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WEIGHING CONSERVATION OBJECTIVES: MAXIMUM EXPECTED COVERAGE VERSUS ENDANGERED SPECIES PROTECTION

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Abstract. Decision makers involved in land acquisition and protection often have multiple conservation objectives and are uncertain about the occurrence of species or other features in candidate sites. Models informing decisions on selection of sites for reserves need to provide information about cost-efficient trade-offs between objectives and account for incidence uncertainty. We describe a site selection model with two important conservation objectives: maximize expected number of species represented, and maximize the likelihood that a subset of endangered species is represented. The model uses probabilistic species occurrence data in a linear-integer formulation solvable with commercial software. The model is illustrated using probabilistic occurrence data for 403 terrestrial vertebrates in 147 candidate sites in western Oregon, USA. The trade-offs between objectives are explicitly measured by incrementally varying the threshold probability for endangered species representation and recording the change in expected number of species represented. For instance, in the example presented here, we found that under most budget constraints, the probability of representing three endangered species can be increased from 0.00 (i.e., no guaranteed protection) to 0.90 while reducing expected species representation ~2%. However, further increasing the probability of endangered species representation from 0.90 to 0.99 results in a much larger reduction in species representation of ~14%. Although the numerical results from our analysis are specific to the species and area studied, the methodology is general and applicable elsewhere.

Key words: conservation; endangered species; goal trade-offs; optimization; Oregon; site selection model; species representation.

Introduction

Recognizing limited resources and land use pressures from population and economic expansion, biologists, economists, and operations researchers have recently explored ways to rationalize the choice of biological reserve networks (e.g., Pressey et al. 1993, Church et al. 1996, Csuti et al. 1997, Margules and Pressey 2000). One outcome of this exploration was the development of models supporting decisions on reserve site selection, which aim to provide case-specific information on the efficient trade-offs between conservation goals and reserve costs. Site selection models assume that species or other conservation features are distributed among potential reserve sites and typically employ species representation objectives (see ReVelle et al. 2002 and Rodrigues and Gaston 2002*a* for summaries of published studies). The pioneering applications selected the minimum number of sites that represented all of the species (Margules et al. 1988, Saetersdal et al. 1993). Later applications maximized the number of species that could be represented within a given number of sites (e.g., Church et al. 1996, Csuti et al. 1997, Stokland 1997). Recognizing other conservation objectives, analysts have formulated site selection models that maximize phylogenetic diversity (e.g., Faith 1992, Solow et al. 1993, Polasky et al. 2001, Rodrigues and Gaston 2002*b*), ecosystem representation (e.g., Schmidt 1996, Pressey et al. 1997, Snyder et al. 1999), and endangered species protection (e.g., Dobson et al. 1997, Ando et al. 1998).

Continuing this line of research, we address three important limitations of reserve site selection models by formulating a model that incorporates multiple conservation objectives, uncertainty about species occurrence, and cost of reserve designation. Most formulations include a single conservation objective, and analysts evaluate that objective under varying fiscal constraints. In practice, however, decision makers may have multiple conservation objectives, and multiobjective site selection models are needed to investigate opportunities for simultaneously meeting those objec-

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tives (Rothley 1999, Church et al. 2000). In addition, most site selection models assume that species or feature occurrences within sites are known with certainty. In practice, there is a great deal of uncertainty about where species or features occur (e.g., Flather et al. 1997). Some recent reserve site selection models explicitly account for incidence uncertainty (Haight et al. 2000, Camm et al. 2002), and we use those formulations as a foundation for our model. Finally, most site selection models assume that costs of protecting sites of the same size are identical. In reality, the market value of land varies widely across sites. Reserve costs can be incorporated into a reserve site selection model by using a budget constraint related to site-specific market land values (e.g., Faith and Walker 1996, Ando et al. 1998).

The purpose of this paper is to describe and demonstrate a reserve site selection model that can be used to quantify the trade-offs between two important conservation objectives: maximizing the expected number of species represented in the selected sites, and maximizing the likelihood that a subset of endangered species is represented. Recognizing that our knowledge of species distributions across the landscape is uncertain, we formulated the model using probabilistic species occurrence data. By combining logic from single-objective, probabilistic formulations (Haight et al. 2000, Camm et al. 2002), we obtained a linear-integer model that can be solved using commercial software. We used the model with a budget constraint to evaluate the cost of a conservation strategy that targets protection for large numbers of species, represented by expected coverage. We imposed additional constraints setting minimum coverage probabilities for endangered species to evaluate the cost of a conservation strategy that targets protection of individual species. By varying the levels of the constraints, we measured the cost of increasing protection for endangered species both in terms of forgone market value and in terms of forgone expected coverage. We illustrate the method using data on terrestrial vertebrates and land values in western Oregon, USA. Using this example, we show that trade-offs exist between the two conservation objectives and demonstrate a general methodology for evaluating them.

