CHAPTER

A Review of Methods for Quantifying Wildlife Habitat in Large Landscapes

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Spatially explicit information about land use and vegetation composition and structure is now available for landscapes (i.e., areas of large spatial extent) around the world. Advancements in remote sensing and related technologies have increased the resolution and quantity of landscape data, and efforts have been made to increase the availability of landscape data (e.g., national Gap Analysis Program; Scott et al. 1993, Jennings 2000). Advancements also have been made in desktop computers and software to model vegetation dynamics [e.g., LANDIS (He et al. 1999, 2005; Mladenoff and He 1999), FVS (Dixon 2002)] and quantify spatial patterns [e.g., FRAGSTATS (McGarigal and Marks 1995, McGarigal et al. 2002)]. Geographic information system (GIS) software allows managers and researchers to study the spatially explicit effects of management decisions and other disturbances on vegetation at large spatial scales and allows researchers to include complex spatial processes in models of wildlife–habitat relationships (Roloff et al., this volume).

For practitioners to take advantage of relatively recent advances in information about landscapes and the means of processing, they must select from among the many different methods of quantifying habitat quality in large landscapes. Fortunately, part of the reason so many options exist is that methods have been developed for a variety of uses related to the management of land and wildlife (Beck and Suring, this volume). Some methods are designed to provide a general index of habitat quality, whereas others attempt to use measures of habitat quality to predict animal presence, population density, or population viability. Also, methods have been developed to incorporate increasingly complex interactions between wildlife and landscapes and to reduce various technical limitations, such as statistical assumptions.

Papers addressing the topic of quantifying wildlife habitat in large landscapes occur in a wide range of primary literature, from wildlife and other ecology journals to those in remote sensing and urban planning, so reviews of this material are needed. Roloff et al. (2001*b*) provided an overview of models used in wildlife management and included guides to help managers select an appropriate category of habitat model for a specific use. Guisan and Zimmermann (2000) reviewed the steps of predictive habitat distribution modeling, including theoretical and technical aspects of model formulation and calibration, and they reviewed some specific statistical methods. Guisan and Thuiller (2005) discussed the history of, recent advances in, and methodological issues (e.g., how to select an appropriate spatial scale) related to species distribution modeling. None of these reviews, however, focused on the variety of GIS-based methods for quantifying the quality and quantity of wildlife habitat in large landscapes.

Our primary goal is to provide a synopsis of available techniques to help managers and other practitioners become aware of the many alternatives that exist. We provide a context for understanding the various techniques for quantifying the quality and quantity of habitat in landscapes by organizing them in a progression of increasing complexity in terms of their objectives, minimum data requirements, and key assumptions. These three criteria are useful when considering which modeling approach might be best for a specific management question or problem. We also provide citations for numerous examples of different modeling approaches.

COMPLEXITY GRADIENT

We classified methods of modeling wildlife habitat into five general approaches that correspond to common objectives in habitat studies (Table 9-1). These approaches generally follow a complexity gradient that represents increasing levels of potential realism in the models. More complex habitat models also tend to be more mechanistic rather than descriptive, and they often rely on more data to estimate parameter values for the purported wildlife–habitat relationships (Fig. 9-1). More complex models, however, are not necessarily better than less complex models (Starfield 1997; Millspaugh et al., this volume); the utility of a model depends only on how well suited it is for its intended use.

The order in which we discuss the five approaches follows the admittedly imperfect complexity gradient with one exception. Models for predicting the presence or absence of wildlife can be quite simple (e.g., a dichotomous habitat quality index) or much more complex (e.g., logistic regression), but we chose to discuss predicting presence in the same section as the probability of occurrence. Likewise, the correlation between model complexity and the modeler's reliance on data is somewhat contrived because the degree to which wildlife–habitat relationships in a model are supported by data rather than expert opinion can vary. The conceptual framework represented in Fig. 9-1, however, provides a practical starting point for considering the options currently available for habitat modeling in a GIS.

Table 9-1 Specific Techniques and Examples for Five General Approaches to Evaluating the Quality of Wildlife Habitat Over Large Landscapes Using a Geographic Information System (GIS). Some Main Strengths of Each Approach Include the Potential Applications, Whereas Some Main Weaknesses Include the Minimum Data Requirements and Assumptions.

General Approach	Objective	Specific Techniques	Potential Applications[a]	Minimum Data Requirements[b]	Key Assumptions[c]	Citations for Examples
Presence or absence	Predict presence Estimate species richness	Designate only 2 habitat quality categories Logistic regression	Mapping species distributions Identifying biodiversity hotspots	Expert opinion supporting putative wildlife–land cover associations	Habitat influences animal distribution	White et al. 1997 Smith et al. 1998
Habitat quality indexing	Quantify habitat quality	Habitat evaluation procedures revised for GIS Weighted linear combination procedures Object-oriented programming	Development mitigation or compensation Evaluating site quality for restoration	Expert opinion supporting putative wildlife–habitat relationships	All significant habitat variables are included	Rickers et al. 1995 Hepinstall et al. 1996 Rickel et al. 1998 Clevenger et al. 2002
Probability of occurrence	Predict presence Estimate species richness Quantify probability of occurrence	Logistic regression Occupancy estimation Discrete choice Mahalanobis distance Resource selection functions (RSF) Artificial neural networks	Mapping important resources Evaluating interspecific interactions	Habitat measures at used and often random locations	Habitat influences animal distribution Animal use estimates are accurate All significant habitat variables are included	Clark et al. 1993 Cooper and Millspaugh 1999 Mace et al.1999 Özesmi and Özesmi 1999 Cooper and Millspaugh 2001 Fleishman et al. 2001 MacKenzie et al. 2002

