Predicting Species Occurrences

Issues of Accuracy and Scale

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CHAPTER

16

Wildlife Habitat Modeling in an Adaptive Framework: The Role of Alternative Models

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Habitat relationship models (e.g., Verner et al. 1986b; henceforward habitat models) purport to establish a quantitative relationship between measures of the physical and vegetation characteristics of a *habitat* (Morrison and Hall, Chapter 2), including vegetation composition, structure, and spatial arrangement of surrounding habitats, and the presence or absence, abundance, or persistence of one or more species in a *landscape* (Morrison and Hall, Chapter 2). With the rapid development of geographic information systems (GIS) and associated computing algorithms, it is now possible to encode mathematical rules describing presumed habitat-population relationships and to rapidly perform complex analyses of the predicted impacts of various arrangements of land cover and vegetation characteristics. For instance, presumed habitat-species occurrence relationships are a crucial part of gap analysis (Scott et al. 1993), as well as forest-planning tools such as FORPLAN (Johnson et al. 1980).

In this chapter, we review some approaches used to evaluate the accuracy and predictive ability of habitat models. We suggest that standard model validation approaches are ambiguous and that assessment of the reliability of habitat models is most meaningful when models are a part of formal optimization procedures in which management actions are selected so as to achieve a specific, quantitative objective. Decision theoretical methods allow for the incorporation of sources of uncertainty in this process, one of which is model reliability. Finally, we think that most conservation decisions are based on a relatively small number of assumptions about ecological pattern and process, and that formal consideration of models based on alternative assumptions is needed. Habitat models can be thought of as tools for translating alternative assumptions into testable predictions, and management can be thought of as the means of providing the experiment under which model predictions can be tested and models and decisions adaptively improved.

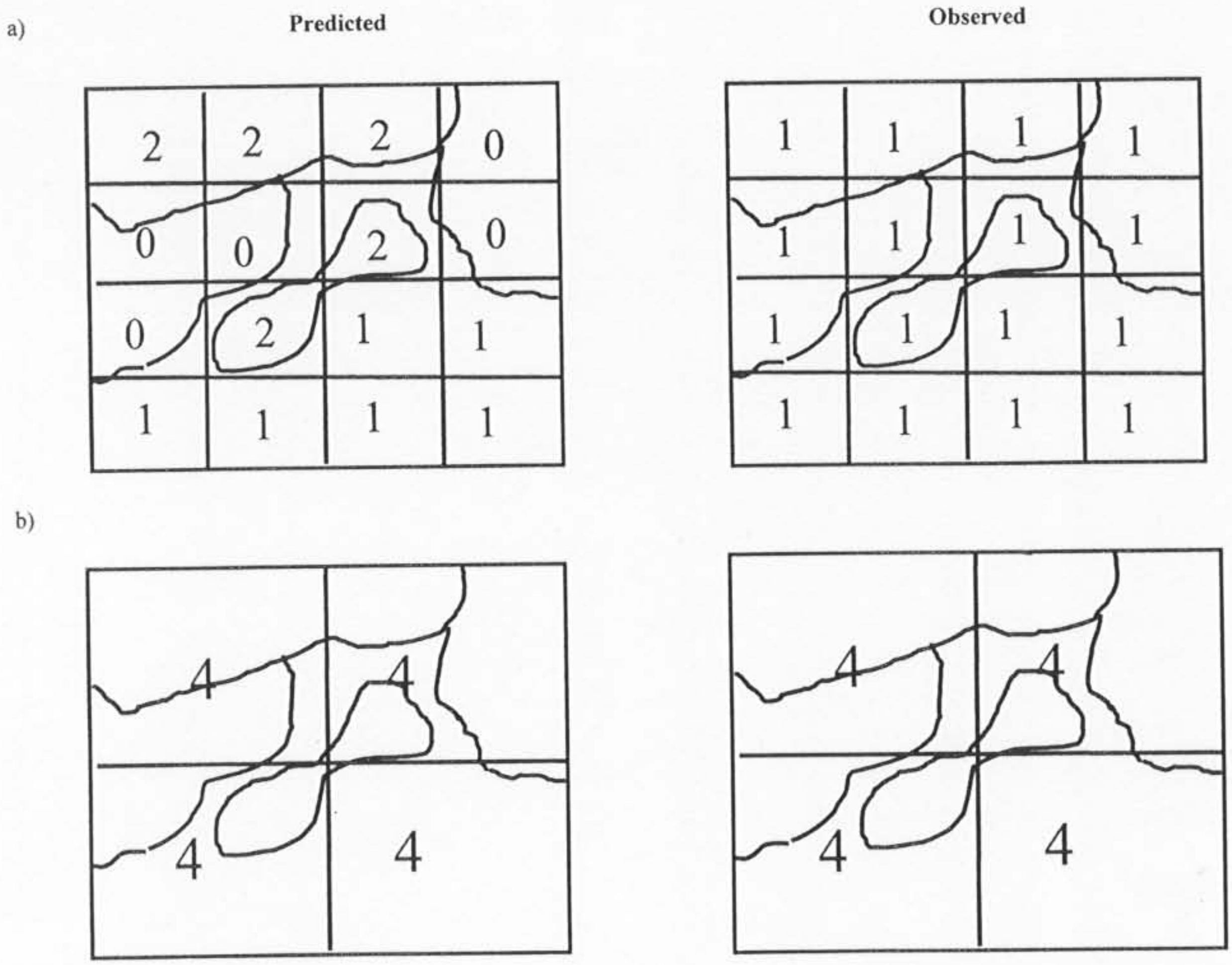
Assessing Model Reliability

It is not our intent to provide an exhaustive review either of model assessment in general or of habitat models in particular. Nonetheless, several commonly agreed-upon principles will be relevant to the ensuing discussion. Model *parameterization*, *verification*, and *calibration* (Morrison and Hall, Chapter 2) are all critical parts of model development (Conroy et al. 1995). In practice, each of these steps, even if taken, may be inadequate to assure a model's reliability. For example, model verification demonstrates neither the truth nor the usefulness of a model, only the model's internal consistency; thus, a verified model may nonetheless be inadequate for management if it is based upon faulty assumptions or logic. Likewise, statistical estimates of model parameters often cannot be obtained, especially when key model states or parameters simply cannot be observed, as is frequently the case for highly parameterized models (e.g., spatially explicit population models; Conroy et al. 1995; Dunning et al. 1995; Pulliam et al. 1992). One approach is to use values based on general knowledge or assumptions about the animal's life history, which are then adjusted so as to provide overall model agreement with observations. However, the resulting parameter values are not bona fide statistical estimates, are likely not unique, and may not have biological meaning. A more serious concern is the likelihood that prediction beyond the range of data used to calibrate the model, frequently necessary in management, may prove unreliable.

