are called states-of-nature nodes, and each node of this type has an associated *conditional probability table* (CPT). CPTs represent the probability or frequency with which a node takes on each discrete state, given the states of any antecedent (“parent”) nodes that interact with it. CPTs can be derived and updated from empirical information, expert judgment, or case examples; we used all three sources but relied mostly on expert judgment. Probabilities associated with proxy variable nodes (shell 2) represent the probabilities of various states associated with each planning choice in the decision node. Species experts were used to help craft the causal web of key environmental correlates and to provide the probabilities in the CPTs, not to assign values to species outcomes.

Decision and utility nodes do not have CPTs. Utility nodes are linked to the population response or outcome node (node shell 5) and have values representing the utility of each possible outcome state (population level). Utilities can be expressed as gross or net, social or economic costs or benefits of each outcome.

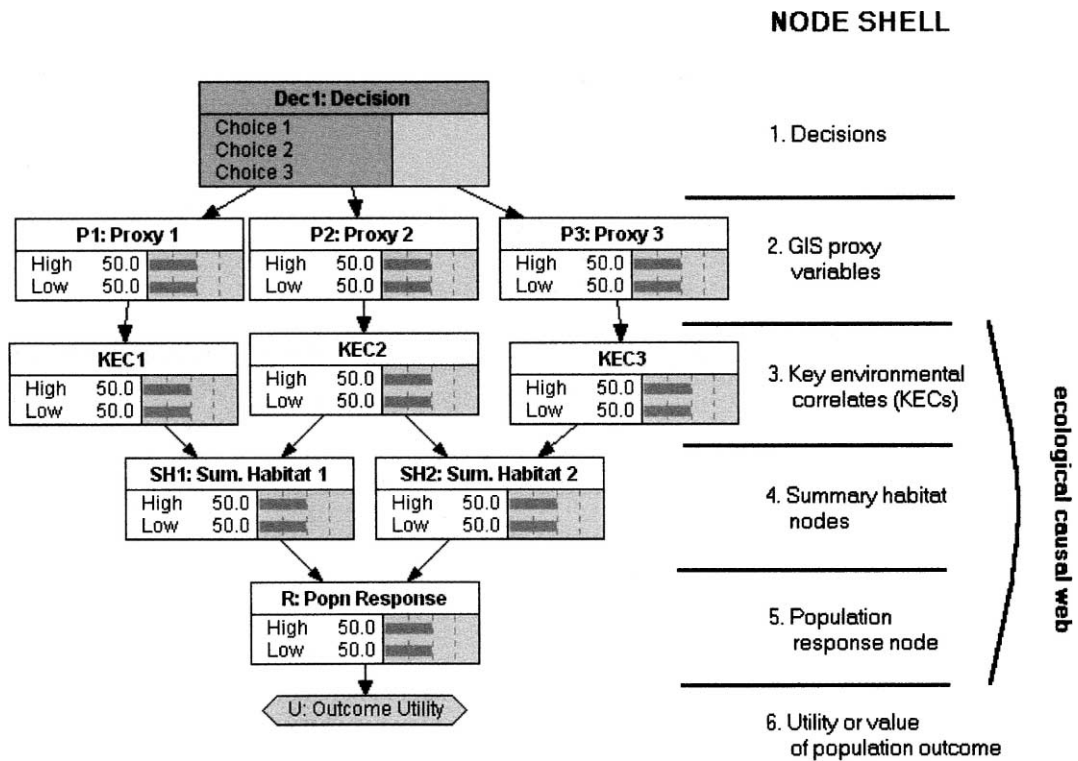


Fig. 1. General structure of a BBN model for evaluating population viability outcomes of wildlife species, showing six shells of nodes. See Appendix A for description of node names. The state of nature nodes (shells 2–5) can depict parameters as multiple discrete values (as shown here) or as continuous values.

Decision nodes can be used to set values of states-of-nature nodes and to determine the expected outcome utility of each decision choice. BBNs without decision and utility nodes are still useful for expressing ecological relations among KECs and resulting likelihoods of population outcomes. BBNs with decision and utility nodes, however, also can be used to help explicitly judge optimal decision pathways that maximize outcome utilities and to help prioritize for monitoring the uncertainties associated with each decision choice.

3. Results and discussion

We present here a set of models for one example wildlife species (see Rieman et al., 2001 for a fish example) to illustrate the three scales of BBN models, the six shells of nodes in the models, the content of the

CPTs for each node, and a potential use of decision and utility nodes for informing and guiding management. We also show how sensitivity testing of the BBN can help guide monitoring in an adaptive management context.

3.1. Example BBNs for evaluating and managing for viable populations

Illustrated here is an example set of BBNs for depicting potential population response of Townsend's big-eared bat (*Corynorhinus townsendii*) in the Basin at three levels of geographic resolution (Fig. 2a–c). The models at each geographic level run independently, but they also can be nested within one seamless evaluation process.