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Table 9-1 Specific Techniques and Examples for Five General Approaches to Evaluating the Quality of Wildlife Habitat Over Large Landscapes Using a Geographic Information System (GIS). Some Main Strengths of Each Approach Include the Potential Applications, Whereas Some Main Weaknesses Include the Minimum Data Requirements and Assumptions. *cont...*

General Approach	Objective	Specific Techniques	Potential Applications[a]	Minimum Data Requirements[b]	Key Assumptions[c]	Citations for Examples
Density	Predict abundance Predict density	Home range or territory mapping Application of RSF Pattern recognition Linear regression	Estimating carrying capacity Evaluating land management alternatives	Habitat measures at locations with varying animal density Density estimates at the locations	Animal density estimates are accurate Population and habitat quality are in equilibrium All significant habitat variables are included	Roloff and Haufler 1997 Bellamy et al. 1998 Boyce and McDonald 1999 McClain and Porter 2000 Penhollow and Stauffer 2000
Population viability	Determine if area is large enough for a viable population Evaluate the level of viability	Quantify availability of high-quality habitat Bayesian belief networks Demographic simulation Estimate population growth rates directly	Identifying limiting factors Endangered species risk assessment or recovery planning	Habitat measures at locations with individuals of varying fitness Fitness estimates of individuals at the locations	Animal fitness estimates are accurate Population and habitat quality are in equilibrium All significant habitat variables are included	Liu et al. 1995 Akçakaya and Raphael 1998 Edelmann et al. 1998 Moilanen and Hanski 1998 Marcot et al. 2001

[a] *Potential applications are examples that are not necessarily exclusive to a single general approach.*

[b] *All listed techniques require a digital map of each habitat characteristic. The presence or absence approach may require only a land cover map.*

[c] *All listed techniques require an assumption that the habitat maps are accurate.*

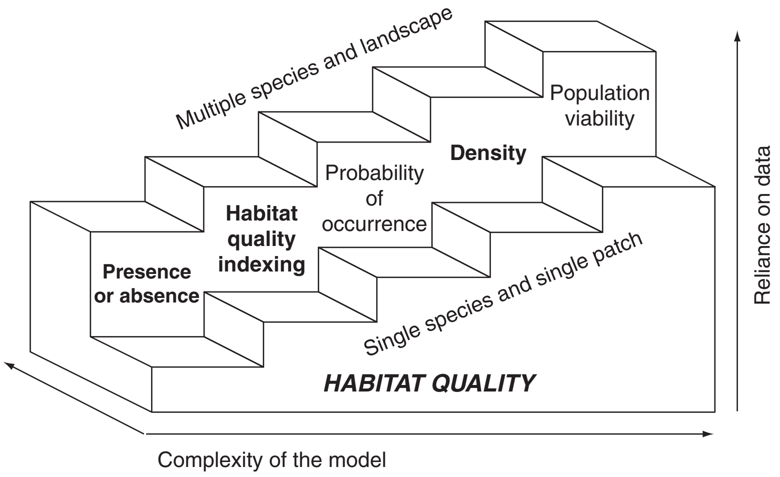

FIG. 9-1

A conceptual framework for GIS-based techniques used to evaluate the quality of wildlife habitat over large landscapes. Habitat quality forms the foundation of all analyses, and as the complexity of a model increases, so does the reliance on data to specify appropriate wildlife–habitat relationships. Additional methodological advancement is necessary for multispecies analyses, which are more complex than their single-species analogs.

Indexing Habitat Quality

Habitat Suitability Index (HSI) models are the basis of the Habitat Evaluation Procedure (HEP) developed by the U.S. Fish and Wildlife Service (1980, 1981) and constitute a basic mathematical technique for quantifying the quality of wildlife habitat. Expert opinion (Crance 1987) and published literature are used to develop functional relationships between the value of habitat attributes (e.g., % canopy cover) and index values between 0 (= not habitat) and 1 (= habitat of highest quality). In the HEP, which was the most common practice for modeling habitat until the 1990s, it was expected that a biologist applying the model collected field-based data to calculate HSI scores. This labor-intensive approach might limit the size of study sites and historically resulted in a focus on microhabitat characteristics (e.g., percent visual obstruction, density of woody stems). Now, however, it is common to use aerial photographs or satellite images of potentially large areas (e.g., 10s to 1000s of km^2) to quantify habitat attributes for use in HSI models (Breininger et al. 1991, Rempel et al. 1997, White et al. 1997, McClain and Porter 2000). Such remotely sensed data have also been used to directly define areas that provide suitable habitat and areas that do not (White et al. 1997). Models of wildlife–habitat relationships based on remotely sensed data often emphasize patch- and landscape-level characteristics rather than smaller-scale characteristics, but the distinction between microhabitat and landscape approaches is becoming less clear. Remotely sensed attribute data can be of high resolution (e.g., <1 m), field measurements of microhabitat characteristics from a sample can be extrapolated across a landscape based on cover types defined in a GIS, and habitat models can contain variables from different scales (Mitchell et al. 2001).