Regardless of the method of model calibration, there remains the issue of whether the model will in fact be useful for making management decisions (Van Horne, Chapter 4). *Validation* (Morrison and Hall, Chapter 2) probes beyond whether the model appears reasonable, and fits data; it also examines how well the model might perform under conditions different from those in which the model was constructed. However, validation can be difficult in practice, for several reasons. First, statistical uncertainty in the data, imprecision in model predictions, or both may result in low power of statistical validation tests to discriminate between observations and predictions (Mayer and Butler 1993). Thus, failure to reject the null hypothesis that the model and data agree is weak support in favor of the model; in fact, it might simply be an artifact of insufficient sampling effort. Second, field measurements must be of appropriate resolution to validate a habitat model. Consider an artificial example of a species existing in a landscape containing three habitat types, each with different predicted values (under a habitat model) for the species, depending on the *habitat quality* (Morrison and Hall, Chapter 2): high (predicted number = 2/10 hectares), marginal (predicted number = 1/10 hectares), and low (predicted number = 0/10 hectares) (Fig. 16.1a). Suppose we are capable of exactly enumerating the population in each 10-hectare block, and we observe one animal in each block. Under this scenario, we would have obtained a poor correspondence between the model predictions and observations, with the numbers agreeing in only 44 percent (six of sixteen) of the comparisons. We would probably conclude that this model was "invalid," or in other words was a poor representation of the relationship between habitat and abundance. Suppose instead that we were only capable of counting the total number of animals on each 40-hectare block (but could do so without error) and were incapable of assigning these counts to habitats other than the array of habitats occurring in each 40-hectare block (Fig. 16.1b). Under this scenario, we would have 100-percent agreement between the model predictions and observations and might be inclined to consider this a valid model.

The above artificial example, while highly contrived, illustrates the point that the selection of the spatial scale is a subjective matter (Trani, Chapter 11) but one that may strongly influence the outcome of model validation (Laymon and Reid 1986; Elith and Burgman, Chapter 24). Reliance upon presence/absence statistics in lieu of counts is another form of coarsening of the data that may result in apparent concurrence between model and data when finer resolution of the latter may have resulted in model rejection. At an even finer resolution, predictions based on abundance or density alone will be inadequate for validating source-sink or other models in which habitat quality cannot be inferred from density, regardless of spatial scale (Pulliam 1988; Van Horne 1983; Conroy and Noon 1996; Maurer, Chapter 9).

Sensitivity analysis (Morrison and Hall, Chapter 2) is often advocated as a practical alternative to true validation. However, these arguments are frequently not convincing, particularly if a model is to be used in decision making. Rather than assuring decision makers of the robustness of the model and of GIS, insensitivity to input errors should be a warning that the model also may be insensitive with respect to making predictions. For some applications, it may be sufficient that the model is capable of ordering alternative management actions, with respect to their relative impact on the resource objective (Hamilton and Moller 1995). However, we are less sanguine than Hamilton and Moller (1995) about even this utility for models and instead propose that unverified assumptions and unreliable parameter values may render as unreliable



a) Predicted

2	2	2	0
0	0	2	0
0	2	1	1
1	1	1	1

a) Observed

1	1	1	1
1	1	1	1
1	1	1	1
1	1	1	1

b) Predicted

4	4
4	4

b) Observed

4	4
4	4

Figure 16.1. Hypothetical comparison between predictions of a simple landscape model and observations under a null model of no habitat affinity; cell values represent predicted and observed counts (a) by 10-hectare block, (b) by 40-hectare block.

even ordinal statements about the relative impacts of various management alternatives; an example of how this might occur follows.

The Role of Alternative Models

As seen in the previous section, validation of habitat models presents serious methodological challenges. However, validation alone cannot resolve whether the model under consideration is superior to a plausible alternative model, in particular, a model that may imply a different course of management. We address this issue in a more appropriate decision-making context. Assume that we have a model (M) and an alternative model (M'), and that both models are plausible, that is, at least some theoretical or empirical support exists for each (e.g., Pascual et al. 1997). It may be that we have performed model validation tests and both models are valid (i.e., neither model is rejected in comparison to the data available). A natural question for a decision maker is: what difference will it make to my decision if I place full faith in model M versus if I place full faith in model M'?

A simple illustration can be used to make this point by returning to the artificial example in Figure 16.1. Suppose that M corresponds to the model predicting that the species has specific affinities, as predicted by the map in Figure 16.1a ("*Predicted*") and that model

M' corresponds to the situation in Figure 16.1a ("*Observed*") in which the species is distributed perfectly evenly among the sixteen 10-hectare blocks. Clearly, belief in one or the other of these models will make a difference in how habitats should be managed. Under the M scenario, management presumably would be directed toward certain habitats—in other words those that are preferred by the species, assuming a goal of conserving this species. Under the M' scenario, management favoring these habitats would appear to be unwarranted, particularly given that such management would no doubt have inherent costs (e.g., tradeoffs with other objectives). Clearly, from the standpoint of decision making, injudicious choice of the spatial scale for model prediction might potentially result in a critical loss of information.

Note that, depending on the scale at which observations are made, the models are both valid and therefore equally plausible (Fig. 16.1b), or one model appears to have more empirical support than the other (Fig. 16.1a). Thus, the usual approach for validation—of comparing predictions with independent observations—may be indeterminate, depending on the scale chosen. Also, note that sensitivity analysis contributes little to the resolution of model uncertainty. The fact that either model, or both, depending on the spatial scale, is relatively more or less sensitive to changes in parameter values sheds no light upon the question of which (if either) model will better inform decision making.

Decision Making under Uncertainty

If habitat or other models are to be useful to managers, they must be capable of making predictions about the consequences of management decisions that are better than the educated guesses that managers would make on their own in the absence of models. The fact that mathematical algorithms can join together hundreds or thousands of habitat models and rapidly display the results using GIS should be small comfort if critical model components are poorly substantiated by evidence (Van Horne, Chapter 4). Even in those cases where models seem to do a reasonable job of prediction, our earlier discussion should convince readers of the risks of blind application of valid models to decision-making problems.