The subwatershed BBN (Fig. 2b) is used to estimate the class of ecological density of the species within each of the subwatersheds in the species' range within

the overall Basin, accounting for broad-scale biophysical conditions and broad-scale human disturbance effects (see Appendix A). We calculated habitat density (node HD1 in Fig. 2b) outside the BBN as part of

preprocessing in GIS, although it is possible to do this calculation within the BBN itself by passing subwatershed-specific data on habitat area and mean home range size of the species into the model. An example

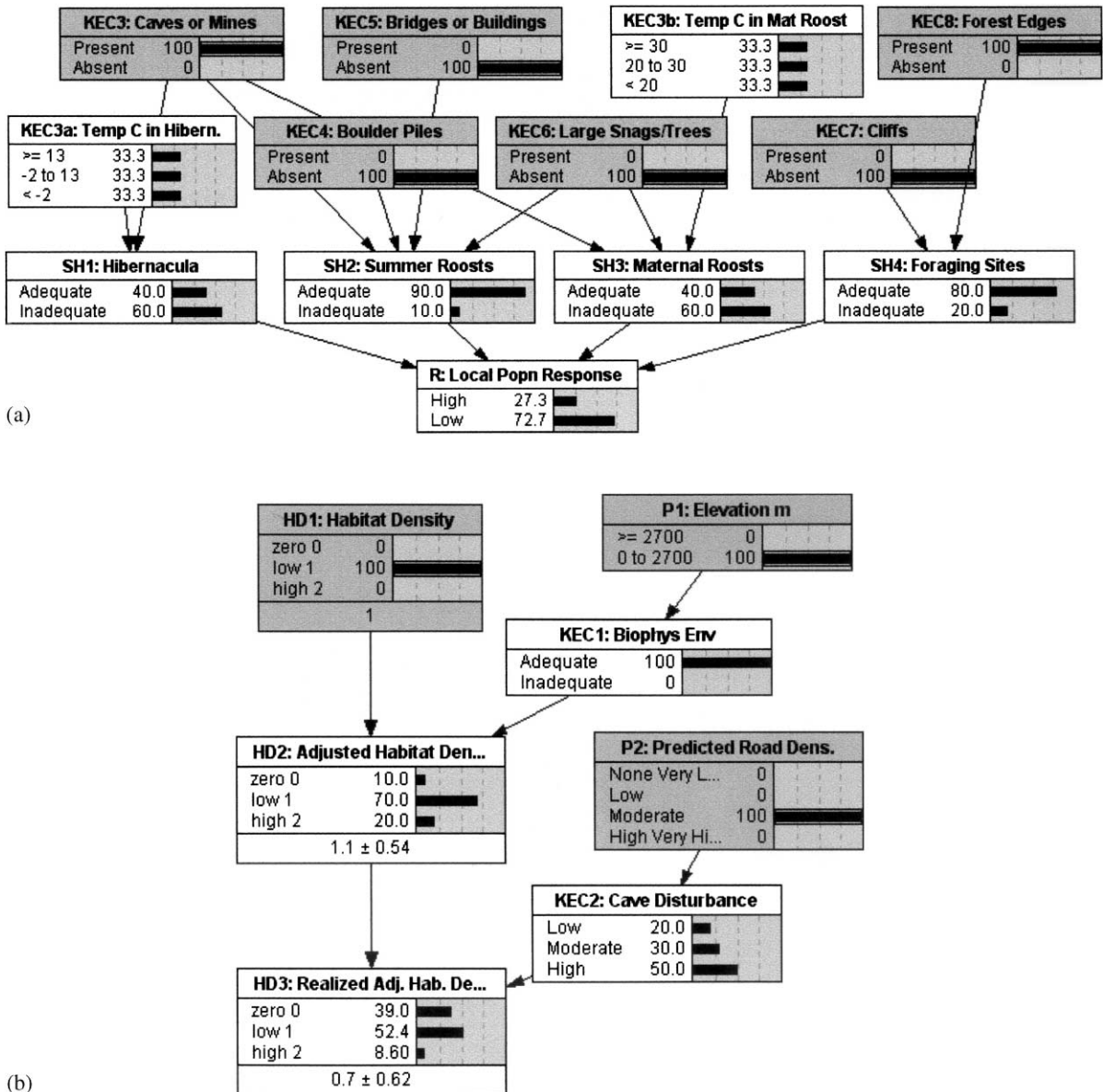


Fig. 2. Example BBNs depicting population response of a wildlife species, Townsend's big-eared bat (*C. townsendii*), in the interior Columbia River basin, USA, at three levels of geographic resolution. (a) Site-specific BBN model: relations of site-specific key environmental correlates (KECs). (b) Subwatershed BBN model: relations of subwatershed-scale KECs and their GIS proxies. (c) Basin BBN model: overall population outcome. See Appendix A for description of node names.