Geographic information system technology has transformed HSI modeling by allowing biologists to easily incorporate spatial structure (e.g., minimum area requirements, effects of habitat edges, juxtaposition of or distance to multiple life requisite resources, proportion of different land cover types), which is often appropriate and desirable (Donovan et al. 1987, Rickers et al. 1995, McClain and Porter 2000). For example, Gustafson et al. (1994) developed a proximity index ([size$_i$/nearest-neighbor distance$_i$] for all patches i=1 to n within a 300 m buffer) to incorporate the spatial configuration of forest patches in a habitat model for wild turkeys (*Meleagris gallopavo*). Another common technique to incorporate spatial structure is to evaluate habitat quality in a portion of the landscape (i.e., an analysis window) and then move the window across the landscape systematically (Riitters et al. 1997). Assuming a raster GIS is used, the HSI score for each window can be assigned to the central cell (= map pixel) or to all cells in the window, and the window can be moved 1 or many cells at a time. Window size (Roloff and Haufler 1997, Ortega-Huerta and Medley 1999, McClain and Porter 2000), percent window overlap, method of calculating the mean or interpolating HSI scores between window centers, and treatment of landscape boundaries are important considerations that may influence the results of a moving window habitat analysis (Hepinstall et al. 1996), but have not been studied comprehensively. We think window size should be ecologically meaningful, usually the scale at which the animal is believed to perceive, evaluate, and be influenced by habitat quality (e.g., home range size; Hildén 1965). Multiple window sizes relating to different aspects of habitat selection (e.g., nest site, foraging) could be used within a model for a single species. Given the high processing rate of modern desktop computers, we recommend moving windows 1 cell at a time because moving them any greater distance (e.g., with only 50% window overlap) requires interpolation and introduces unnecessary error in results of the moving window analysis.

Weighted linear combination (WLC) procedures for multicriteria evaluations (Voogd 1983) provide an alternative framework to HEP for habitat quality indexing (HQI). When WLC procedures are implemented in raster GIS (Eastman et al. 1995), values in maps of habitat attributes are standardized to the same unitless scale (e.g., 0–1). Then a matrix of pairwise comparisons between habitat variables is created from knowledge of or hypotheses about the relative importance of the individual variables to overall habitat quality (Saaty 1977). The principal eigenvector of the matrix contains weights that sum to 1. A habitat quality map is created by calculating the weighted mean of the standardized habitat variable scores in each raster cell. The advantages of the WLC approach are that pairwise-comparison matrices can simplify model development, most GIS software provides tools for implementing such models, and WLC is easily incorporated in a formal decision analysis (Eastman et al. 1995). Clevenger et al. (2002) used WLC procedures to incorporate expert opinion from individuals and published literature into assessments of black bear (*Ursus americanus*) habitat in Banff National Park, Alberta, Canada. They found that the literature-based model performed acceptably and similarly to a discriminant function when compared to independent data about where bears crossed a road, but the expert opinion model performed poorly.

An empirical alternative for indexing habitat quality involves calculating the Mahalanobis distance (D^2), or lack of similarity, which can be recoded to a 0–1 scale, between a vector of attributes of a raster cell (x) and the vector of mean attribute values from locations where animals have been observed (u), often obtained by radio-tracking (Clark et al. 1993). A main benefit of D^2 relative to other multivariate methods is that it incorporates the covariance matrix to standardize across variables and account for correlations among them. Knick and Rotenberry (1998), however, discovered that it was inappropriate to apply u and its covariance matrix in landscapes that were not sampled because differences in habitat characteristics (e.g., patch size) always result in greater D^2, even if a difference is in the direction of better habitat. They proposed as a solution using only the partitioned components of D^2 that vary the least and therefore represent a minimum rather than purportedly optimum set of habitat requirements (Rotenberry et al. 2002). Thatcher et al. (2006) and Browning (2005) provided recent examples of both approaches. As with other statistical models, it is important to include only habitat attributes that have hypothesized relationships to habitat quality to avoid spurious correlations.

The use of fuzzy systems and object-oriented programming (OOP) is a more sophisticated approach that allows for high-level abstractions of wildlife–habitat relationships and may represent the real world better than procedural programming (Booch et al. 1999). Fuzzy logic also can be used to incorporate the accuracy of spatial classification into habitat assessments. Although OOP is used to model animals and habitat patches as interacting objects, the approach is similar to other HQI modeling techniques because degree of membership scores, ranging from 0 to 1, are assigned to habitat patches based on the presumed quality of their habitat characteristics (Rickel et al. 1998). Furthermore, the main output, mean degrees of membership for a habitat patch, is analogous to an HSI score, which is usually a weighted mean of multiple suitability index scores on a 0–1 scale. A fundamental difference exists, however, between the theories underlying habitat models that are based on discrete categories of index values and those based on ambiguous, or fuzzy, categories (Hill and Binford 2002).

Predicting Presence and Probability of Occurrence

In some cases, models for predicting the presence or absence of a species in an area are less complex and require less data than an HQI model (Fig. 9-1) because one can simply define only two categories on the landscape: areas that provide habitat (= present) and areas that do not (= absent). Category definitions often are based on land use or land cover classifications (Aspinall and Veitch 1993, White et al. 1997, Smith et al. 1998), but they could be based on a minimum habitat quality threshold below which it is presumed the species will not occur (Table 9-1). For example, Browning et al. (2005) maximized the predictive gain by using as a threshold the index value at which the vertical distance between cumulative frequency distributions for percentage of study area and percentage of used sites was greatest. Liu et al. (2005) used common model assessment indices (e.g., sensitivity, overall prediction success) to compare 12 different approaches for determining a threshold value, assuming errors due to false positive species occurrences and false negative occurrences were equally important. They determined that the observed prevalence of species occurrence, mean predicted suitability (or probability of occurrence), and several joint functions of sensitivity and specificity (e.g., maximizing their sum) performed best. Maximizing the Kappa statistic performed worse, and subjective thresholds were worst. Regardless of category definitions and thresholds, using mutually exclusive categories to simplify habitat assessments can be problematic because true wildlife responses are unlikely to match the categories.