On the other hand, we recognize that decisions must be made and that imperfect models, validated at inappropriate scales of resolution, or perhaps not at all, may be all that are available. Even under ideal circumstances, assumptions about biological mechanisms will not be perfectly understood, and thus it will not be possible to make unambiguous predictions about the impacts of management decisions whether or not models are used to make these predictions. Obviously, biological systems, even if well understood, are subject to intrinsic variability, but of special concern here is what we term *structural uncertainty*. That is, more than one mechanism (or model) might plausibly explain and predict the potential response of the system to management, and we are uncertain as to which is better *for a given management goal*. Formally, we are faced with making a decision or action, a, from a set of possible or feasible decisions $a \in \{a_1, a_2, \ldots, a_n\}$. Any decision we make will result in an outcome that will have a value to us, which we will denote as $u(a)$. This value may be in terms of species conservation, economic gain, or perhaps a tradeoff between one or more goals (e.g., species conservation versus economic gain). Assuming that such an objective value can be ascertained or agreed upon, a rational decision maker (Lindley 1985) will seek to select that decision that will result in the greatest value for the objective. However, uncertainty exists as to what the actual objective value or utility will be for any decision. First, consider uncertainty induced by environmental or demographic variability. Let $\mathrm{E}[u(a|\theta)]$ represent the average or expected value or utility of decision a, assuming that a particular model or parameter value (represented by θ) is known to be true. This value is obtained by averaging over the statistical distribution of uncertain outcomes x resulting from each possible decision a

$$E[u(a|\theta)] = \int_x u(a|x; \theta)\, f(x|\theta)\, dx \quad \text{for } a \in \{a_1, a_2, \ldots, a_n\}$$

where $u(a|x; \theta)$ is the value of decision a given outcome x under model θ and $f(x|\theta)$ is a statistical distribution of these outcomes, where θ is assumed known.

Until this point, we have assumed that the model (as expressed by $f(x|\theta)$) is correctly specified, and that any deviations of model predictions from outcomes must be due to environmental or demographic factors.

Here we switch our focus to structural (model) uncertainty. Let $p(\theta_i)$ represent a probability distribution reflecting our uncertainty in θ, which takes on values θ_i, $i = 1, \ldots, m$ under each of m alternative models. This uncertainty may include statistical error, but more generally includes bias due to incorrect model assumptions. The average value of the decision is now

$$E[u(a)] = \sum_{i=1}^{m} \int_{x} u(a|x;\theta_i)\, p(\theta_i) f(x|\theta_i) dx \qquad (16.1)$$

$$\text{for } a \in \{a_1, a_2, \ldots, a_n\}$$

$\sum_{i=1}^{m} p(\theta_i) = 1$; when θ is continuous, the summation operator changes to integration over θ. By definition, the optimal decision satisfies

$$\max_{a} E[u(a)]$$

and must be found by averaging over the uncertain environmental and demographic conditions (i.e., values of x) and structural uncertainty (i.e., values of θ). Ignoring either source of uncertainty will result in suboptimal decision making. Conversely, reduction of either source of uncertainty will improve decision making. Obviously, there is little that can be done about environmental and demographic uncertainty, beyond including components of each in the decision-making model.

On the other hand, structural uncertainty *can* be reduced, theoretically to zero, if additional information (data) can be obtained that places higher probability on certain model structures (values of θ) than on others. We describe below how this source of uncertainty can be reduced via adaptive management. For now, we focus on the impact of structural uncertainty on decision making. Consider a case where an optimal decision a is sought, and consider only the average response across environmental and demographic conditions, assuming that a given model of ecological processes is true. Suppose that there are two alternative models of this process, which we shall label θ_1 and θ_2, and that our degree of belief in each model is $p(\theta_1)$ and $p(\theta_2) = 1 - p(\theta_1)$, respectively. The expected value of any candidate decision a, taking into account only structural uncertainty, is

$$E[u(a)] = u(a|\theta_1)p(\theta_1) + u(a|\theta_2)p(\theta_2).$$

Clearly, structural uncertainty exists any time that $0 < p(\theta_1) < 1$. However, notice that this uncertainty is only important in the decision-making process to the extent that the values of the resulting decisions would be different, or in other words

$$u(a|\theta_1) \neq u(a|\theta_2).$$

Conversely, if the models predict the same outcome for any given decision, or if that outcome is equally valued to the decision maker, then uncertainty about the ecological process is not relevant to the decision process. This can be illustrated by a simple numerical example. Suppose that for each of the above two model structures we obtain values for decision a of $u(a|\theta_1) = 4$ and $u(a|\theta_2) = 7$. Suppose that there is a competing decision, a', for which the corresponding values are $u(a'|\theta_1) = 6$ and $u(a'|\theta_2) = 4$. If there is complete uncertainty about which model correctly describes the process, then $p(\theta_1) = p(\theta_2) = 0.5$ and the values for each decision are given by

$$E[u(a)] = 4(0.5) + 7(0.5) = 5.5$$

and

$$E[u(a')] = 6(0.5) + 4(0.5) = 5.$$

Therefore, the optimal decision is a. Suppose however that additional knowledge accumulates (e.g., from a monitoring program carried out on the managed system) so as to place more faith in model 1, such that $p(\theta_1) = 0.8$. Now the decision values are

$$E[u(a)] = 4(0.8) + 7(0.2) = 4.6$$

and

$$E[u(a')] = 6(0.8) + 4(0.2) = 5.6$$

and the optimal decision is now a'. This approach thus places the issue of model reliability (and its resolution) squarely in the context of optimal decision making. That is, we are no longer comparing a single model to an arbitrary measure of accuracy but instead are asking which decision should we make given two or more plausible models and an assessment of relative belief in each model. In some cases (e.g., where theory or data provide justification), we may be justified in giving one model more weight; in others (e.g., either model is theoretically justifiable, and both seem valid given current data), we may not. In either instance, we have an objective means for making a decision, taking into account model uncertainty.

Adaptive Management

As shown above, model uncertainty must be considered, along with other sources of uncertainty, in making optimal conservation decisions. Because our knowledge of systems will always be imperfect, and parameters will always be estimated with error, model uncertainty can never be eliminated. However, model uncertainty can and should be reduced. One method to reduce model uncertainty is adaptive optimization, as incorporated as a part of adaptive resource management (Walters 1986). The basic steps of adaptive optimization are

1. Define a resource objective (e.g., species conservation, as above)
2. Delineate a set of feasible management alternatives $\{a_1, a_2, \ldots, a_n\}$
3. Develop models $\theta \in \{\theta_1, \theta_2, \theta_3, \ldots, \theta_m\}$ that predict the impact of the decision on the objective
4. Identify and quantify the relevant sources of uncertainty in (3)
5. Implement the decision that appears to be optimal given (4)
6. Compare predictions under each model to data ($\underline{x}$) collected following management
7. Compute a likelihood $L(\underline{x}|\theta)$ for each model given these data; these likelihoods reflect the relative agreement of the observed data to the predictions of each model
8. Update the model probabilities from Bayes' Theorem

   $$p(\theta_i|\underline{x}) = \frac{p(\theta_i)L(\underline{x}|\theta_i)}{\sum_{j=1}^{m} p(\theta_j)L(\underline{x}|\theta_j)}; \theta_i \in \{\theta_1, \theta_2, \ldots, \theta_m\}, \quad (16.2)$$

   where $p(\theta_i \mid \underline{x})$ is the posterior probability of θ_i, conditioned on having observed the data $\underline{x}$
9. Incorporate these new model weights in prediction and decision making at the next decision opportunity

Thus, adaptive resource management provides a mechanism for feedback of information following management, which in turn reduces model uncertainty and promotes further understanding of system processes. Because of the long-term nature of many conservation problems, that feedback may be slow or may not occur at all at a given location (e.g., once a reserve is built, there will likely be little interest in revisiting the decision). However, knowledge gained through monitoring one system should inform future decision making in similar systems. In other conservation problems, for instance those involving forest cutting practices, decisions may be regularly revisited and the information gained from one decision cycle will provide direct feedback for future decision cycles.