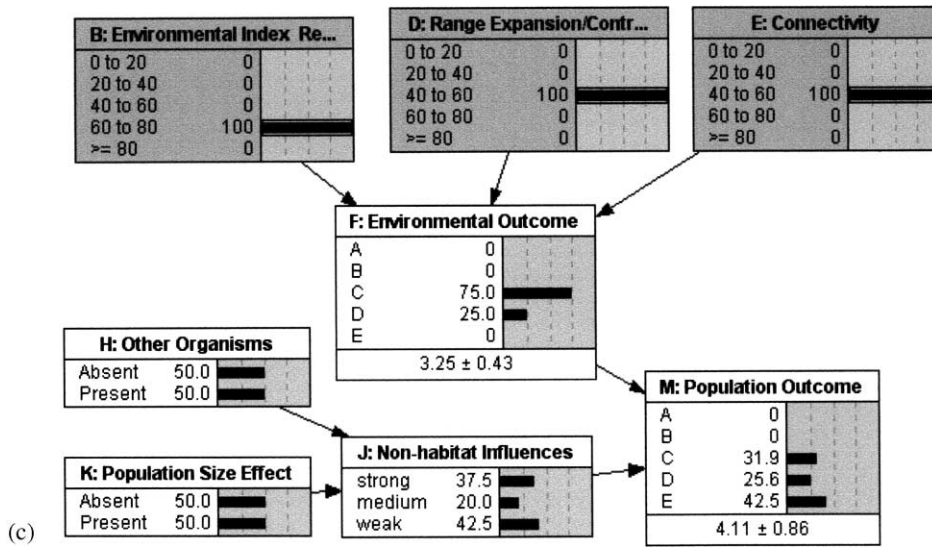


Fig. 2. (Continued).

run for the subwatershed BBN (Fig. 2b), where initial calculation of habitat density (node HDI) was “low,” mean elevation (node P1) was <2700 m, and predicted road density (node P2) was “moderate,” resulted in a probability distribution of realized adjusted habitat density of 39.0, 52.4, and 8.6% of zero, low, and high states, respectively. We used such qualitative states of habitat density instead of continuous values because we did not feel confident in expressing outcomes as absolute population numbers. Note that the significant figures shown in the BBN models (Fig. 2) result from the BBN calculations rather than from frequency data.

Once the user has ascertained that a particular subwatershed has at least non-zero realized adjusted habitat density (see Appendix A), the site-specific BBN (Fig. 2a) can then be used to determine the degree to which local conditions and substrates specifically provide for the species. This site-specific BBN can be part of a procedure to implement the chosen planning alternative. The site-specific BBN accounts for habitat features and conditions too fine-grained to depict in the GIS database at the subwatershed level of geographic resolution.

For wildlife analyses, the subwatershed BBN was designed to run in batch mode (the “process cases” function in Netica) across all subwatersheds (although this function was not used for the fish BBNs). Results

are passed back to GIS where each subwatershed is then mapped according to its expected value of realized adjusted habitat density. The overall pattern of realized adjusted habitat density across all subwatersheds is then summarized in GIS, and this summary is passed to the input nodes of the Basin wildlife BBN model (Fig. 2c). This model is used to determine the likely overall population viability response across all subwatersheds and is designed to explicitly evaluate the three major factors that influence persistence of wildlife metapopulations: habitat concentration (node B in Fig. 2c), percent of range occupied (node D), and connectivity of habitats (node E). The Basin wildlife BBN analyzes habitat concentration and percent of range occupied by comparing current or projected patterns with historic patterns. The Basin fish model (Rieman et al., 2001) similarly addressed aquatic habitat capacity and connectivity.

The Basin model provides a first-level evaluation of population viability response based on these habitat patterns (node F “environmental outcome” in Fig. 2c), and also a second-level evaluation given additional influences of non-habitat factors including population size and other organisms (predators, symbionts, etc.). The final outcome (node M “population outcome” in Fig. 2c) represents the likelihood distribution among the five population outcome classes for the species

across all lands, given both habitat and non-habitat influences. Both the environmental outcomes and population outcomes were carried into the environmental impact statement effects analysis.

Site-specific BBN and subwatershed BBN models were crafted for each species according to their individual ecological causal webs, that is, the unique array of KECs affecting their presence or abundance at these two scales. The Basin BBN was mostly a generic model applied to all species we evaluated. We chose to use a generic approach in part because there was neither time nor information available to customize population viability analyses for each species individually. Also, we suggest that the main components in our general Basin BBN model represent conditions common to all the species we evaluated that can affect viability of metapopulations: viz., extent of overall distributional range of the species, population concentration centers (“sources and sinks”), and dispersion or degree of isolation of populations (Fagen, 1988; Quinn and Hastings, 1987; Gilpin and Hanski, 1991; Grasman and Hillerislambers, 1997). We recognize the generality of our approach and welcome focused autoecological studies and species-specific viability analyses.