Probabilistic Expected Coverage Model

The model formulation combines the conservation objectives of two previously developed models: maximizing expected number of species covered (Camm et al. 2002) and attaining minimum threshold coverage probabilities for endangered species (Haight et al. 2000). The motivation for the combined model is that it allows for the *quantification* of the trade-offs between these two conservation objectives. Specifically, the new model retains the objective of maximizing expected species covered found in Camm et al. (2002), but with the addition of minimum threshold constraints for endangered species as studied by Haight et al. (2000). The new model provides a methodology for explicitly measuring trade-offs between objectives; for example, the loss in expected number of species covered as the minimum thresholds for endangered species are increased.

Model development

We develop the model as follows. Let I represent the set of species under consideration, J represent the set of potential reserve sites, and $E \subseteq I$ represent the set of species listed as threatened or endangered. Define the binary variable X_j for all $j \in J$ as follows:

$$X_j = \begin{cases} 1 & \text{if site } j \text{ is selected for protection} \\ 0 & \text{if site } j \text{ is not selected.} \end{cases}$$

Let p_{ij} be the probability that species $i \in I$ exists at site $j \in J$. We make two assumptions on the probabilities p_{ij}. First, relaxing the definition of probability, we assume that p_{ij} is less than one; i.e., $0 \leq p_{ij} < 1$. In the linear model described below, some constraints are undefined for $p_{ij} = 1$ (see Eqs. 6 and 7.). However, an adjustment to the model that allows $p_{ij} = 1$ is given in Camm et al. (2002). Second, we assume for each species i and any two distinct sites j and k that the probabilities p_{ij} and p_{ik} are independent. It is possible to model dependencies across sites, though doing so considerably complicates the analysis. Further, there is often not the necessary data to model such dependencies accurately.

Defining w_i as the probability that species i is *not* covered in the sites selected for protection, we can write

$$w_i = \prod_{j \in J} (1 - p_{ij})^{X_j} \qquad i \in I. \tag{1}$$

Eq. 1 follows since the selected set of sites fails to cover a given species i if and only if that species is absent from all of the selected sites. Note that the independence assumption allows us to write w_i as a product over all sites. The problem is to determine the values of the site selection variables $X_J \in \{0,1\}$ $j \in J$ to maximize the expected number of species covered (expected coverage, EC):

$$\text{Max EC} = \sum_{i \in I} (1 - w_i) \tag{2}$$

subject to Eq. 1 and

$$1 - w_i \geq h_i \qquad i \in E \tag{3}$$

$$\sum_{j \in J} c_j X_j \leq B \tag{4}$$

where

h_i = the minimum probability that species $i \in E$ must be included in the selected sites,
c_j = the cost of protecting site j,
B = the budget allocated to site protection.

Eq. 2 is the objective function, which is to maximize

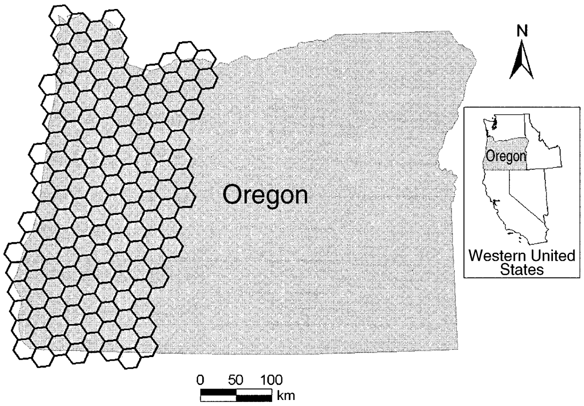

FIG. 1. Partitioning of western Oregon into 147 hexagonal cells using the grid system employed by the EPA Environmental Modeling and Assessment Program.

expected coverage over the set of species, I (derived from Camm et al. 2002). Eq. 3 ensures that species that are listed as threatened or endangered, $i \in E$, meet or exceed minimum coverage probability thresholds, h_i (derived from Haight et al. 2000). Note that by setting $h_i = 0$ for all $i \in E$, the problem is one of maximizing expected coverage. Setting higher values for h_i requires greater assurance of protection for threatened and endangered species. Eq. 4 ensures that the cost of site protection does not exceed the budget, B. Both previous studies constrained the number of sites included in the reserve network rather than the budget allocated to site protection.

The problem in Eqs. 1–4 is nonlinear and cannot be converted to an equivalent linear integer program because the objective function is the sum of terms that involve the products of the decision variables X_j. Nevertheless, solving a linear approximation of the nonlinear problem can yield good solutions to problems of large enough size to have practical significance. We used the linearization procedure of Camm et al. (2002) to create a linear approximation. With the assumption that $0 \leq p_{ij} < 1$ for all i and j and $h_j < 1$ for all $i \in E$, we can take the natural logs of Eqs. 1 and 3 to obtain an equivalent problem:

$$\text{Max EC} = \sum_{i \in I} (1 - w_i) \tag{5}$$

subject to

$$\ln(w_i) = \sum_{j \in J} X_j \ln(1 - p_{ij}) \qquad i \in I \tag{6}$$

$$\sum_{j \in J} X_j \ln(1 - p_{ij}) \leq \ln(1 - h_i) \qquad i \in E \tag{7}$$

$$\sum_{j \in J} c_j X_j \leq B. \tag{8}$$

This model is linear in the decision variables X_j and w_i, except for the term $\ln(w_i)$. To create the linear approximation for $\ln(w_i)$, we note that $0 < w_i \leq 1$ and define a set of K break points to approximate the interval L to 1, where $L > 0$ is the lowest possible probability of species absence if as many sites were protected as possible. Let B_k be the kth break point and $\lambda_{ik} \geq 0$ be a continuous variable that weights the kth break point for species i. Letting $w_i = \Sigma_{k=1}^{K} B_k\lambda_{ik}$, $\ln(w_i) = \Sigma_{k=1}^{K} \ln(B_k)\lambda_{ik}$ and $\Sigma_{k=1}^{K} \lambda_{ik} = 1$ be the substitutions required for the linear approximation of w_i, the new model is

$$\text{Max EC} = \sum_{i \in I} (1 - w_i) \tag{9}$$

subject to

$$\sum_{k=1}^{K} \ln(B_k)\lambda_{ik} = \sum_{j \in J} X_j \ln(1 - p_{ij}) \qquad i \in I \tag{10}$$

$$w_i = \sum_{k=1}^{K} B_k \lambda_{ik} \qquad i \in I \tag{11}$$

$$\sum_{j \in J} X_j \ln(1 - p_{ij}) \leq \ln(1 - h_i) \qquad i \in E \tag{12}$$

$$\sum_{j \in J} c_j X_j \leq B \tag{13}$$

$$\sum_{k=1}^{K} \lambda_{ik} = 1 \qquad i \in I \tag{14}$$

where $X_j \in \{0,1\}$ $j \in J$ and $\lambda_{ik} \geq 0$ $i \in I$, $k \in K$ are the decision variables. We solved this linear approximation of the expected coverage problem to analyze the effects of alternative budgets and required coverage probabilities on optimal site selection strategies.

STUDY AREA AND DATA

We illustrate the probabilistic expected coverage model and our method for evaluating trade-offs among conservation objectives and opportunity cost using probabilistic data on species occurrences and land value for western Oregon between the crest of the Cascade Range and the Pacific Ocean (Fig. 1). This application is used to illustrate the results obtainable from the methodology and not for on-the-ground conservation planning in a particular place. The area was partitioned into 147 hexagonal cells using the grid system employed by the EPA Environmental Monitoring and Assessment Program (White et al. 1992). Each hexagon is ~63 500 ha. Because we had estimates of species occurrence and average land value for each hexagon, we assumed that each hexagon represented a potential reserve site, forming set J. In practice, geographic analysis of land cover, habitat, and ownership would be required to identify the location and size of potential reserves, species occurrence, and land values.

Data on the occurrence of 403 terrestrial vertebrate species, set I, were obtained from Master et al. (1995). Each species was assigned to one of the following occurrence categories in each hexagon based on actual occurrence records and expert opinion about the likelihood of occurrence:

1) *Confident*.—There was a verified sighting of the species in the hexagon has occurred in the past two decades (probability of 0.95–1.0).

2) *Probable*.—The hexagon contains suitable habitat for the species, there have been verified sightings in nearby hexagons and, in the opinion of a local expert, it is highly probable that the species occurs in the hexagon (probability of 0.8–0.95).

3) *Possible*.—No verified sightings have occurred in the hexagon, the habitat is of questionable suitability for the species, and in the opinion of a local expert, the species might occur in the hexagon (probability of 0.1–0.8).

4) *Not present*.—Habitat in the hexagon is unsuitable for the species (probability of 0.0–0.1).

Assuming that each hexagon represented a potential reserve site, we set the occurrence probability, p_{ij}, for each species i in each site j equal to the midpoint of the corresponding occurrence category (0.975 for confident, 0.875 for probable, 0.45 for possible), except we used 0.00 for not present. In a few instances, a species had two different (but adjacent) occurrence category assignments for a site. We set the occurrence probability for these equal to the midpoint of the union of the two categories (e.g., for possible and probable, p_{ij} = midpoint of (0.1, 0.95) = 0.525).

Set E consists of three terrestrial vertebrate species that are present in the study area and listed as endangered either by the U.S. Fish and Wildlife Service under the Endangered Species Act of 1973 or by the Oregon Fish and Wildlife Service under the Oregon Endangered Species Act of 1987 (Public Communication: Rare, threatened and endangered plants and animals of Oregon, Oregon Natural Heritage Program, 2001 [*available online*]).[7] These species are the Columbian white-tailed deer (*Odocoileus virginianus leucurus*), the gray wolf (*Canis lupus*), and the American Peregrine Falcon (*Falco peregrinus anatum*). The probable locations of the endangered species are mapped in Fig. 2. The Columbian white-tailed deer occurs in two sites with $p_{ij} = 0.975$, eight sites with $p_{ij} = 0.875$, and five sites with $p_{ij} = 0.45$. The gray wolf occurs in 21 sites, all with $p_{ij} = 0.45$, and the American Peregrine Falcon in 24 sites all with $p_{ij} = 0.875$. Ten sites had positive occurrence probabilities for two endangered species, and one site had positive probabilities for all three species. If all sites were selected for protection, the expected coverage would be ~398 species and the probability of coverage of each endangered species would exceed 0.99.

