Habitat Models for Land-Use Planning: Assumptions and Strategies for Development

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Introduction

Wildlife managers have long recognized that management goals must be constrained by the availability and suitability of habitat. This recognition, combined with ever increasing land development pressures, has resulted in environmental legislation emphasizing systematic approaches to collection and analysis of habitat information. Wildlife planners have responded with a variety of approaches to the development of models that quantify habitat requirements.

The use of habitat models in wildlife management is certainly not a new concept. Early models attempted to relate habitat quality and quantity as defined by various life requisites (Trippensee 1948). Conceptually, these early approaches are identical to many contemporary efforts directed at modeling habitat.

This paper has two objectives related to contemporary habitat modeling approaches. The first objective is to characterize the assumptions and limitations inherent to operational habitat models. Various approaches to habitat modeling, some of which will be discussed at this conference, are described in their own terminology—which tends to obscure the fact that they have common ideals and are subject to the same sets of limitations.

The second objective of this paper is to describe a strategy for development of habitat models consistent with these potential limitations. There seems to be two divergent perspectives on operational habitat models. The first is an ideal perspective, which views operational habitat models with skepticism because the current state of habitat knowledge is limited. The second is a pragmatic perspective, which recognizes that available habitat information, no matter how incomplete, can be used to improve the credibility of a land-use decision. The strategy outlined in this paper is directed toward the latter perspective but may help to bridge the gap between the pragmatic and ideal.

The Habitat Approach to Land-Use Planning

Habitat has many definitions (Coulombe 1977) but has been defined theoretically as the location that supports a wildlife population including space, food, cover, and other animals (Giles 1978) and often is characterized by vegetation, landform, and hydrology (Odum 1971). Variations in food, cover, and physical features of habitat often are paralleled by observed differences in animal abundance. As a possible explanation for these variations, the concept of habitat preferences has been devised (Ricklefs 1973). The supporting logic for this concept is that populations display genetically determined preferences for habitats that favor their survival and reproduction. Wildlife managers attempt to decipher the causal relationships associated with habitat preference and then use this knowledge for land use planning.

Application of habitat concepts to land-use planning requires systematic methods of relating habitat conditions to potential population abundance, i.e., a habitat model. A model is a representation of a system or phenomenon and contains information in a predetermined form intended to be interpreted in accordance with predetermined rules (Thesen 1974). In order to accomplish its objectives, a model must be structured in a form that allows the user to interpret its output. The output of a habitat model must, therefore, at least have implicit units of measure that address characteristics of both the wildlife population and its habitat, i.e., "a land parameter measured in animal units" (Giles 1978:194). The concept of carrying capacity is often used in this context.

Carrying capacity as used in the field of population ecology is the density of organisms at which the net reproductive rate equals unity (Pianka 1974). In this context, carrying capacity is dynamically defined as an equilibrium between population birth and death rates which are regulated by the interaction of habitat variables and the population itself (Figure 1).

The habitat approach to land-use planning is focused at assessing potential wildlife population limits. A distinctive aspect of the habitat approach is that the wildlife manager can perform the analyses without case-by-case measurement of the wildlife population. However, carrying capacity, as defined previously, may be unmanageable because of extensive data requirements and the unknowns concerning specific relationships. But since it is a broad concept and accounts for all environmental factors that limit wildlife populations, we can use it as a standard