Case Study: Habitat Management for Population Persistence under Uncertainty

We illustrate the above principles with an example of landscape management in which the objective is the maintenance of populations of two forest species. The two species have resource needs that pose a potential conflict for management in the sense that provision of resources for one species may remove resources for the other. This example, although hypothetical, is similar to a problem we are currently investigating involving forest management in the Piedmont National Wildlife Refuge (PNWR) in central Georgia. At PNWR, a primary management emphasis is that of maintaining viable populations of the endangered red-cockaded woodpecker (*Picoides borealis*, henceforth woodpeckers), with the long-term goal of tripling the 1998 refuge population (Richardson et al. 1998). However, concern exists that aggressive management favoring woodpeckers, including maintenance of low densities of understory and midstory vegetation via prescribed burning, may adversely affect species of birds and other organisms that depend on these vegetative strata for shelter, foraging, or nesting. Previous research (Powell et al. 2000) has addressed the specific concern that woodpecker habitat management reduces fitness of the wood thrush (*Hylocichla mustelina*, henceforth thrushes) as measured by adult and juvenile survival and reproduction rates. Results to date suggest that woodpecker management, at least as currently practiced at PNWR, has minimal if any impact on thrush fitness. However, this system exhibits great spatial and temporal variability in demographic parameters, which together with estimation error induces uncertainty in these conclusions. Further, there is no assurance that results observed by Powell et al. (2000) would extend to a more aggressive management regime than that which occurred during the study. Current understanding of the effects of woodpecker management (e.g., Richardson et al. 1998) may be inadequate to accurately predict whether such management would enhance the long-term viability of woodpeckers—the primary goal of its management. These factors, taken together, suggest that forest management at PNWR and similar systems, in addition to being influenced by system uncertainty and statistical error, may be relatively sensitive to structural assumptions in models used to predict the impact of management decisions on objective values that include both a woodpecker component and a component reflecting other resource goals.

We describe a simplified, artificial system that nonetheless captures some of the essential elements of management at PNWR. Here we reduce the resource management objective to a tradeoff between a species favored by understory vegetation reduction (represented by woodpeckers) and another favored by its retention (represented by thrushes). However, the statements that "woodpeckers are favored by burning" and "thrushes are favored by exclusion of burning" result from assumptions in the models underpinning the decision analysis. We thus formulated explicit alternatives to these assumptions to mimic extremes in the relationship between population response and management that might be consistent with real field data. Specifically, we considered alternatives that propose that populations do not respond to management actions. We incorporated these different hypotheses in eight alternative models, as described below.

System Features and General Assumptions

The landscape was represented as a 10×10 square grid. Any cell in the grid could be occupied by a woodpecker, a thrush, or by both species. From an initial distribution of woodpeckers within the landscape, models predict a resulting distribution of woodpeckers following a single 10-year time step. These models alternatively suggest that woodpecker population growth is, or is not, dependent on distance to nearest-neighbor source sites, and is, or is not, dependent on woodpecker response to habitat management through controlled burning. In contrast, we model thrush occupancy only in a habitat-suitability context and do not consider an initial distribution of thrush. That is, following management a thrush occurs in a cell with probability that does, or does not, depend on the burning status of that cell. Generally, we want to maximize population growth of woodpeckers and density of thrushes through appropriate selection of one of a few decision alternatives. Our aim is to look at every alternative for each combination of models and for certain initial distributions of woodpeckers.

Habitat-occupancy Models

For the woodpecker, we modeled single-time-step cell occupation probabilities conditional on current cell occupation status, habitat treatment, and distance to nearest occupied cell. That is, we built expressions for the conditional probabilities

$$\Pr\{X_i(1) = x_1 | X_i(0) = x_0,\ d_i(0) = d_0,\ H_i = h_i\},$$

where $X_i(t)$ is a random variable indicating occupation status of landscape cell i at time t, $x_t = 0$ (unoccupied) or 1 (occupied), $d_i(0)$ is the decision variable for cell i, d_0 is the decision value (1 = burned, 0 = not burned), H_i is a random variable, and h_i is a distance value.

Given that landscape cell i is currently occupied by a woodpecker (i.e., $X_i(0) = 1$), we used the following expression as the model of cell occupancy probability at time 1:

$$\Pr\{X_i(1) = 1 \mid X_i(0) = 1, d_i(0) = d_0\} = \begin{cases} p_0,\ d_0 = 1 \\ p_0',\ d_0 = 0 \end{cases} \qquad (16.3)$$

where p_0 and p_0' are user-selected probabilities. Because $x_t = 0$ or 1, $\Pr\{X_i(1) = 0 \mid X_i(0) = 1,\ d_i(0) = d_0\} = 1 - \Pr\{X_i(1) = 1 \mid X_i(0) = 1,\ d_i(0) = d_0\}$. Thus, the probability of woodpecker persistence is sensitive to the management decision, where the degree of sensitivity is reflected in the difference $p_0 - p_0'$.

Given that landscape cell i is not currently occupied by a woodpecker, we expressed the probability of cell i being colonized at time 1 as a function of distance h_i to the nearest occupied cell and burning status for cell i:

$$\Pr\{X_i(1)=1 \mid X_i(0)=0, d_i(0)=d_0, H_i=h_i\} = \begin{cases} e^{-h_i/\beta}, & d_0=1 \\ e^{-h_i/\alpha\beta}, & d_0=0 \end{cases} \tag{16.4}$$

where α and β are user-controlled parameters. Thus, woodpecker colonization probability is partially dependent on the spatial distribution of woodpeckers. We proposed an alternative model in which colonization probability was not sensitive to h_i:

$$\Pr\{X_i(1)=1 \mid X_i(0)=0, d_i(0)=d_0\} = \begin{cases} \beta(1-e^{-a/\beta})/a, & d_0=1 \\ \alpha\beta(1-e^{-a/\alpha\beta})/a, & d_0=0 \end{cases} \tag{16.5}$$

where a is a user-controlled parameter. We derived this model by integrating the functions in equation 16.4 over the interval 0 to a and then dividing the result by the length of the interval to obtain a uniform probability mass over 0 to a.