Average land value was used to represent the opportunity cost c_j of protecting site j. The methods and data used to estimate average land values are described in Garber-Yonts and Polasky (1998). Land value was estimated by the assessed market value for private land and the net present value of resource use (using forest inventory, site quality, and livestock forage productivity data) for public land. Public land allocated to wilderness or park (hence, not available for commodity production) was assumed to have no opportunity cost. Urban and tribal lands were excluded from the analysis. Estimated land values ranged from $363 to $48 765 per ha and were highest near major cities (Fig. 3). The least expensive land was in the eastern and southern parts of the study area, which were dominated by public land.

[7] ⟨http://www.natureserve.org/nhp/us/or⟩

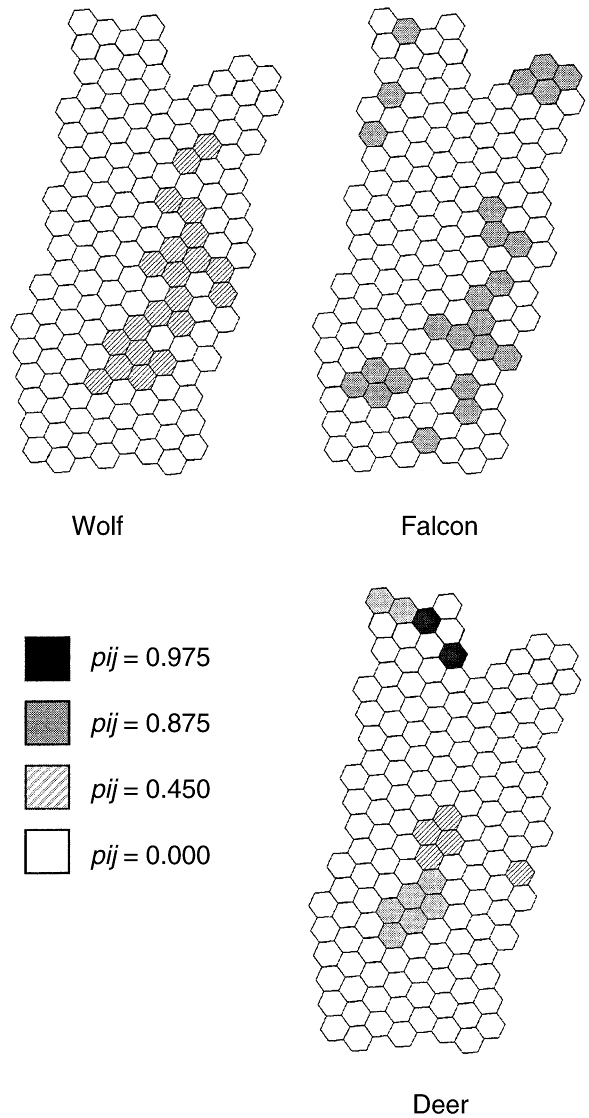

FIG. 2. Occurrence probabilities for three endangered species in western Oregon: the gray wolf (*Canis lupus*), the American Peregrine Falcon (*Falco peregrinus anatum*), and the Columbian white-tailed deer (*Odocoileus virginianus leucurus*).

SOLUTION METHOD

The model specified in Eqs. 9–14 was solved on an IBM Pentium III computer using the integrated solution

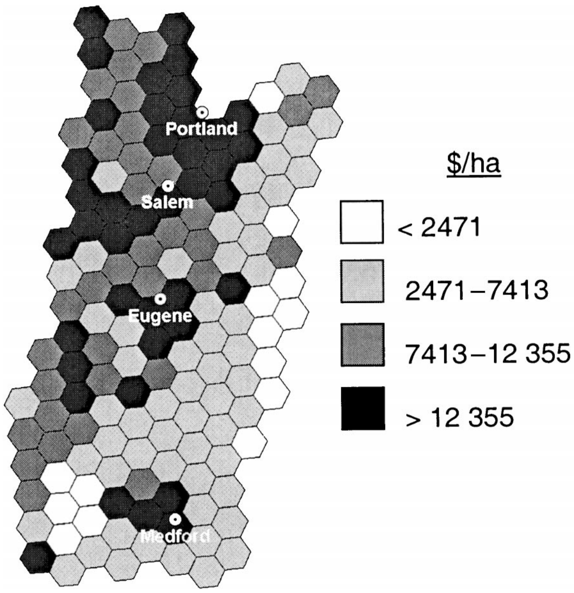

FIG. 3. Average land value estimates in western Oregon (Garber-Yonts and Polasky 1998).