3.2. *Internal structure of the BBNs*

In each BBN, the input nodes (those without arrows pointing to them; also called parentless nodes) variously represented data taken from GIS themes, from inventories, as analyzed from other BBNs, or from expert judgment. That is, the input nodes in the site-specific BBN (Fig. 2a) would be taken from a site-specific inventory in the field. The input nodes in the subwatershed BBN (Fig. 2b) are taken from database calculations of habitat density (node HDI), or from GIS data (nodes P1 and P2) serving as proxies for the true KEC of the species (nodes KEC1 and KEC2). The habitat input nodes in the upper portion of the Basin BBN (nodes B, D, and E in Fig. 2c) are all taken from GIS post-processing of the subwatershed BBN across the entire study area, and the non-habitat input nodes in the lower portion of the Basin BBN (nodes H and K) can be taken from external population models or from expert judgment on potential small population effects and presence of other influential organisms.

CPTs for the example site-specific BBN are shown in Appendix B. CPTs can be defined using expert judgment by running the model, in part or whole, until each part of the model behaves according to expectations. CPTs also can be established or updated with empirical data of case examples, as available.

3.3. *Using BBNs for managing fish and wildlife*

We are using BBN species models to evaluate effects on fish and terrestrial vertebrates of planning alternatives for managing federal public lands within the Basin (Rieman et al., 2001; Raphael et al., 2001). BBN species models also can be used to help refine the planning alternatives by providing a feedback for determining conditions suited to given partial specification of the model. One way this can be done is by running the models in “most probable explanations” mode, which shows the most likely states for each node for which values are not explicitly specified.

A more reliable way to use the BBN species models for decision-making is to determine the decision with the highest utility given a stated outcome. This is done by incorporating the decision and utility nodes and specifying a desired outcome, such as 80% probability of a “high” population response. Through back-calculation in the model, the probability belief bars in the decision node then show the decision with the highest likelihood of producing that outcome. This approach assumes that the decision maker can accurately express their preference for one outcome over another, and for some acceptable probability of an outcome. The BBN presents another piece of information — the probability — that must be understood and interpreted by the decision-maker biologically and in socio-political terms.

3.4. *Representing uncertainty and prioritizing monitoring for adaptive management*

Mostly, however, the BBN species models provide a means of articulating what we ecologists think we know about the ecological causal web influencing vertebrate species. The model is a tool and an aid to help us represent ecological causal influences and uncertainties.

BBNs can help represent several kinds of uncertainty. In a sense, the probability distribution (CPT) in

Table 1
CPT for the node representing cave disturbance (node KEC2) in the example subwatershed wildlife BBN model (Fig. 2b)^a

Value of input node, predicted road density (node P2)	Probability of cave disturbance		
	Low	Moderate	High
None to very low	70	30	0
Low	40	40	20
Moderate	20	30	50
High to very high	10	30	60

^a Probabilities in this node denote the degree to which the GIS data on predicted road density (node P2) truly represent cave disturbance.

each node is a depiction of uncertainty. For example, in the subwatershed BBN model (Fig. 2b), the CPT for the node representing cave disturbance (node KEC2) represents the degree to which the GIS proxy variable of predicted road density (node P2) actually depicts cave disturbance. Although this was the best available GIS proxy variable, it provides a fairly poor prediction of cave disturbance, as the spread of probability values show (Table 1). Solving the network then represents, in a sense, how the propagation of that uncertainty affects the probability distribution of the final outcome. The probability distributions in the key environmental correlate nodes are unconditional probabilities, that is, not based on other random variables (although they can link to GIS proxy variables). The values of these prior probabilities can be determined by analyzing existing inventory or monitoring data to determine frequency distributions among the states for each environmental correlate. We used uniform priors because the actual value of each environmental correlate was provided for each site or subwatershed during analysis.

Another kind of uncertainty shown by BBNs is sampling error as denoted by a mean \pm standard deviation (S.D.) within individual nodes that are depicted as range states. Examples are shown at the bottom of some of the node boxes in Fig. 2b and c, where the values refer to the expected value and spread of uncertainty (S.D.) of the number of the states in each box. For example, in Fig. 2b, notice how the spread of uncertainty (S.D. values) increase in nodes HD1 (S.D. = 0), HD2 (S.D. = 0.54), and HD3 (S.D. = 0.62), as other factors are brought into the calculations.

A third type of uncertainty pertains to the sensitivity of specified nodes to values of other nodes. Sensitivity

testing can be used, for example, to determine the relative influence on a species outcome from an array of KECs, including human and natural disturbances. This is best done in BBNs by first setting probabilities to uniform for each input node and then running a sensitivity analysis. Sensitivity is defined as the expected reduction in variation of some query variable due to the conditional probability structure of the BBN and the specific value of the parent nodes.