For both the woodpecker persistence and the colonization models, we considered forms in which occupation probabilities were not dependent on the habitat decision. For the persistence model, we used the expression

$$\Pr\{X_i(1) = 1 \mid X_i(0) = 1\} = (p_0 + p_0')/2. \tag{16.6}$$

For the spatially dependent colonization model, we used the expression

$$\Pr\{X_i(1) = 1 \mid X_i(0) = 0, H_i = h_i\} = (e^{-h_i/\beta} + e^{-h_i/\alpha\beta})/2 \tag{16.7}$$

and for the non-spatially dependent model, we used

$$\Pr\{X_i(1) = 1 \mid X_i(0) = 0\} = [\beta(1 - e^{-a/\beta}) + \alpha\beta(1 - e^{-a/\alpha\beta})]/2a. \tag{16.8}$$

Combinations of these model structures provided four alternative models for the woodpecker response to management and woodpecker spatial distribution:

1. model W_{DS}—decision-sensitive and spatially sensitive; equations 16.3 and 16.4.
2. model $W_{D.}$—decision-sensitive and spatially insensitive; equations 16.3 and 16.5.
3. model $W_{.S}$—decision-insensitive and spatially sensitive; equations 16.6 and 16.7.
4. model $W_{..}$—decision-insensitive and spatially insensitive; equations 16.6 and 16.8.

Unlike probability in the woodpecker models, the thrush occupation probability of cell i at time 1 was considered to be solely dependent on habitat treatment in one model alternative (T_D)

$$\Pr\{Y_i(1) = 1 \mid d_i(0) = d_0\} = \begin{cases} q_0, & d_0 = 1 \\ q_0', & d_0 = 0 \end{cases} \tag{16.9}$$

where Y_i is the thrush occupation status (either 0 or 1) of cell i at time 1, and q_0 and q_0' are probabilities set by the user. An alternative model ($T_{.}$) to reflect decision-insensitivity for thrushes is

$$\Pr\{Y_i(1) = 1\} = (q_0 + q_0')/2 .$$

Thus, the four woodpecker model alternatives in combination with each of the two thrush model alternatives yielded eight alternative system models.

Landscape Simulation

We simulated effects of decisions under each of the species models over a range of initial woodpecker conditions. We considered four types of initial condition: (1) low woodpecker occurrence (n = 5 cells occupied), highly clumped; (2) low occurrence, highly dispersed; (3) high occurrence (n = 20), highly clumped; and (4) high occurrence, highly dispersed. We used a rejection procedure to generate clumped and dispersed distributions. We calculated an index of clumping K (Krishna Iyer 1949; Pielou 1977) for each randomly generated candidate distribution of n occupied cells, and we assumed that the index followed a normal distribution under random mingling of cells. We accepted the distribution as a clumped distribution if $K \geq 1.282$ (normal critical value at 90th percentile) and as a dispersed distribution if $K \leq -1.282$. We continued this process until we had generated one hundred distributions of each type on the landscape grid.

For each initial distribution of woodpecker occupancy, we simulated a set of management decisions under each of the alternative models. The burning status for cell i, $d_i(0)$, was a random outcome of the decision variables $d^{(1)}$, the proportion of woodpecker-vacant habitat burned, and $d^{(2)}$, the proportion of woodpecker-occupied habitat burned. For a fixed selection of $d^{(1)}$ and $d^{(2)}$, $(100 - n)d^{(1)}$ cells were randomly chosen for burning from the set of woodpecker-vacant cells, and $nd^{(2)}$ cells were chosen at random from the set of woodpecker-occupied cells. We considered four settings of $d^{(1)}$ and $d^{(2)}$:

1. $\{d^{(1)}, d^{(2)}\} = \{0.2, 0.2\}$
2. $\{d^{(1)}, d^{(2)}\} = \{0.2, 0.8\}$
3. $\{d^{(1)}, d^{(2)}\} = \{0.8, 0.2\}$
4. $\{d^{(1)}, d^{(2)}\} = \{0.8, 0.8\}$

Given an initial distribution of woodpecker and values of $d^{(1)}$ and $d^{(2)}$, we drew one hundred random arrangements of the $d_i(0)$. Thus, each of the sixteen combinations of initial conditions and decision variables provided ten thousand random distributions of woodpecker occupancy and burning activity.

All simulations were conducted over a single ten-year time step. Values 0.904 and 0.665 for p_0 and p_0', respectively, correspond to annual persistence rates of 0.99 and 0.96; in other words, annual risk of extirpation is four times as likely for an unburned cell than for a burned cell. We chose values of 0.8 and 0.25 for β and α, respectively, which render colonization unlikely in any burned cell not adjacent to an occupied cell. For unburned cells, colonization is extremely unlikely for any nearest-neighbor distance. We chose values of 0.1 and 0.6 for the thrush occupation probabilities q_0 and q_0', respectively.

For each of the decision simulations, we recorded the woodpecker population growth as $\lambda = \Sigma X_i(1)/n$, and we calculated $w = \Sigma Y_i(1)/100$, the proportion of habitat occupied by thrushes. We combined these quantities in the objective function

$$J = \{\max(0, \lambda - 1)\}^u w^v,$$

where u and v were set to the values 1.0 and 0.2, respectively. These values imply that woodpecker population growth is rewarded approximately linearly as long as thrushes occupy a minimum threshold (about 20 percent) of the landscape. Rewards are minimal if the decision grows one species at the expense of the other. We obtained means and variances of ten thousand objective function evaluations for each of 128 initial condition × model alternative × decision alternative combinations.

Simulation Results

Because initial conditions, the decision action, and population responses were all realizations of stochastic processes, values of the objective function were also stochastic. Therefore, for any given population model, each decision was superior to the others in least one simulation simply by chance (Tables 16.1, 16.2). However, the large number of simulations clearly indicated that certain decisions provided the greatest expected value of the objective function and that others were consistently inferior.

The optimal decision depended on accurate identification of the underlying management response model (Tables 16.1, 16.2; Fig. 16.2). For example, given that initial woodpecker population size is 20, then the decision to burn 20 percent of both woodpecker-vacant and woodpecker-occupied landscape cells is the best decision only if one correctly presumes that thrushes respond negatively to fire and that woodpeckers do not respond at all (Fig. 16.2d–f). However, this same decision is the worst that can be made if, in fact, woodpeckers respond positively to fire (Fig. 16.2d–f). The four decisions were equally adequate only in the special case in which neither species responded to fire management.