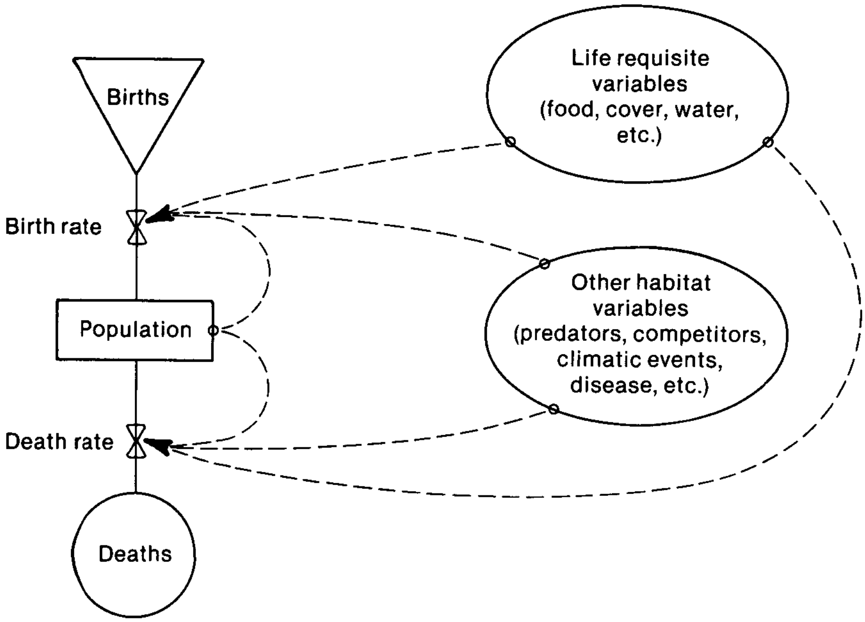

Figure 1. Diagrammatic view of carrying capacity, defined as existing populations, which is determined by birth and death rates.

against which operational definitions of habitat and associated carrying capacity estimates are based.

Assumptions and Limitations of Operational Habitat Models

Operational habitat models include only a subset of the variables required by theoretical definitions of habitat. Habitat models are frequently constructed around easily measured physical and floristic variables thought to represent food, cover, and reproductive needs of a wildlife population. Operational habitat models may exclude some types of habitat information (e.g., other species populations) that may have a more subtle and, in some cases, perhaps a more influential effect on population limits.

The model builder and model user must constantly be aware of the void between theoretical and operational definitions of habitat. The unreliability of operational habitat models in accurately depicting population limits may arise from a combination of situations involving the kinds of habitat information excluded from the model. For purposes of discussion, habitat models can be characterized by breadth and depth of detail. Model breadth is proportional to the number of habitat components (e.g., seasonal habitat, food, cover, other animals) addressed. Model depth is proportional to the number and kinds of variables chosen to describe each habitat component. Habitat models almost always emphasize either depth or breadth, rather than both simultaneously. A habitat model with depth but little breadth of detail, for example, might include many variables related to food energetics (i.e., a food carrying capacity model), including those that define the allocation of food resources to food competitors. If sufficient data were available, the model might be expected to produce reasonable estimates of observed populations under conditions when food resources impose limits on the population. Of course, the potential limitation of this model is that the population may be limited by habitat variables other than those directly related to food, and the model excludes information of concern to the wildlife manager.

More commonly, operational habitat models consider a relatively large breadth of habitat components such as food, cover, and reproductive requirements, with each component being assessed with little detail. Thermal cover, for example, may be measured by vegetation structure only. However, the significance of various conditions of vegetation structure for determining the suitability of thermal cover may be dependent on other environmental variables that contribute to determination of energy budgets and thus population growth rates (Kendeigh et al. 1977).

The potential limitation of models with little depth is that numerous weakly supported assumptions are required in the model, and it may be difficult for the model user to define conditions under which the model is likely to succeed or fail in providing accurate estimates of population limits.

The problems of restricted model breadth or depth are amplified when existing information is used to construct a model. Wildlife populations are subject to limits imposed by the total environment, yet the entire spectrum of variables composing the total environment is never described. In addition, individual studies are often site-specific and unrelated, making generalizations concerning habitat model relationships difficult. Synthesizing available data into model relationships involves considerable judgment and often requires subjective decisions. As the number of assumptions that must be made in this data synthesis increases, the probability that a habitat model will be unreliable in accurately depicting population limits also increases.