As an example, in the site-specific BBN (Fig. 2a), we determined the sensitivity of local population response (node R) to the various KECs modeled for the species, that is, caves or mines, boulder piles, bridges or buildings, large snags or live trees, cliffs, and forest edges (Table 2). Since the BBN nodes have categorical states, the values in Table 2 are calculations of entropy reduction; with continuous value

Table 2

Results of a sensitivity analysis of the example site-specific wildlife BBN model (Fig. 2a). Values are calculations of entropy reduction^a; the greater the value, the greater the influence on the parameter of interest, in this case local population response (node R)

Influencing node	Entropy reduction value
KEC3: caves or mines	0.02902
KEC6: large snags or live trees	0.00953
KEC8: forest edges	0.00599
KEC7: cliffs	0.00599
KEC5: bridges or buildings	0.00063
KEC4: boulder piles	0.00002

^a Entropy reduction describes the expected reduction I in mutual information of a query variable Q due to a finding F , and is calculated as $I = \sum_q \sum_f P(q,f) \log[P(q,f)/P(f)]$, where q is a state of the query variable Q , f a state of the findings variable F , and the summations refer to the sum of all states q or f of variables Q or F .

states, one would use equivalent calculations for variance reduction (Pearl, 1991). Results suggest that the KEC having the greatest influence on local population response is caves and mines (node KEC3), which are critical for winter hibernacula and are also used as maternal roosts. Next most influential are snags and large trees. The least influential KEC is boulder piles. Thus for this species, the manager might want to prioritize local inventory efforts on caves and mines, and trees and snags, rather than on the other KECs listed in the model. Such a use of sensitivity analysis could be expanded to help the manager compare and select the best standards and guidelines for producing a desired outcome.

Sensitivity analysis can help identify the most influential decisions and KECs as one basis for guiding decision-making and for prioritizing monitoring activities. As data are gathered and incorporated as case files, thereby updating the CPTs within the model, new sensitivity tests can be run to determine the next most important factor to monitor or study. In this way, BBN species models, sensitivity testing, and prioritizing of monitoring studies can fit well into an adaptive management framework of incrementally learning by doing and testing.

4. Conclusions and recommendations

We found that BBNs were helpful for challenging us to articulate what we know about ecological influences on vertebrate species at various levels of geographic resolution, and to knit those influences into ecological causal webs. This is not often done in ecological modeling but, in our view, is a necessary first step in species viability analysis. We found that BBNs could be quickly structured and made operational by combining empirical information with expert experience to specify the probability tables for each node. BBN models can use categorical, ordinal scale, and continuous data in the same model, and can be easily updated with new data and from expert review.

Like many models in ecology, BBNs are crafted after an expert's mental map of how biological systems operate. We have not shown this here, but if experts disagree on the fundamental causal web underlying a species' response, each web can be modeled in

tandem and tested with empirical data for their prediction accuracy. Mostly, however, BBNs should be viewed as decision-aiding tools helpful for combining expert experience with available empirical data.

In the case of our models, we sought peer review and help from taxon-specific experts individually and in panels, outside our science team, to build and evaluate the site-specific and subwatershed models. With some general peer review, we developed the Basin BBN model to evaluate overall species viability. It is easy to build BBN models that reflect personal biases; we recognized this and sought extensive peer review and participation from outside experts throughout the process. At their best, BBNs, like any expert evaluation should be neither arbitrary nor mere opinion; it should provide solid rationale, synthesize existing data with experts' experience, and provide explicitly quantifiable hypotheses to be tested with validation studies. They should also provide a basis for understanding the types, sources, degrees, and implications of uncertainties in existing data and expert understanding.

We also found that incorporating decision and utility nodes and using sensitivity analysis greatly extended the models' usefulness as a basis for evaluating and refining planning alternatives and prioritizing species–environmental parameters for monitoring and further study. In this way, BBNs can be valuable tools for decision-making. Although, we did not find it necessary in our analysis, variants of a species model can be developed based on different experts or sets of experts, should there be legitimate disagreement on interpreting available data. These “competing models” can represent the range of expert opinion on causal webs of, and management effects on, a given species. In this way, the types and degrees of scientific uncertainty should be clearly explained to decision-makers. In some cases, where empirical data are truly lacking, a BBN is no better than a simpler statement of an educated guess, and in such cases we would not promote the use of BBNs per se, although they may still serve a useful purpose of organizing thinking and posing testable hypotheses.

However, we also found that many of the subwatershed scale BBN models began to look alike for different wildlife species because there was only a small pool of potential terrestrial GIS variables from which to draw. That is, most of the KECs in each

wildlife species' ecological causal web could not be analyzed with GIS data at the subwatershed scale, and would have to be relegated to site-specific BBN modeling.