The theory and practice of modeling the presence of wildlife and estimating the probability of a site being occupied has advanced recently (Scott et al. 2002, MacKenzie et al. 2006). Logistic regression models (Coker and Capen 1995, Bellamy et al. 1998, Penhollow and Stauffer 2000, Fleishman et al. 2001), resource selection function (RSF; Manly et al. 2002) models (Mace et al. 1999), multiple-visit detection-nondetection surveys (MacKenzie et al. 2002), and artificial neural network models (Anderson 1995, Özesmi and Özesmi 1999) can be used to predict probability of occurrence or use from vegetation, landscape, and other habitat characteristics. Johnson and Gillingham (2005) directly compared Mahalanobis distance, RSF, and ecological niche models using the same training, habitat, and validation data. They also evaluated a qualitative HSI model that was based on expert opinion. Correlations between model predictions and validation data were high for the quantitative models ($r > 0.88$, $p \leq 0.02$) and lower for the HSI model ($r = 0.51$, $p = 0.30$). The quantitative models differed in how well they predicted areas of high versus low probabilities of occurrence, which resulted in low similarity among models in the spatial distribution of mapped habitats (Kappa $\leq$ 0.19). Dettmers et al. (2002) also compared multiple modeling methods (i.e., logistic regression, Mahalanobis distance, classification and regression tree [CART; Breiman et al. 1984], and discriminant function models), with a few qualifications mostly related to how the different models were applied to produce comparable results. Which model(s) performed best differed among the six bird species considered, but in general the discriminant function models performed well on the original study site but not when tested with independent data from another site; logistic regression and Mahalanobis distance models performed well at predicting probabilities of occurrence but performed worse at predicting presence, likely due to the need to apply a threshold value to define presence; and CART models were best at predicting bird presence.

Whereas the simplest models of presence and HQI models may be based solely on expert opinion, predicting probability of occurrence or use generally requires statistical models that are fit to data (Table 9-1). It is difficult to determine the absence of a species in a particular area, and presence is not perfectly related to habitat quality or quantity because the existence of habitat is a necessary but not sufficient condition for animal presence. Information about the presence or absence of a species, regardless of the modeling approach used for prediction, may be desired when species richness, rather than density or viability of any single species, is the response variable of interest (if so, see "Multispecies Approaches" later).

Estimating Population Density

When data exist or assumptions are justified to predict population density from habitat variables or index values, all the methods discussed in the preceding sections, especially RSF modeling, can be used to estimate density (Boyce and McDonald 1999). Even if seemingly appropriate data exist, several key assumptions are necessary to link habitat attributes to population density (or even presence). One must assume that knowledge of all limiting factors is included in the model, empirical data accurately reflect wildlife–habitat relationships, animals always select habitat perfectly, temporal fluctuations in habitat quality are adequately incorporated in the model, and the population has equilibrated with the habitat (Boyce and McDonald 1999). It also might be important to account for spatial autocorrelation in statistical models because different spatial scales of variation in wildlife abundance and habitat variables can affect inferences about wildlife–habitat relationships (Keitt et al. 2002). Relationships that allow the use of HQI models or models of species presence to make inferences about animal density (Gaston et al. 2000, Royle and Nichols 2003), however, should not be assumed to exist. In fact, the processes and variables that determine presence and density may differ, and even if positive relationships between presence and density exist, these relationships may change over time (Nielsen et al. 2005).

Various methods have been used to model densities of wildlife. Bellamy et al. (1998) used a 6-point scale of availability of large hardwoods to define suitable and unsuitable habitat for nuthatches (*Sitta europaea*) in woodlots of eastern Britain. Then they applied a nonlinear regression model developed for nuthatches in the Netherlands to predict expected number of breeding pairs from the area of suitable habitat in the woodlot and the surrounding landscape. Pereira and Itami (1991) multiplied the land area in each of several probability-of-occurrence categories by the mean density of squirrel activity areas in those categories to estimate habitat equivalents (U.S. Fish and Wildlife Service 1980), which represented the potential density of squirrels in portions of the landscape. McClain and Porter (2000) predicted population-density potential for white-tailed deer (*Odocoileus virginianus*) directly using pattern recognition (PATREC) methods (Williams et al. 1978), which seek patterns in habitat variables that are associated with areas of high and low animal abundance. Deer harvest data corrected for land accessibility, snow depth, and variation in hunting intensity at the scale of townships were used to develop the PATREC model and as a source of independent data for model validation. The PATREC model explained approximately twice as much of the variability in the independent deer harvest data as did an HSI model containing the same variables but parameterized based on a published study conducted in the same region. An advantage of the HSI model, however, was its greater spatial resolution.

Relative abundance of wildlife can be modeled using count data. Penhollow and Stauffer (2000) used multiple linear regression models to relate the mean number of detections of 23 bird species during point counts to GIS-based habitat characteristics, including forest age, overstory cover type, and eight metrics from FRAGSTATS. The species-specific models had adjusted R^2 values of 0.17–0.77, demonstrating how variable the success of applying a particular type of model can be among species. Royle et al. (2002) developed a statistically rigorous method for extrapolating information from counts of animals at points to a map of relative abundance over an entire region. The method accounts for spatial correlation in counts, incorporates habitat and other covariates, and allows for a spatially explicit assessment of uncertainty, which can be used to improve the allocation of subsequent survey effort. Thogmartin et al. (2004) applied this method to explore habitat relationships and map the relative abundance of cerulean warblers (*Dendroica cerulea*).