The parameter values that we chose for the objective function heavily rewarded management directed toward woodpeckers, and this was reflected in how the decision patterns varied among management response models. For the four model types in which woodpeckers were not assumed to respond to fire management (models W..T., W..T$_{\mathrm{D}}$, W.$_{\mathrm{S}}$T., W.$_{\mathrm{S}}$T$_{\mathrm{D}}$), models W..T. and W.$_{\mathrm{S}}$T. provided no trend in mean objective value as extent of burning increased in the landscape, whereas the thrush response models (W..T$_{\mathrm{D}}$ and W.$_{\mathrm{S}}$T$_{\mathrm{D}}$) provided a negative trend as more of the landscape was burned (Fig. 16.2). However, all woodpecker response models provided a positive trend in mean objective value, though the rate of increase was slower when the thrush response was considered (Fig. 16.2, models W$_{\mathrm{D}}$.T$_{\mathrm{D}}$ and W$_{\mathrm{DS}}$T$_{\mathrm{D}}$) than when it was not (Fig. 16.2, models W$_{\mathrm{D}}$.T. and W$_{\mathrm{DS}}$T.). As objective value parameters are altered to bring management desires for the two species into greater conflict, we would expect the trend in objective value over the decisions under the

TABLE 16.1.

Mean and approximate 99% confidence interval for objective value (J) and frequency of optimality (n_{Opt}) for four decisions under eight alternative system models and two types of spatial arrangements of woodpeckers (dispersed versus clumped), given an initial population of five woodpeckers.

	Decision[a]											
	$d^{(1)} = 0.2,\ d^{(2)} = 0.2$			$d^{(1)} = 0.2,\ d^{(2)} = 0.8$			$d^{(1)} = 0.8,\ d^{(2)} = 0.2$			$d^{(1)} = 0.8,\ d^{(2)} = 0.8$		
Model[b]	J	**99% CI**	n_{Opt}	J	**99% CI**	n_{Opt}	J	**99% CI**	n_{Opt}	J	**99% CI**	n_{Opt}
Initial woodpecker population size = 5, highly dispersed												
$W_{..}T_{.}$	0.384	(0.376–0.392)	2440	0.385	(0.378–0.393)	2400	0.386	(0.378–0.394)	2537	0.388	(0.381–0.396)	2469
$W_{..}T_{D}$	0.412	(0.404–0.420)	2941	0.414	(0.406–0.422)	2868	0.347	(0.340–0.354)	2095	0.345	(0.338–0.352)	2005
$W_{D.}T_{.}$	0.175	(0.169–0.180)	438	0.254	(0.248–0.260)	809	0.521	(0.512–0.530)	3518	0.631	(0.622–0.640)	5124
$W_{D.}T_{D}$	0.187	(0.182–0.193)	713	0.267	(0.261–0.274)	1154	0.471	(0.462–0.479)	3395	0.559	(0.551–0.567)	4664
$W_{.S}T_{.}$	0.632	(0.622–0.641)	2529	0.626	(0.616–0.635)	2423	0.631	(0.621–0.640)	2436	0.633	(0.623–0.642)	2501
$W_{.S}T_{D}$	0.674	(0.664–0.684)	3059	0.674	(0.664–0.684)	3056	0.576	(0.567–0.584)	1994	0.557	(0.548–0.565)	1825
$W_{DS}T_{.}$	0.161	(0.156–0.167)	25	0.237	(0.231–0.242)	45	1.045	(1.033–1.056)	4254	1.158	(1.147–1.169)	5622
$W_{DS}T_{D}$	0.174	(0.168–0.179)	59	0.256	(0.250–0.262)	107	0.939	(0.929–0.950)	4269	1.031	(1.020–1.041)	5488
Initial woodpecker population size = 5, highly clumped												
$W_{..}T_{.}$	0.385	(0.377–0.393)	2447	0.386	(0.378–0.393)	2483	0.388	(0.380–0.396)	2441	0.388	(0.380–0.396)	2487
$W_{..}T_{D}$	0.414	(0.406–0.423)	2972	0.409	(0.401–0.418)	2881	0.346	(0.339–0.353)	2060	0.341	(0.335–0.348)	2013
$W_{D.}T_{.}$	0.178	(0.173–0.184)	512	0.252	(0.246–0.258)	812	0.515	(0.506–0.524)	3500	0.625	(0.616–0.634)	5050
$W_{D.}T_{D}$	0.189	(0.183–0.195)	728	0.270	(0.263–0.276)	1141	0.471	(0.462–0.479)	3392	0.559	(0.551–0.567)	4670
$W_{.S}T_{.}$	0.474	(0.465–0.482)	2468	0.475	(0.466–0.483)	2447	0.475	(0.466–0.483)	2467	0.476	(0.468–0.485)	2494
$W_{.S}T_{D}$	0.506	(0.497–0.515)	2971	0.505	(0.496–0.514)	2934	0.433	(0.426–0.441)	2046	0.428	(0.420–0.436)	1977
$W_{DS}T_{.}$	0.115	(0.111–0.119)	56	0.182	(0.177–0.187)	107	0.784	(0.773–0.794)	4000	0.903	(0.892–0.913)	5761
$W_{DS}T_{D}$	0.122	(0.117–0.127)	97	0.192	(0.187–0.198)	191	0.707	(0.698–0.717)	4080	0.799	(0.790–0.808)	5548

[a] Expressed as proportion of ninety-five woodpecker-vacant cells ($d^{(1)}$) and proportion of five woodpecker-occupied cells ($d^{(2)}$) burned. Each decision was simulated one hundred times under one hundred random woodpecker occupancy distributions.

[b] Model expressed as a character triplet $W_{ij}T_{k}$, where i indicates woodpecker colonization and persistence probabilities are (i = D) or are not (i = **.**) sensitive to burning, j indicates woodpecker colonization probability is (j = S) or is not (j = **.**) sensitive to distance from a nearest-neighbor source cell, and k indicates thrush occurrence probability is (k = D) or is not (k = **.**) sensitive to burning.

TABLE 16.2.

Mean and approximate 99% confidence interval for objective value (J) and frequency of optimality (n_{Opt}) for four decisions under eight alternative system models and two types of spatial arrangements of woodpeckers (dispersed versus clumped), given an initial population of twenty woodpeckers.