BBN modeling has the disadvantage of not allowing feedback loops among variables, particularly from the response variable back to predictor variables. It is difficult to represent temporal or spatial dynamics and interactions in BBN models, and it is potentially easy to unduly overemphasize uncertain expert opinion. Where data exist, simulation models such as spatially explicit models of metapopulation dynamics (Pulliam and Dunning, 1995), which can better represent temporal or spatial dynamics, can nicely complement use of BBN models.

We found that several aspects of BBN model structure influence model operation and outcome: model depth (number of nodes from top to bottom); number of states in each node (as influencing sensitivity to input conditions); and how the CPTs are parameterized, that is, as either normalized probabilities (the usual case with expert opinion) or as absolute probabilities (as with empirical data).

In conclusion, BBNs can be useful for quickly modeling species influences, especially where empirical data on population demography are lacking. BBNs also provide a means of modeling fish and wildlife species in similar ways and provide a trackable, reviewable means of comparing effects of management decisions on vertebrate populations.

Acknowledgements

We benefited greatly from discussions and consultation with Tim Haas, David Cleaves, and Bruce Rieman. We also thank the members of an invited peer review panel of biologists and statisticians for their helpful discussions and suggestions: David Cleaves, Lisa Croft, Edward Guerrant Jr., Tim Hass, Andy Hansen, Danny Lee, Wayne Owen, Terry Rich, Nathan Schumacher, Bill Thompson, and Barb Wales.

Appendix A

BBN node levels and names as used in the figures.

We designed wildlife species BBN models with three levels of geographic resolution and six node shells.

Levels of geographic resolution:

1. Site-specific BBN model: local substrates and environmental conditions.
2. Subwatershed BBN model: subwatershed to sub-basin scale habitat capability and disturbances.
3. Basin BBN model: effects of basin-wide habitat distribution and abundance, and other disturbances on population viability.

Node shells and designations (and short names) (Fig. 1):

- Shell 1: decision nodes (Dec);
- Shell 2: GIS proxy nodes (P);
- Shell 3: key environmental correlate nodes (KEC);
- Shell 4: summary habitat nodes (SH);
- Shell 5: population response node (R);
- Shell 6: utility node (U)

Also, three HD nodes were used in the subwatershed BBN model (Fig. 2b):

- HD1 = habitat density
 - calculated as total area of suitable habitat divided by mean home range size;
- HD2 = adjusted habitat density
 - HD1 adjusted for broad-scale biophysical conditions;
- HD3 = realized adjusted habitat density
 - HD2 adjusted for broad-scale human disturbance effects.

The four BBN models presented in Figs. 1 and 2 for use with Netica (Norsys) are available at <http://www.spiritone.com/~brucem/bbns.htm>.

Appendix B

Conditional probability tables (CPTs) from the site-specific BBN example model on Townsend's big-eared bat (*C. townsendii*) in the interior Columbia River basin, USA (Fig. 2a). Utility, proxy, and decision nodes are not explicitly shown in this particular model.

Note that two parentless nodes in Fig. 2a (KEC3a and KEC3b) are shown as having uniform prior probabilities, and the other parentless nodes (KEC3–KEC8) are shown in Fig. 2a forced to one state, even though their

prior probability distributions as listed below are also uniform. This is because Fig. 2a shows one possible model run for a hypothetical location where the states of all KECs are known except for cave temperature.

B.1. Shell 3: key environmental correlate nodes

KEC3: caves or mines (type of node: state of nature with discrete states)	
Present	0.5
Absent	0.5
KEC3a: temperature (°C) in hibernacula (type of node: state of nature with continuous value states)	
More than 13	0.333333
–2 to 13	0.333333
Less than –2	0.333333
KEC3b: temperature (°C) in maternal roosts (type of node: state of nature with continuous value states)	
More than 30	0.333333
20–30	0.333333
Less than 20	0.333333
KEC4: boulder piles (type of node: state of nature with discrete states)	
Present	0.5
Absent	0.5
KEC5: bridges or buildings (type of node: state of nature with discrete states)	
Present	0.5
Absent	0.5
KEC6: large snags or live trees (type of node: state of nature with discrete states)	
Present	0.5
Absent	0.5
KEC7: cliffs (type of node: state of nature with discrete states)	
Present	0.5
Absent	0.5
KEC8: forest edges (type of node: state of nature with discrete states)	
Present	0.5
Absent	0.5

B.2. Shell 4: summary habitat nodes (SH) and habitat density nodes (HD)

Adequate	Inadequate	KEC3	KEC3a
SH1: hibernacula (type of node: state of nature, with discrete states)			
0.1	0.9	Present	More than 13
1	0	Present	–2 to 13
0.1	0.9	Present	Less than –2
0	1	Absent	More than 13
0	1	Absent	–2 to 13
0	1	Absent	Less than –2

B.2. Shell 4: (Continue)