Roloff and Haufler (1997) developed a method of mapping home ranges that results in an estimate of population density. In their approach, home ranges are delineated using a GIS to accumulate a minimum number of habitat units (i.e., the area of a patch multiplied by its HSI score, summed over all patches of interest). The process begins with cells of the highest habitat quality and essentially follows an ideal free distribution (Fretwell and Lucas 1970). Furthermore, the mean HSI score of the focal cells for a home range must exceed a predefined habitat quality threshold of viability (Roloff and Haufler 1997). The population density is the product of the number of viable home ranges and the mean number of individuals in a home range divided by the total area of interest. Roloff and Haufler (2002) applied the same approach to the mapping of bird territories.

Evaluating Population Viability

Approaches to evaluating the viability of a population using habitat data fall into four categories: assessing availability of high-quality habitat, Bayesian belief networks (BBNs; Oliver and Smith 1990), population simulation, and estimating population growth rates directly. Availability of high-quality habitat can be estimated with home range mapping procedures (Roloff and Haufler 1997). First, a minimum viable population size must be specified. An area is then deemed sufficient to support a viable population if it is large enough to contain the minimum number of adequate home ranges. This approach may be useful for assessing the suitability of a reserve of limited size for animals that have large home ranges or territories. It can also be used to evaluate more subtle changes in viability due to changes in habitat quality (Roloff and Haufler 2002).

A BBN "depicts the logical or causal relations among ecological factors that influence the likelihood of outcome states of some parameter(s) of interest" (Marcot et al. 2001:30). Habitat-based BBN models can be used to predict virtually any habitat or population performance measure (i.e., from an index of habitat quality to population viability). To evaluate wildlife population viability, Marcot et al. (2001) specified input (e.g., habitat) variables and assigned them prior probabilities of being in a given state. The probability that intermediate (e.g., life requisite) variables were in a given state was conditional on (i.e., linked to) input and other intermediate variables that affected them. The final, posterior probability was the likelihood of a population being in one of five qualitative viability categories. The BBN models developed by Marcot et al. (2001) were integrated with GIS and were used to evaluate habitat at multiple scales.

Simulating population growth is a common method for population viability analysis (PVA; Beissinger and Westphal 1998; Beissinger et al., this volume; Akçakaya and Brook, this volume). Models for PVA range from deterministic, single population matrix projections (Caswell 2001) to stochastic, spatially explicit metapopulation simulations (Hanski and Simberloff 1997), with increasing complexity and data requirements. Although each type of model can be used to evaluate the effects of habitat quality and quantity on vital rates and the effects of vital rates on population viability, it is often easiest to account for spatial variability in habitat quality and vital rates in metapopulation models. Incidence function models (Hanski 1994) predict whether or not metapopulation units (i.e., patches) are occupied, usually from individual extinction and colonization probabilities (E_i and C_i) for each patch. Incidence function models often base E_i and C_i predominantly on patch size and interpatch distances, respectively. Moilanen and Hanski (1998) used patch-specific habitat quality information to influence the effective patch size and interpatch distances in their incidence function model. More specifically, they multiplied E_i and C_i by parameters that were, in turn, defined by third order polynomial functions of habitat quality variables. Donovan and Thompson (2001) used a modified matrix model to estimate metapopulation growth rates of a generalized migratory songbird in landscapes composed of various proportions of high- and low-quality habitat that differed in the reproductive success rates of birds nesting in them. Akçakaya and Raphael (1998) used a home range mapping procedure to define habitat patches (and their carrying capacity for northern spotted owls [*Strix occidentalis*]), which were then used as population units in a spatially explicit, habitat-based metapopulation simulation model (RAMAS GIS; Akçakaya 2000*a*, 2006; Akçakaya et al. 2004*a*). Nickelson and Lawson (1998) used regression models to estimate potential production and survival rates of coho salmon (*Oncorhynchus kisutch*) smolts for specific stream reaches from habitat data. Then they combined the vital rates for smolts with estimates of other population parameters in a reach-specific metapopulation simulation model. Liu et al. (1995) used habitat-specific fecundity in a third type of spatially explicit population simulation model, an individual-based model, to evaluate the population viability of Bachman's sparrows (*Aimophila aestivalis*). Liu (1993*a*) also discussed how the initial distribution of individual sparrows among patches that vary in habitat quality and the length of time each patch provides habitat can influence population viability.

As an alternative to data- and computer-intensive population simulations, population growth rates can be estimated directly using habitat quality data. Growth rates are indicators of viability, but they may not account for factors such as density dependence when they are estimated from habitat data. Fortunately, models relating habitat quality to population growth rates are flexible enough to overcome many potential drawbacks. Edelmann et al. (1998) developed regression models to estimate sage grouse (*Centrocercus urophasianus*) vital rates for each cell in a raster GIS from habitat data. A second type of regression model was used to estimate population growth rates (λ) from the cell-specific vital rates. Evaluation of population viability was based on the frequency distribution of λ in all cells. Similarly, Moore et al. (2000) used a quadratic function of stand age and basal area to model λ directly for a hypothetical forest bird metapopulation. They simulated stand-specific population sizes, recalculated λ at each time step because habitat quality changed over time, and incorporated source-sink dynamics (Pulliam 1988).

ADDITIONAL CONSIDERATIONS

Selecting and applying methods for quantifying the quality and quantity of wildlife habitat in landscapes involves consideration of more than just the gradient of model complexity. Additional considerations should include whether to use a multispecies model rather than multiple single-species models, how to make comparisons of habitat quality among different landscapes, and how to evaluate the habitat model.