	Decision[a]											
	$d^{(1)} = 0.2$, $d^{(2)} = 0.2$			$d^{(1)} = 0.2$, $d^{(2)} = 0.8$			$d^{(1)} = 0.8$, $d^{(2)} = 0.2$			$d^{(1)} = 0.8$, $d^{(2)} = 0.8$		
Model[b]	J	**99% CI**	n_{Opt}	J	**99% CI**	n_{Opt}	J	**99% CI**	n_{Opt}	J	**99% CI**	n_{Opt}
Initial woodpecker population size = 20, highly dispersed												
$W..T.$	0.016	(0.015–0.017)	1441	0.016	(0.015–0.017)	1517	0.016	(0.015–0.017)	1499	0.015	(0.014–0.016)	1429
$W..T_D$	0.018	(0.017–0.019)	1614	0.017	(0.016–0.018)	1554	0.016	(0.015–0.017)	1417	0.015	(0.014–0.015)	1365
$W_D.T.$	0.002	(0.001–0.002)	124	0.015	(0.014–0.016)	1179	0.016	(0.015–0.017)	1151	0.060	(0.058–0.061)	4837
$W_D.T_D$	0.002	(0.002–0.002)	175	0.015	(0.014–0.015)	1285	0.015	(0.014–0.016)	1169	0.056	(0.054–0.057)	4725
$W._ST.$	0.208	(0.205–0.212)	2557	0.205	(0.202–0.209)	2409	0.207	(0.203–0.210)	2525	0.205	(0.202–0.209)	2430
$W._ST_D$	0.224	(0.220–0.227)	3146	0.218	(0.215–0.222)	2867	0.194	(0.191–0.197)	2122	0.185	(0.182–0.188)	1845
$W_{DS}T.$	0.015	(0.014–0.016)	1	0.061	(0.059–0.063)	8	0.363	(0.359–0.367)	2964	0.478	(0.475–0.482)	6993
$W_{DS}T_D$	0.017	(0.016–0.018)	3	0.066	(0.064–0.068)	19	0.344	(0.340–0.348)	3374	0.427	(0.424–0.430)	6576
Initial woodpecker population size = 20, highly clumped												
$W..T.$	0.016	(0.015–0.017)	1478	0.017	(0.016–0.018)	1515	0.016	(0.015–0.017)	1498	0.017	(0.016–0.018)	1463
$W..T_D$	0.018	(0.017–0.019)	1595	0.018	(0.017–0.019)	1631	0.016	(0.015–0.017)	1441	0.015	(0.014–0.016)	1392
$W_D.T.$	0.002	(0.002–0.002)	137	0.015	(0.014–0.016)	1156	0.016	(0.015–0.017)	1086	0.061	(0.059–0.063)	4872
$W_D.T_D$	0.002	(0.002–0.002)	169	0.015	(0.014–0.016)	1299	0.015	(0.014–0.016)	1173	0.055	(0.053–0.056)	4702
$W._ST.$	0.149	(0.146–0.152)	2473	0.151	(0.148–0.154)	2505	0.150	(0.147–0.153)	2502	0.148	(0.145–0.151)	2426
$W._ST_D$	0.160	(0.157–0.164)	2970	0.157	(0.154–0.160)	2765	0.141	(0.138–0.144)	2261	0.133	(0.130–0.136)	1964
$W_{DS}T.$	0.009	(0.008–0.010)	3	0.045	(0.043–0.046)	37	0.270	(0.266–0.274)	2844	0.383	(0.379–0.386)	7071
$W_{DS}T_D$	0.010	(0.009–0.010)	6	0.046	(0.045–0.048)	56	0.251	(0.248–0.255)	3070	0.342	(0.339–0.345)	6836

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[a] Expressed as proportion of eighty woodpecker-vacant cells ($d^{(1)}$) and proportion of twenty woodpecker-occupied cells ($d^{(2)}$) burned. Each decision was simulated one hundred times under one hundred random woodpecker occupancy distributions.

[b] Model expressed as a character triplet $W_{ij}T_k$, where i indicates woodpecker colonization and persistence probabilities are (i = D) or are not (i = .) sensitive to burning, j indicates woodpecker colonization probability is (j = S) or is not (j = .) sensitive to distance from a nearest-neighbor source cell, and k indicates thrush occurrence probability is (k = D) or is not (k = .) sensitive to burning.