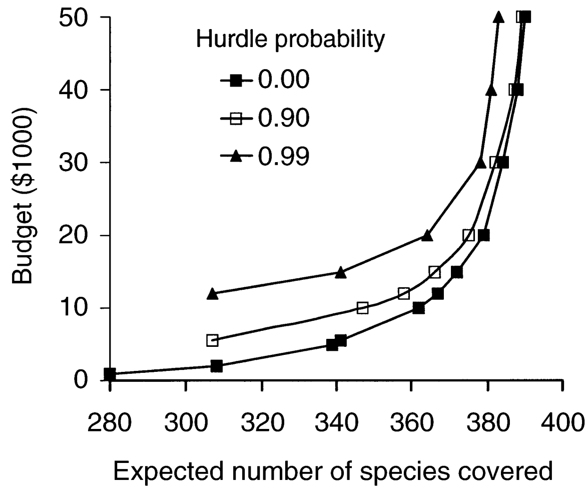

FIG. 4. Budget (or opportunity cost) required to achieve given levels of expected number of species covered, EC, under three hurdle probabilities for endangered species: h_i = 0.00, h_i = 0.90, and h_i = 0.99.

package GAMS/OSL 2.25 (GAMS Development Corporation 1990), which was designed for large and complex linear and mixed integer programming problems. Input files were created using GAMS (General Algebraic Modeling System), a program designed to generate data files in a format that standard optimization packages can read and process. The model was solved using a revised simplex algorithm in conjunction with a branch and bound algorithm for integer-variable problems. Both of these algorithms are part of IBM's optimization subroutine library, a FORTRAN-based subroutine library designed to solve optimization problems.

The model was solved for 10 budget levels, B, from \$1000 to \$50 000 and 7 levels of coverage probability thresholds, h_i, from 0.00 to 0.99. We assumed that equal area was reserved in each of the selected sites and that reserved areas would be representative of the site in terms of species occurrence and cost. We reported budget limits for the cost of reserving 0.407 ha (one acre) from each of the selected sites. While this is insufficient area for virtually all species, the cost of larger reserve sizes can be obtained by simply scaling the budget limit accordingly under our assumption of equal area.

As the number of break points in Eqs. 10 and 11 is increased, the model provides a more accurate approximation of the nonlinear expected coverage problem, but at the expense of more real variables λ_{ik}. We defined a set of 16 break points to approximate the interval L to 1.0, where $L = 8.3 \times 10^{-65}$ was the minimum probability of species absence if 40 sites were protected and the probability of absence was 0.025 in each site. Forty was the maximum number of sites that could be protected with a budget of \$50 000. After experimentation, we settled on a set of 8 break points in the interval [L, 0.1] and 8 break points in the interval [0.1, 1.0]. The objective function values obtained using these linear approximation break points were within 1% of corresponding values computed using the nonlinear Eqs. 1 and 2. Each solution was obtained in less than an hour of computer execution time.

RESULTS

We observed trade-offs between three objectives: cost (size of budget), B; the expected number of species covered, EC; and threshold protection levels for threatened and endangered species, h_i, $i \in E$ (Figs. 4 and 5). Cost curves for EC for three levels of the coverage probability thresholds (h_i = 0.00, 0.90, and 0.99) showed the impact that changing levels of species pro-

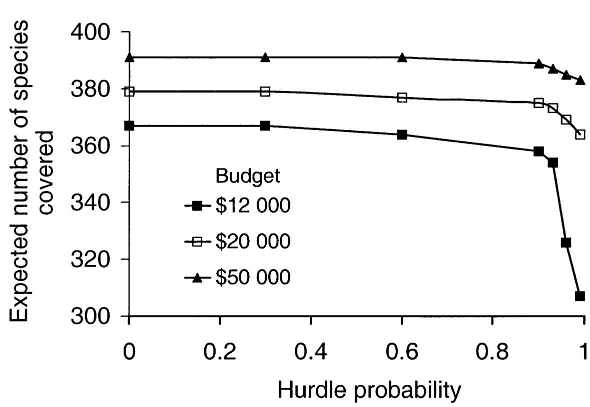

FIG. 5. Bound on the set of feasible combinations of expected coverage, EC, and endangered species hurdle probability, h_i (known as the production possibilities frontier). The figure shows trade-offs between the two conservation objectives for three budget limits: B = \$12 000, B = \$20 000, and B = \$50 000.

tection had on both the minimal budget required to achieve protection and the trade-offs between the conservation objectives (Fig. 4). With $h_i = 0.00$ (thereby imposing no constraint on minimal endangered species protection), EC ranged from 281 to 390 species as the budget limit, B, varied from \$1000 to \$50 000. The minimum budget level required to achieve the coverage probability thresholds for $h_i = 0.90$ was \$5500 and for $h_i = 0.99$ was \$12 000. The slope of the cost curve is the marginal cost, showing the cost of each additional increment in EC. Marginal cost increases dramatically once EC exceeds ~380 species for all three levels of h_i. That is, EC becomes much more costly to increase as its upper bound of coverage is approached.