Multispecies Approaches

Several investigators have incorporated >1 species in their habitat evaluations, but most deal with each species separately rather than quantifying habitat quality for groups of species (Kliskey et al. 1999; Marzluff et al. 2002; Noon et al., this volume). For example, a computer program developed by Li et al. (2000) contains habitat models for hundreds of species, but effects of differences among landscapes are not integrated across species. Van Horne and Wiens (1991) discussed difficulties they encountered in their evaluation of the feasibility of combining HSI models for 16 forest bird species into a single, more general model. An approach proposed by Hansen et al. (1999:1461) "integrates aspects of species prioritization, dynamic habitat modeling, and PVA" in an effort to balance coarse filter and fine filter methods under time and budget constraints imposed on managers. Using this approach, species are ranked by risk of extinction at continental to watershed scales based on population status and threats to habitat. A few species with the highest ranks (i.e., lowest viability) are targeted for local demographic research and quantitative PVA. Habitat quality models are developed for several species with the next highest rankings. Then alternative management strategies based on species rankings are evaluated (Hansen et al. 1999). Fine filter models for ecological indicator species (Morrison et al. 1998:337) can also be used to evaluate coarse filter habitat quality for multiple members of a community.

One way to evaluate habitat availability for multiple species directly is to link habitat characteristics to the species richness or diversity of wildlife. White et al. (1997) evaluated the diversity of terrestrial vertebrates based on habitat relationships, and they summarized their results in terms of species richness and habitat abundance (i.e., area of suitable habitat summed across species). A habitat model tested by Flather et al. (1992) predicted avian species richness in landscapes of the eastern United States. Similarly, Penhollow and Stauffer (2000) developed linear regression models to relate landscape characteristics to avian species richness and assemblage index values (e.g., Shannon-Wiener). Fleishman et al. (2002) modeled species richness as well as occurrence and persistence in their analysis of butterfly habitat in the Great Basin of the western United States. However, a concern with modeling species richness for conservation planning is that all species are treated equally, and common species tend to contribute the most to richness (Flather et al., this volume).

Occupancy models (MacKenzie et al. 2004) and artificial neural networks (ANN; Anderson 1995) have potential for multispecies habitat modeling. Both types of models can predict probabilities of occurrence for >1 species simultaneously, thereby incorporating interactions among them. Unlike occupancy models, in which probabilities of occurrence are calculated jointly for all species, ANN models calculate the probabilities separately for each species, so the output is summarized as species richness. Özesmi and Özesmi (1999) developed a two-species ANN model for bird nest site habitat and implemented it in a GIS, but it was based on microhabitat variables that typically are not available for large areas (e.g., height and density of herbaceous stems).

Akçakaya (2000*b*:S80) proposed a unique way to use habitat-based, single-species models of population viability to produce a "multispecies conservation value" map. Each cell in the map contains the weighted mean of HSI scores for all species at that location. The weighting factor accounts for the probability of extinction or decline of each species (presumably, any index of species importance could be substituted) and the contribution of the location to the viability of each species, which is the difference in extinction probability between a model that includes the location and one that does not (Akçakaya 2000*b*). The weighted linear combination procedure described by Eastman et al. (1995) could be used to weight species importance for subsequent inclusion in Akçakaya's (2000*b*) multispecies conservation map or for combining habitat quality maps for multiple species in the absence of quantitative viability information.

In addition to maximizing species richness or a weighted mean HSI score, Hof and Raphael (1993) recognized two other multispecies objectives. The main objective of a management plan could be to maximize the minimum probability of viability among all wildlife species of interest or to maximize the joint probability of viability across all species of interest. Hof and Raphael (1993) assumed in their model that viability was linearly or logistically related to relative abundance. They demonstrated, however, that results differed depending on which objective was satisfied.

Comparing Landscapes

Spatial Comparisons.—Habitat analysis can be used to evaluate a single landscape, but often it is used to compare ≥2 landscapes across spatial or temporal (Rickers et al. 1995) intervals. Habitat suitability index values have been summarized across a landscape by calculating the mean (Donovan et al. 1987, Rickers et al. 1995), multiplying patch size by HSI score to obtain habitat units (Rickers et al. 1995, Marzluff et al. 2002), or providing the quantity of area in distinct HSI value categories (Herr and Queen 1993; Hepinstall et al. 1996; Riitters et al. 1997; Kliskey et al. 1999; Ortega-Huerta and Medley 1999; Dijak and Rittenhouse, this volume). Further summarization may also be useful, such as calculating the ratio of "optimal" to "marginal" patch area, which may influence some populations (Lidicker 1988).

It would be more informative to provide the entire cumulative frequency distribution of HSI values in the landscape (Gustafson 1998). The generic GIS model developed by Ortigosa et al. (2000) to calculate values for HSI models creates a frequency table of mutual occurrence (based on a cell-by-cell comparison) of HSI categories, which is analogous to comparing cumulative distribution functions of HSI values. These simple summaries fail to make full use of available GIS technology because they do not fully characterize spatial differences among landscapes. Riitters et al. (1997) used landscape metrics (e.g., connectivity, contagion, fractal dimension) and mean patch size of suitable habitat to elaborate their summary of habitat quality, and Trani (2002) demonstrated the effect of spatial resolution on landscape metrics. Mitchell (1997:129) used Moran's I coefficient (see Cliff and Ord 1973, Cressie 1993) as an index of spatial continuity (i.e., autocorrelation) in HSI values for his landscape comparisons. More recently, Johnson et al. (2004) used a local quadrat variance method to identify spatial patterns in land cover, and similar methods could be used to quantify patterns among patches of habitat. Perhaps most comprehensively, elaborations of the Kappa statistic can be used to compare both the quantity and location of differences in model predictions at multiple spatial resolutions in raster maps of categorical data (Pontius 2000, 2002; Hagen 2003), but see the critique and an alternative for presence-absence comparisons by Allouche et al. (2006).