Adequate	Inadequate	KEC4	KEC5	KEC3	KEC6
SH2: summer roosts (type of node: state of nature, with discrete states)					
1	0	Present	Present	Present	Present
0.95	0.05	Present	Present	Present	Absent
0.9	0.1	Present	Present	Absent	Present
0.85	0.15	Present	Present	Absent	Absent
0.95	0.05	Present	Absent	Present	Present
0.95	0.05	Present	Absent	Present	Absent
0.8	0.2	Present	Absent	Absent	Present
0.05	0.95	Present	Absent	Absent	Absent
1	0	Absent	Present	Present	Present
0.9	0.1	Absent	Present	Present	Absent
0.9	0.1	Absent	Present	Absent	Present
0.8	0.2	Absent	Present	Absent	Absent
0.95	0.05	Absent	Absent	Present	Present
0.9	0.1	Absent	Absent	Present	Absent
0.7	0.3	Absent	Absent	Absent	Present
0	1	Absent	Absent	Absent	Absent
Adequate	Inadequate	KEC3	KEC6	KEC3b	
SH3: maternal roosts (type of node: state of nature with discrete states)					
0.8	0.2	Present	Present	More than 30	
1	0	Present	Present	20–30	
0.8	0.2	Present	Present	Less than 20	
0.1	0.9	Present	Absent	More than 30	
1	0	Present	Absent	20–30	
0.1	0.9	Present	Absent	Less than 20	
0.7	0.3	Absent	Present	More than 30	
0.7	0.3	Absent	Present	20–30	
0.7	0.3	Absent	Present	Less than 20	
0	1	Absent	Absent	More than 30	
0	1	Absent	Absent	20–30	
0	1	Absent	Absent	Less than 20	
Adequate	Inadequate	KEC8	KEC7		
SH4: foraging sites (type of node: state of nature with discrete states)					
1	0	Present	Present		
0.8	0.2	Present	Absent		
0.8	0.2	Absent	Present		
0	1	Absent	Absent		

B.3. Shell 5: population response node (R)

High	Low	SH2	SH4	SH3	SH1
R: local (site-specific) population response (type of node: state of nature with discrete states)					
1	0	Adequate	Adequate	Adequate	Adequate
0.2	0.8	Adequate	Adequate	Adequate	Inadequate
0.2	0.8	Adequate	Adequate	Inadequate	Adequate
0.2	0.8	Adequate	Adequate	Inadequate	Inadequate
0.2	0.8	Adequate	Inadequate	Adequate	Adequate
0.2	0.8	Adequate	Inadequate	Adequate	Inadequate
0.1	0.9	Adequate	Inadequate	Inadequate	Adequate
0.1	0.9	Adequate	Inadequate	Inadequate	Inadequate
0.2	0.8	Inadequate	Adequate	Adequate	Adequate
0.2	0.8	Inadequate	Adequate	Adequate	Inadequate
0.1	0.9	Inadequate	Adequate	Inadequate	Adequate
0.1	0.9	Inadequate	Adequate	Inadequate	Inadequate
0.1	0.9	Inadequate	Inadequate	Adequate	Adequate
0.1	0.9	Inadequate	Inadequate	Adequate	Inadequate
0	1	Inadequate	Inadequate	Inadequate	Adequate
0	1	Inadequate	Inadequate	Inadequate	Inadequate

References

- Boyce, M., 1992. Population viability analysis. *Ann. Rev. Ecol. Syst.* 23, 481–506.
- Castillo, E., Gutierrez, J.M., Hadi, A.S., 1997. *Expert Systems and Probabilistic Network Models*. Springer, New York, 605 pp.
- Charniak, E., 1991. Bayesian networks without tears. *AI Mag.* 12 (4), 50–63.
- Cohen, Y., 1988. Bayesian estimation of clutch size for scientific and management purposes. *J. Wildl. Manage.* 52 (4), 787–793.
- Crome, F.H.J., Thomas, M.R., Moore, L.A., 1996. A novel Bayesian approach to assessing impacts of rain forest logging. *Ecol. Appl.* 6 (4), 1104–1123.
- Dennis, B., 1996. Discussion: should ecologists become Bayesians? *Ecol. Appl.* 6 (4), 1095–1103.
- Dixon, P., Ellison, A.M., 1996. Introduction: ecological applications of Bayesian inference. *Ecol. Appl.* 6 (4), 1034–1035.
- Ellison, A.M., 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. *Ecol. Appl.* 6 (4), 1036–1046.
- Fagen, R., 1988. Population effects of habitat change: a quantitative assessment. *J. Wildl. Manage.* 52, 41–46.
- FEMAT, 1993. *Forest ecosystem management: an ecological, economic, and social assessment*. Report of the Forest Ecosystem Management Assessment Team. US Government Printing Office, Washington, DC (chapters numbered separately).
- Gilpin, M.E., Hanski, I. (Eds.), 1991. *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, Orlando, FL, 336 pp.
- Grasman, J., Hillerislambers, R., 1997. On local extinction in a metapopulation. *Ecol. Model.* 103, 71–80.
- Haas, T.C., 1991. Partial validation of Bayesian belief network advisory systems. *AI Appl.* 5 (4), 59–71.
- Haas, T.C., 1992. A Bayes network model of district ranger decision making. *AI Appl.* 6 (3), 72–88.
- Haas, T.C., Mowrer, H.T., Shepperd, W.D., 1994. Modeling aspen stand growth with a temporal Bayes network. *AI Appl.* 8 (1), 15–28.
- Heckerman, D., Geiger, D., Chickering, D.M., 1994. Learning Bayesian networks: the combination of knowledge and statistical data. In: de Mantaras, R.L., Poole, D. (Eds.), *Uncertainty in Artificial Intelligence*. Proceedings of the 10th Conference. Morgan Kaufmann, San Francisco, CA, University of Washington, Seattle, WA, pp. 293–301.
- Jensen, F.V., 1996. *An Introduction to Bayesian Networks*. Springer, New York.
- Lee, D.C., Rieman, B.E., 1997. Population viability assessment of salmonids by using probabilistic networks. *N. Am. J. Fish. Manage.* 17, 1144–1157.
- Lehmkuhl, J.F., Raphael, M.G., Holthausen, R.S., Hickenbottom, J.R., Naney, R.H., Shelly, J.S., 1997. Historical and current status of terrestrial species and the effects of the proposed alternatives. In: Quigley, T.M., Lee, K.M., Arbelbide, S.J.