The vertical distance between the three cost curves in Fig. 4 measures the cost of increasing h_i while maintaining EC. For example, at EC = 308, the cost of increasing h_i by 90 percentage points, from 0.00 to 0.90, is \$3300. But the next additional 9 percentage points (i.e., increasing h_i from 0.90 to 0.99) costs more than twice as much, \$6660. As with EC, h_i becomes more costly to increase as the upper bound is approached.

The trade-off between the alternative conservation objectives, expected coverage and endangered species protection, is measured by the horizontal distance between the cost curves in Fig. 4. This distance is the change in EC as h_i is increased, for a given budget, B. In Fig. 5, this trade-off is shown explicitly by the bound on the set of feasible combinations of EC and h_i (known as the production possibilities frontier) for three budget limits, B = \$12 000, B = \$20 000, and B = \$50 000. Note that EC is not affected by increasing h_i from 0.00–0.30, regardless of budget, and little is lost by increasing h_i from 0.30–0.90. Large decreases in EC occur as h_i is increased above 0.90.

The trade-off between the two competing conservation objectives becomes more marked as total conservation resources, B, become more limiting. For example, at B = \$50 000, the cost of increasing h_i from 0.90 to 0.99 is six species, or <2% of the maximum attainable expected coverage at this budget level (EC = 391). But at B = \$12 000, the cost of increasing h_i from 0.90 to 0.99 is 51 species, or 14% of the maximum attainable expected coverage at this budget level (EC = 367). At high budget levels, it is possible to provide higher levels of protection for virtually all species, including most endangered species, so the constraint that endangered species must be covered to a certain threshold probability is not very costly in terms of the expected total number of species covered. When B = \$50 000 and $h_i = 0.00$ (so that no thresholds were required), the optimal solution still results in coverage probabilities of 0.98 for the Peregrine Falcon, 0.93 for the white-tailed deer, and 0.70 for the gray wolf. However, with B reduced to \$12 000 and h_i still at 0.00, the resultant coverage probabilities remained high for the Peregrine Falcon (0.998), but dropped markedly for the white-tailed deer (0.45) and the gray wolf (0.45). Because endangered species often have limited ranges that may not coincide with centers of species richness, forcing high levels of coverage of endangered species with limited budgets will result in a loss in overall species coverage. With larger budgets, both a strategy to cover as many species as possible and a strategy focused on protecting endangered species will tend to converge on the same priority areas for conservation.

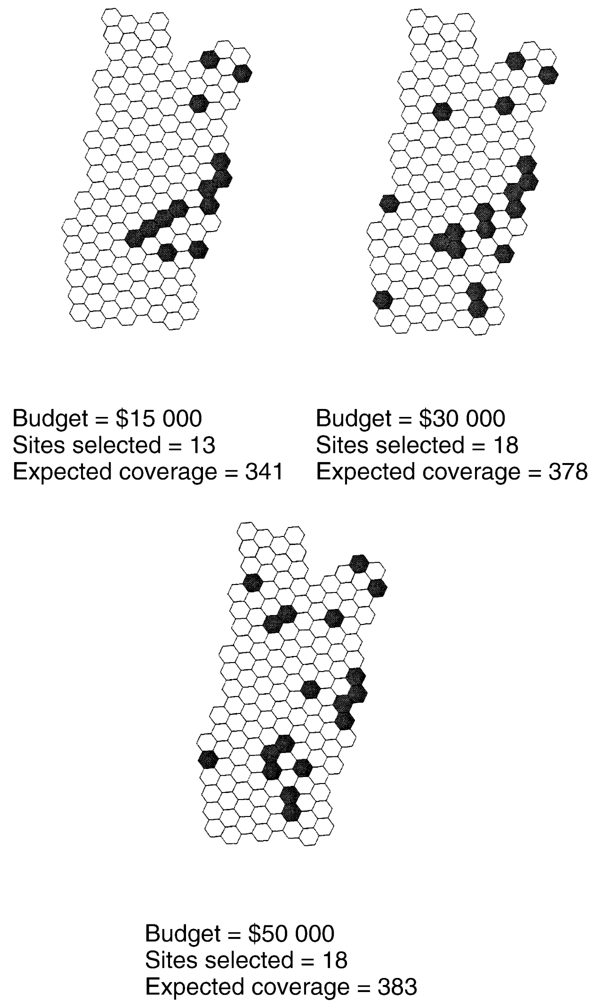

FIG. 6. The number and location of hexagons selected as part of the reserve network for the hurdle probability for endangered species ($h_i = 0.99$) and for three budget limits: B = \$15 000, B = \$30 000, and B = \$50 000. Selected hexagons are dark.