Predicted animal densities or metrics of population viability can be used to compare landscapes when habitat-based models of density or viability are used. Data relating HSI values to animal density also can be used to summarize landscape quality in these terms (Breininger et al. 1991). Once the quality or quantity of habitat or the density or viability of a wildlife population is summarized for a landscape, spatial comparisons among landscapes can be made using the corresponding summary statistics of greatest interest.

Temporal Comparisons.—A further level of sophistication in landscape comparisons involves simulating the habitat or population-level effects of vegetation dynamics and alternative management decisions over time. Several studies provide examples of simulating forest growth and harvest followed by or linked with an evaluation of wildlife habitat quality. Kliskey et al. (1999) used a GIS-based HSI model to compare habitat suitability for marten (*Martes americana*) and woodland caribou (*Rangifer tarandus*) among four timber harvest scenarios for a large watershed in British Columbia. Marzluff et al. (2002) used a similar approach to evaluate habitat suitability for three nongame species under five management scenarios for a 566 ha forest in western Washington. Bettinger et al. (1996) modeled the effect of several timber management options on a habitat effectiveness index for elk (*Cervus elaphus*; Ager and Hitchcock 1994) in a watershed in northeastern Oregon. LEEMATH evaluates alternative forest management strategies in terms of habitat potential for many bird, reptile, and amphibian species (Li et al. 2000). Some of these species models also incorporated other landscape planning considerations such as stream fish habitat and economics.

Temporal comparisons of habitat values also can be made at higher levels of the complexity gradient. Olson and Orr (1999) developed a model that tracks the presence and absence of wildlife species as a function of the size, density, and species composition of trees within the forest stands of a timber growth and yield model (FREIGHTS; Krumland 1990). Boyce and McDonald (1999:271) advocated the use of RSFs to compare wildlife population sizes at different points in time, but they acknowledged that "RSF coefficients might change as resource availability changes."

Few models of which we are aware simultaneously simulate habitat dynamics (e.g., forest succession and harvest) and habitat-dependent population viability. The model developed by Moore et al. (2000) incorporated an optimization framework that defined timber harvest strategies (i.e., a series of decisions about where, when, and how much to harvest) to maximize bird abundance at the end of a planning horizon. Birds within a stand were treated as a population whose growth rate was a quadratic function of stand age and basal area. ECOLECON (Liu 1993*b*) used habitat-specific fecundity to directly link an individual-based population simulation with a forest growth and yield subroutine in a spatially explicit landscape (Liu et al. 1995). Similarly, RAMAS Landscape (Applied

Biomathematics, Setauket, New York), which is available commercially, integrates a landscape vegetation model, LANDIS (He et al. 2005), with a wildlife metapopulation model, RAMAS GIS (Akçakaya 2006; Akçakaya and Brook, this volume). RAMAS Landscape has been used to evaluate the effect of timber harvest regimes on the viability of sharp-tailed grouse (*Tympanuchus phasianellus*) populations in Wisconsin (Akçakaya et al. 2004*b*) and the effect of different fire-return intervals on the viability of Bell's sage sparrow (*Amphispiza belli*) in California (Akçakaya et al. 2005). Larson et al. (2004) modeled the viability of ovenbird (*Seiurus aurocapillus*) populations in Missouri using LANDIS and RAMAS GIS separately.

Model Evaluation

Habitat models are developed to satisfy a variety of objectives. Each model, therefore, should be evaluated by the degree to which it accomplishes the specified objectives, not by its complexity, or the degree to which it represents reality (Millspaugh et al., this volume). A basic objective of most habitat models is to predict some aspect of a wildlife population (e.g., presence, density, survival), so assessing predictive ability is a critical component of model validation (Vaughan and Ormerod 2005). This requires wildlife-use data that are independent of those from which the model was developed. Some evaluation procedures are related to specific methods for habitat modeling (e.g., Boyce et al. 2002, Fielding 2002) or the type of data available for model building and testing (e.g., Ottaviani et al. 2004). It is informative not only to evaluate model predictions with new observations from the original study site but also to evaluate predictions in new geographic areas (Mladenoff et al. 1999). Vanreusel et al. (2007) argue that models based on functional resources (e.g., specific foods) rather than environmental surrogates (e.g., topography, climate) are more likely to be transferable to new areas. True validation also addresses other components of the modeling process (Roloff and Kernohan 1999), such as a logical analysis of model formulation (Guisan and Zimmermann 2000).

Beutel et al. (1999) discussed six assumptions inherent in models of presence or abundance—habitat influences animal distribution, the predicted distribution is adequately modeled, habitat is adequately measured, distribution is adequately measured, measured distribution equates with habitat quality, and habitat quality is adequately measured—and ways to test their validity. Roloff and Kernohan (1999) provided a checklist for HSI model validation studies and emphasized that surrogates of fitness (e.g., reproductive rates, survival), rather than presence or abundance, should be used. One of their main concerns was that authors often ignored the variability of input data and its impact on model outputs. Although the presence of sampling error in habitat attribute data gathered in the field is well known, the measurement error associated with remotely sensed data and other GIS databases may not be as widely appreciated (Stoms et al. 1992). Monte Carlo simulation can be used to calculate confidence intervals for HSI scores from uncertainty in input variables (Bender et al. 1996), and fuzzy math (Ferson et al. 1998) can be used to calculate reliability bounds on HSI scores from both statistical and structural uncertainty in the model (Burgman et al. 2001).