- (Tech. Eds.), Evaluation of EIS Alternatives by the Science Integration Team. General Technical Report PNW-GTR-406. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 537–730.
- Marcot, B.G., 1998. Selecting appropriate statistical procedures and asking the right questions: a synthesis. In: Sit, V., Taylor, B. (Eds.), *Statistical Methods for Adaptive Management Studies*. BC Ministry of Forests Research Branch, Victoria, BC, pp. 129–142. <http://www.for.gov.bc.ca/hfd/pubs/docs/lmh/lmh42.htm>.
- Marcot, B.G., Castellano, M.A., Christy, J.A., Croft, L.K., Lehmkuhl, J.F., Naney, R.H., Nelson, K., Niwa, C.G., Rosentreter, R.E., Sandquist, R.E., Wales, B.C., Zieroth, E., 1997. Terrestrial ecology assessment. In: Quigley, T.M., Arbelbide, S.J. (Tech. Eds.), *An Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins, Vol. III*. General Technical Report PNW-GTR-405. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 1497–1713.
- Morawski, P., 1989. Understanding Bayesian belief networks. *AI Expert* (May), 44–48.
- Oliver, R.M., Smith, J.Q. (Eds.), 1990. *Influence Diagrams, Belief Nets and Decision Analysis*. Wiley, Chichester, UK.
- Olson, R.L., Willers, J.L., Wagner, T.L., 1990. A framework for modeling uncertain reasoning in ecosystem management. II. Bayesian belief networks. *AI Appl. Nat. Resour. Manage.* 4 (4), 11–24.
- Pearl, J., 1991. *Probabilistic Reasoning in Intelligent Systems: Networks of Plausible Inference*, 2nd Edition. Morgan Kaufmann, San Mateo, CA.
- Press, S.J., 1989. *Bayesian Statistics: Principles, Models, and Applications*. Wiley, New York, 237 pp.
- Pulliam, H.R., Dunning, J.B., 1995. Spatially explicit population models. *Ecol. Appl.* 5 (1), 2.
- Quinn, J.F., Hastings, A., 1987. Extinction in subdivided habitats. *Conserv. Biol.* 1, 198–209.
- Raphael, M.G., Wisdom, M.J., Rowland, M.M., Holthausen, R.S., Wales, B.C., Marcot, B.G., Rich, T.D., 2001. Status and trends of habitats of terrestrial vertebrates in relation to land management in the interior Columbia River basin. *For. Ecol. Manage.* 153, 29–42.
- Rieman, B., Peterson, J.T., Clayton, J., Howell, P., Thurow, R., Thompson, W., Lee, D., 2001. Evaluation of potential effects of federal land management alternatives on trends of salmonids and their habitats in the interior Columbia River basin. *For. Ecol. Manage.* 153, 43–62.
- Spiegelhalter, D.J., Dawid, A.P., Lauritzen, S.L., Cowell, R.G., 1993. Bayesian analysis in expert systems. *Statist. Sci.* 8 (3), 219–283.
- Wisdom, M.J., Holthausen, R.S., Wales, B.C., Hargis, C.D., Saab, V.A., Lee, D.C., Hann, W.J., Rich, T.D., Rowland, M.M., Murphy, W.J., Eames, M.R., 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia basin: broad-scale trends and management implications. General Technical Report PNW-GTR-485. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Wolfson, L.J., Kadane, J.B., Small, M.J., 1996. Bayesian environmental policy decisions: two case studies. *Ecol. Appl.* 6 (4), 1056–1066.