Increasing the budget from \$15 000 to \$50 000 while holding the hurdle constraint at 0.99 allowed the protection of more sites, especially along the coast and in the Willamette Valley where sites are more expensive (Fig. 6). The gain in expected coverage was 42 species (12%). Increasing the hurdle probability from 0.00 to 0.99 while holding the budget at \$12 000 results in a concentration of the selected sites into one nearly contiguous region of the study area (Fig. 7). A comparison

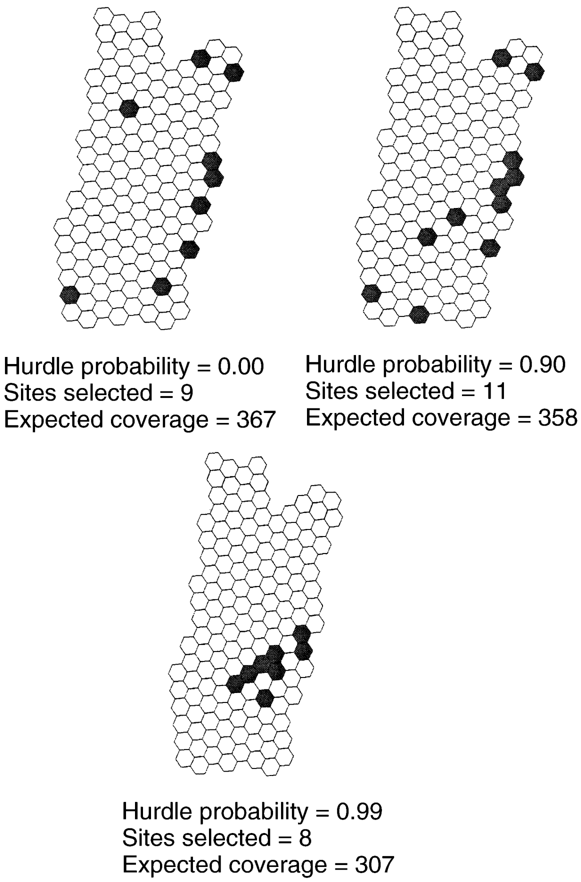

FIG. 7. The number and location of hexagons selected as part of the reserve network for the budget limit, $B = \$12\,000$, and for three hurdle probabilities for endangered species: $h_i = 0.00$, $h_i = 0.90$, and $h_i = 0.99$. Selected hexagons are dark.

of the eight sites selected when $h_i = 0.99$ with maps of endangered species occurrence (Fig. 2) shows that each of these eight sites contains at least one such species with positive probability, most of the sites contain more than one endangered species, and one of the sites is the only site in the study area that contains all three such species. The loss in expected coverage with $h_i = 0.99$ vs. $h_i = 0.90$ was 51 species (14%).

We also identified sites that are likely to contribute to both conservation objectives at least cost (Fig. 8). Optimal site selections were found for 24 problems with budgets of \$12 000 to \$50 000 and hurdle probabilities of 0.90 to 0.99. Solutions were combined to obtain the relative frequency with which each site belonged to the optimal solution. Sites with high inclusion frequencies are likely to be high-priority sites for conservation regardless of the objective or the budget constraint. A high inclusion probability is similar to the notion of irreplaceability (Pressey et al. 1994). The irreplaceability of a site is defined as the percentage of solutions in which that site is included. In our application, five sites on the eastern edge of the study area had inclusion frequencies of >80%. These sites were relatively inexpensive, with three of the five sites being in the five least expensive sites in the study area. All five were in the least expensive 25% of sites. Further examination of the coverage data revealed that the conservation value of these sites comes from their high species richness and not from their coverage of endangered species. Only one of these sites contained two of the endangered species and one other site contained one endangered species, all with probabilities of $p_{ij} = 0.45$. Computed separately, the expected coverage for each of these five sites ranged from 201 to 219, which is above the average across all sites of 192 species per site. The high expected coverage at low cost implies a high return (in terms of species richness) per dollar invested.

DISCUSSION

The primary contribution of our reserve site selection model is to allow the assessment of conservation trade-offs between overall species protection and a narrower focus on protecting a smaller number of endangered species. In our application with species occurrence data for western Oregon, the objectives of maximizing species richness and maximizing endangered species coverage do not closely align except when large conservation budgets allow protection of a large number of sites. In other applications, these conservation objectives may align across a wide range of budget levels so that there is very little trade-off. Quantitative information about the degree of trade-off is important to decision makers, and our model provides that information.