When appropriate data exist, validation of habitat models is straightforward in a GIS framework because correlations can be computed between values in a map of population parameters of interest and values in a habitat quality map (Duncan et al. 1995). Roloff et al. (2001*a*) used the volume of intersection index (Millspaugh et al. 2004) to compare the utilization distribution predicted by a habitat effectiveness model for elk and the utilization distributions of elk herds, which were based on radio-tracking data. Mladenoff et al. (1999) used compositional analysis (Aebischer et al. 1993), comparing habitat use and availability, to validate their logistic regression model of gray wolf (*Canis lupus*) habitat in Wisconsin. Resampling methods (e.g., cross-validation, bootstrapping) provide an alternative to collecting new, independent data for evaluating correct classification rates for models used to predict presence and absence (Verbyla and Litvaitis 1989).

Reducing the resolution of a model or its output (see "Comparing Landscapes" earlier for examples of how to summarize habitat model outputs) for validation purposes may be helpful if independent data about wildlife populations (e.g., harvest indexes, regional surveys) are more readily available at a landscape scale (e.g., township, county, watershed) rather than a patch scale (i.e., an area of relatively homogeneous vegetation). Furthermore, the scale at which land management objectives are most relevant, often the landscape, is also the most relevant scale at which to evaluate model performance. Model validity, however, is currently limited by a lack of information about the spatial components of wildlife habitat (e.g., minimum patch size) and relationships between habitat quality and landscape indices (Li et al. 2000).

Furthermore, model validation alone is not sufficient for determining whether a given model is better or worse than possible alternatives (Conroy and Moore 2002). Adaptive management provides a framework for using repeated collections of new data to reduce the uncertainty about which model is best for predicting the consequences of management decisions (Williams et al. 2002).

CONCLUSIONS

Recent technological advancements in the collection and analysis of spatially explicit data for large geographic areas have facilitated the development of new methods for evaluating wildlife habitat. Currently, our ability to incorporate wildlife population objectives in land management plans is limited more by a lack of knowledge about the relationships between the quality and quantity of habitat and animal use and demographics. We recommend, therefore, that a focus remain on improving our understanding of wildlife-habitat relationships (Morrison 2001), which will require studies of resource use by animals across a wide range of spatial scales. Such information would be most useful if it were summarized and made widely available in published databases (e.g., Wisdom et al. 2000).

Habitat modeling should be encouraged, even when knowledge is imperfect or data are scant, for several reasons. Developing models compels us to formalize our hypotheses about wildlife–habitat relationships. Habitat models organize existing knowledge in a format useful to managers. They also help us identify gaps in existing knowledge and prioritize future research objectives for filling the gaps. Managers and researchers also should be aware of the potential drawbacks of misusing habitat models. All models are imperfect representations of reality, and inferences based on them should be treated as hypotheses, or best estimates, rather than facts. Furthermore, habitat models are more useful for making relative comparisons of habitat quality among landscapes than they are for making accurate predictions about habitat quality at a given place and time.

Given the broad range of objectives for which wildlife habitat models are developed, we expect that the methods and approaches for developing such models will continue to expand rather than narrow to just a few that might be deemed best, or universally applicable. Some specific methodological advancements seem particularly important. Biologists should strive for a comprehensive approach to summarizing the quality, quantity, and spatial structure of habitat over large areas (Gustafson 1998). Summarizing and analyzing changes in those statistics over time may require a different approach. Furthermore, quantifying the uncertainty in the output of models should be more commonly applied. Such practices are necessary to make complete and valid comparisons among management alternatives. We also need to develop additional options for considering >1 species simultaneously at all levels of habitat modeling complexity (see Noon et al., this volume).

A general approach we think continues to hold promise was mentioned by Wiens (2002) as he speculated about the future of habitat modeling: focusing on process. Several processes at the individual and population levels link wildlife populations to the way they use space, and understanding those processes will improve our conceptualization of wildlife habitat. When we consider the processes that produce the patterns we observe, habitat models are more meaningful and the causes of discrepancies between predicted and realized patterns of use can be logically investigated.

Progress in habitat modeling techniques is likely to continue to be driven, or at least accompanied, by increasing quantitative and scientific rigor. The demand for skilled modelers with a sound understanding of the best available methods also may increase. We hope the future also holds the true integration of science and decision making. Not only are the expertise and experience of both researchers and managers necessary for developing most habitat models, resources spent on model development are largely wasted if the model is not used to inform management decisions.

SUMMARY

Recent technological advancements in the collection and analysis of spatially explicit data for large geographic areas have facilitated the development of new methods for evaluating wildlife habitat. We reviewed various methods that have been developed or revised for geographic information systems to evaluate the quality of wildlife habitat or to predict how wildlife populations respond to spatially explicit changes in habitat caused by land management decisions. Our goal was to provide a synopsis of available techniques and organize the methods along a complexity gradient with increasing levels of potential realism in the models. We also discussed multispecies approaches, methods of comparing landscapes, validation of habitat models, and several applications of each method. Further research is needed to advance knowledge of wildlife–habitat relationships; to develop multispecies methods; and to provide a comprehensive approach to summarizing the quality, quantity, and spatial structure of wildlife habitat over large spatial and temporal scales.

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