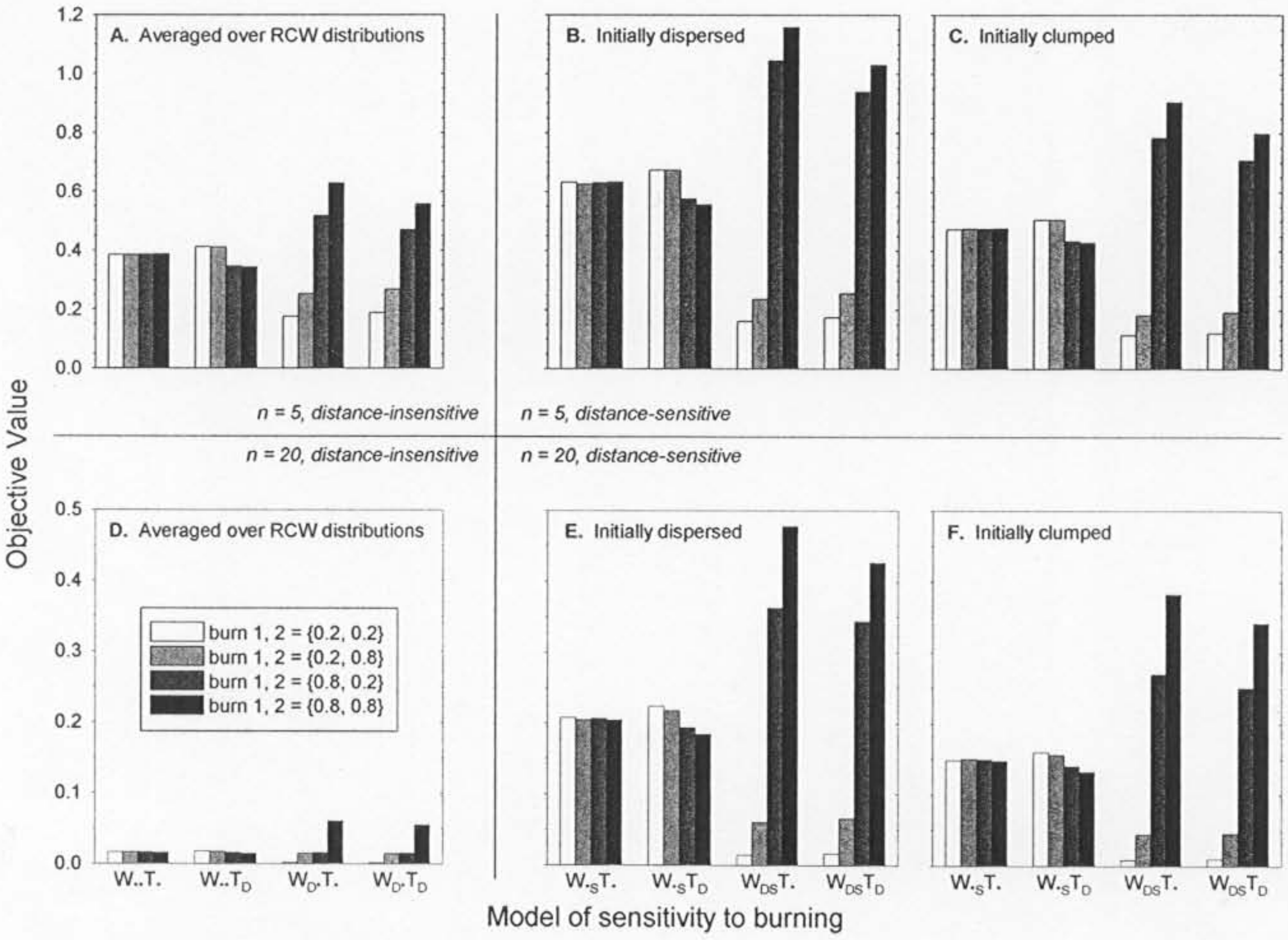

Figure 16.2. Mean objective values for four landscape burning decisions under alternative models of red-cockaded woodpecker (*Picoides borealis*) and wood thrush (*Hylocichla mustelina*) population dynamics. Decisions are expressed in the form $\{d^{(1)}, d^{(2)}\}$, where $d^{(1)}$ represents proportion of woodpecker-vacant habitat burned, and $d^{(2)}$ represents proportion of woodpecker-occupied habitat burned. Shading of decision bars increases from light to dark as extent of landscape burning increases. In each plot, decision results are provided for four models of species response to burning: no response by either woodpeckers or thrushes (model $W_{.i}T_{.}$), response by thrushes only (model $W_{.i}T_D$), response by woodpecker only (model $W_{Di}T_{.}$), and response by both woodpecker and thrushes (model $W_{Di}T_D$), where subscript *i* indicates whether woodpecker colonization probability is (*i* = S, plots *b, c, e, f*) or is not (*i* = ., plots *a, d*) sensitive to distance to nearest source neighbor. Decision outcomes vary according to two initial states of the system: initial population size (plots *a, b, c* for $n = 5$ and plots *d, e, f* for $n = 20$), and initial distribution of woodpeckers (plots *b* and *e* for dispersed distributions and plots *c* and *f* for clumped distributions).

joint woodpecker-thrush response model to become quite flat, almost resembling that for the null response model.

We found that making the optimal decision was not dependent on correctly identifying the appropriate distance-sensitivity mechanism for woodpecker colonization (contrast Fig. 16.2a with Fig. 16.2b–c and Fig. 16.2d with Fig. 16.2e–f), the initial abundance of woodpeckers (contrast Fig. 16.2a–c with Fig. 16.2d–f), or the initial distribution of woodpeckers (contrast Fig. 16.2b with Fig. 16.2c and Fig. 16.2e with Fig. 16.2f). With regard to this latter result, however, we point out that our simulated decisions were carried out by selecting habitat cells completely at random with regard to woodpecker location. Had our decision set also included the selection of cells under some alternative sampling scheme (e.g., probability of selection of woodpecker-vacant cells inversely proportional to distance from woodpecker-occupied cells), we would then expect to find that the optimal decision does depend on correct identification of the initial distribution of woodpeckers.

Discussion

This hypothetical example demonstrates the importance of correct model identification in decision making, or at least the importance of considering a set of reasonable model alternatives. Furthermore, the relative performance of decisions across the model set will vary according to form and parameterization of the objective function.

In our example, we were omniscient observers of the system and could easily understand the implications of each decision under each version of nature. In real systems, however, we are uncertain about the true version of nature, and our observations are incomplete and imprecise, yet we still are faced with making an optimal decision for a management objective. Our real need, therefore, is twofold: to find the decision that maximizes some physical attribute of the system, and to apply the results of the decision action toward the reduction of uncertainty and toward better decision making in the future.

Suppose that we are managing a system that is described by one of the eight models above, but that we are completely uncertain about which model is correct. We will also assume that the initial population of woodpeckers is five and that woodpeckers occur in a dispersed pattern. Then we may apply equation 16.1 to find the optimal decision under uncertainty, using values of J (Table 16.1) for the $\int u(a|x;\theta_i)f(x|\theta_i)dx$ and $p(\theta_i) = 0.125$. The maximum value of $E(a)$ is 0.663, which occurs for decision $\{d^{(1)}, d^{(2)}\} = \{0.8, 0.8\}$.

Following the decision action, the system may be observed for a number of years until the time of the next management action. We assume that data are collected according to some design that yields observations at temporal, spatial, and demographic resolutions that are consistent with model predictions. Suppose that data from the field, collected ten years following the decision action, provided a set of values $L(\underline{x}|\theta)$, the statistical measures of agreement between the data and each model θ (e.g., a sum of squared differences between observations and model predictions scaled by a variance measure). Furthermore, suppose that these values redistributed (through equation 16.2) model weight from the equal allocation of 0.125 for each model to the allocation of 0.79 to the model $W_{\cdot S}T_D$ (woodpecker management-insensitivity, woodpecker distance-sensitivity, thrush management-sensitivity) and 0.03 to the other seven models. Now, if we are again required to choose a management action for the next ten years, and again starting from an initial condition of five dispersed woodpeckers, then reapplication of equation 16.1 under these new weights results in a maximum value of 0.606 for $E(a)$, which occurs for decision $\{d^{(1)}, d^{(2)}\} = \{0.2, 0.8\}$. Thus, at both decision periods we not only made optimal decisions under system uncertainty, we also exploited our decision action and our monitoring data to reduce uncertainty between decision episodes. Note also in this approach that statistical measures of model-to-data agreement are not used to make dichotomous, absolute assignments of model validity or invalidity based on arbitrary criteria. Rather, they are used in a way that allocates more or less credibility to a model over time without ever completely dismissing a contender from the model set.

Summary

We make several observations regarding the use of habitat models in a conservation decision context. First, the assessment of model accuracy (model validation) must be based on observable phenomena so that model predictions can be directly compared to observations. "Suitability," meaning the *potential* of a habitat to provide a portion of the needs of a population, cannot itself be objectively measured, and models dependent on "suitability" as the output cannot be validated (but see Hill and Binford [Chapter 7] for another perspective). Second, even when presence, absence, or numerical abundance can be observed and appear to conform to model predictions, this agreement may constitute weak validation, that is, not exclude competing explanatory or even null habitat models. Weak validation occurs for several reasons, including (1) possible existence of source-sink and other demographic phenomena tending to obscure functional relationships between habitat and populations; (2) weak evidence based on qualitative (e.g., present or absent) versus quantitative comparisons; (3) lack of statistical power; and (4) injudicious choice of spatial scale. Third, arbitrary conventions of accuracy (map or attribute) or precision are irrelevant to decision making and tend to distract from the proper consideration of uncertainty in decision making, which will always be made under uncertainty. The key is to provide tenable alternative models that make different predictions about the relationship between management actions and the objective. Finally, optimal decisions can be made based on current information about the tenability of alternative models (expressed as model weights). Adaptation occurs when uncertainty is reduced (changing model weights) by information feedback obtained in the course of management and monitoring.

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