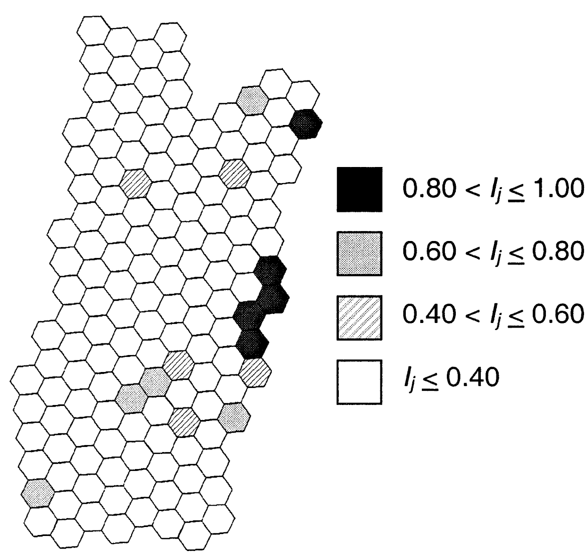

FIG. 8. Frequency with which each hexagonal cell was selected for inclusion in the reserve network in 24 problems with budget levels ranging from $B = \$12\,000$ to $B = \$50\,000$ and hurdle probabilities ranging from $h_i = 0.90$ to $h_i = 0.99$. The shading of the hexagon shows the value of the inclusion index I_j, representing the proportion of the problems in which site j was selected.

Our model directly accounts for uncertainty in species occurrence data and cost of site protection, two innovations that few site selection models address. The ability to handle probabilistic species occurrences is important because, in real-world planning situations, complete information is rare and often prohibitively expensive to obtain. The ability to handle site costs is important because the market value of candidate reserve sites can vary widely across sites. Using logarithmic transformations and linear approximations, we created a linear-integer formulation of the problem that can be solved using off-the-shelf commercial software. In contrast, previous site selection models incorporating uncertainty relied on simple heuristic solution methods (Araújo and Williams 2000, Polasky et al. 2000).

We acknowledge that the structure of our model includes important biological simplifications. First and foremost, the model does not incorporate relationships between species persistence and site protection. As a result, while a species may be present in the selected reserve sites, there is no guarantee that the amount and spatial arrangement of its habitat will support its persistence. One approach to accounting for species persistence is to use surrogate measures such as minimum levels of habitat area, quality, and contiguity (Williams and ReVelle 1996, Church et al. 2000, Nalle et al. 2002, Önal and Briers 2002, Fischer and Church 2003). The mathematical logic in our site selection model could be expanded to incorporate surrogate measures, and the model could be used to attain the desired amount and spatial arrangement of habitat as well as species representation goals. Another approach to handling species persistence is to incorporate models of population dynamics (see Beissinger and Westphal 1998 for review) directly into a site selection formulation. While progress is being made toward incorporating single-species models into optimization frameworks (Montgomery et al. 1994, Bevers et al. 1997, Hof and Raphael 1997, Calkin et al. 2002, Haight et al. 2002, Moilanen and Cabeza 2002), more work is needed to expand optimization frameworks to include dynamics of several species (e.g., Montgomery et al. 1999).

The model also assumes that the probability of species occurrence in a site is independent of its occurrence in neighboring sites. We made this assumption because we had no information on conditional probabilities of species presence given occurrence in neighboring sites. Assuming independence allowed us to compute the likelihood of species occurrence in the set of selected sites as one minus the product of the probabilities of absence in the selected sites. If we had conditional probabilities and found that occurrence probabilities were not independent, then the model would be much more difficult to formulate and solve.

Like most reserve site selection models, ours takes a static approach to conservation planning. The model is designed for a setting in which decision makers seek cost-effective sets of sites to protect biodiversity given current information about species occurrence. Reserves are selected to set aside and are preserved in their current state. This may be a reasonable first-pass approach to the immediate problem of slowing biodiversity loss. However, planning is a dynamic process that incorporates new information as it unfolds. This issue could be addressed by using the basic model in a sequential fashion that is consistent with adaptive planning. The model can be used to recommend a set of sites to protect in the current period. Then, once additional information is gathered to update species occurrence probabilities, the model can be used again to determine the best sites to protect under the new conditions. This recursive procedure gives the decision maker a tool to adapt decisions as better information becomes available. Additionally, the set of protected sites can be shifted over time as conditions change due to climate change or economic change. Costello and Polasky (2004) analyze alternative versions of a dynamic site selection model.

Even with its biological simplifications, we are confident that a probabilistic site selection model can be used to address authentic conservation problems. For example, if we had maps of suitable habitat for target species within potential reserve sites, we could expand our probabilistic formulation to include requirements for the amount and spatial arrangement of habitat area. Another practical application is a survey problem involving probabilistic species occurrence data. In this case, the decision maker needs to identify sites to exclude from development because of the presence of rare species. Because the location of rare species is not known with certainty and resources are limited, not all sites can be surveyed for species presence. The problem is to choose sites to survey to minimize the likelihood of developing sites with rare species present.

Regardless of the modeling approach, it is important to consider the range of conservation objectives held by decision makers, because most applications have no single agreed-upon conservation objective. As Metrick and Weitzman (1998) note,

> *The defining limitation of the economics of biodiversity preservation is the lack of a common denominator or natural anchor. As a society, we have not even come close to defining what is the objective. . . . This is the essential problem confounding the preservation of biodiversity today.*

Different conservation objectives may lead to different conservation strategies. It is our hope that multiobjective models like ours will help decision makers identify opportunities for simultaneously meeting conservation objectives and design strategies that are balanced with respect to competing goals.

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