These considerations provide the basis for several conclusions concerning operational habitat models:

1. A habitat model must have sufficient breadth to encompass components that are instrumental in determining population limits.
2. It is not reasonable to expect a given habitat model to be a universally reliable indicator of population limits because key habitat components may vary between areas of model application.
3. A habitat model with restricted depth may be insensitive to subtle environmental changes and may predict only relative changes in population limits with perhaps a high degree of reliability in predicting the direction of change (+ or −), but a lower degree of reliability in predicting the magnitude of change.
4. A habitat model should be structured for a particular application to enhance its credibility with respect to the above points.
5. Numerous assumptions will be made during model construction, particularly if no new habitat information is collected specifically for the modeling effort.
6. The model assumptions must be clearly stated in order to evaluate the model's credibility in contributing to a land-use decision.

These considerations are integral to the following strategy for model construction.

Strategy for Development of Habitat Models

Land use impacts on wildlife are a function of the habitat variables affected by the particular land use and the degree to which these variables are significant determinants of wildlife population limits. A habitat model developed for land-use planning should define the habitat variables that are likely to be limiting for the population at the model application site and synthesize measures of the variables into a description of habitat that is useful for decision making. The model building strategy outlined below works within these guidelines. This strategy is a synopsis of one described by the U.S. Fish and Wildlife Service (1981) and is based on strategies developed for approaches to ecosystem modeling (Hall and Day 1977, Holling 1978, Innis 1979). The model building strategy is comprised of three basic phases: (1) setting objectives; (2) formulating model relationships; and (3) evaluating model performance.

Model Objectives

Setting clear objectives helps to insure that model construction occurs within well-defined limits and terminates at a pre-selected level of detail appropriate for the problem to be solved. Model objectives generally include statements concerning the kinds of information required to solve a land use problem, but also must take into account limitations of money, time, and data availability. Habitat model objectives discussed herein include: (1) defining an acceptance level for model output; (2) defining the breadth of habitat to be modeled; and (3) defining the geographical area to which the model is applicable.

Defining an acceptance level for model outputs. The ideal habitat model from a technical perspective will produce very precise and accurate estimates of population limits in terms of individuals per unit area. However, an acceptance level for model outputs should be defined because obtaining the ideal may not be technically feasible for reasons discussed earlier or may not be necessary for a land use application. The acceptance level will vary depending on the reliability required in a particular land use study. The acceptance level defines an operational end point of model development; i.e., when the model is suitable for actual use. Clearly stated acceptance levels are a necessary prerequisite for later stages of model development (i.e., model evaluation) and include statements about required precision and accuracy.

Model output precision may be set at two possible levels: (1) unitless outputs in verbal (e.g., rating of poor, good, excellent) or index form; and (2) outputs in measurable units (e.g., individuals per unit area). Many land use studies require model outputs only in the verbal or index form because the needs of these studies can be met by merely ranking alternatives. The advantage of producing only unitless ratings is that precise and accurate data are not required and the number of model assumptions can be kept to a minimum. However, the assumptions that are made must be clearly stated.

Models that must provide outputs in measurable units require accurate and precise empirical information. The data requirements often cannot be met with available information and therefore additional assumptions are required to construct the model. Construction of a model with measurable output units may therefore require additional efforts in testing and reformulating assumptions.

Given an output precision level, a habitat model should meet a prescribed level of accuracy in mimicking reality. There are several possible standards against which a model's reality can be judged. The most defensible test may be a comparison against observed population limits. Although desirable in the long term, it may not be necessary or possible within cost constraints to conduct these tests for many land use studies. Other acceptable standards may be review of the model predictions by study team members or species authorities. If the model predictions reflect the reviewers concept of reality, the model is accepted.

Model breadth. The number of habitat components included in a model should not be overly constrained for reasons discussed earlier. However, setting limits on the habitat components to be included in the model puts bounds on the amount of habitat information required and may reduce the data gathering effort. In constraining model breadth, the model builder must make assumptions about which habitat components are likely to be affected by the land use to the extent that wildlife population limits will be altered. Possible bounds on model breadth include perceived critical seasonal or life stage (e.g., juveniles) habitats.

Geographic area of model applicability. Defining the geographic area of model applicability also will limit the information required to build a model. For a particular land use study, the geographic limits must include the area affected by the land use change. However, if one desires to apply a habitat model to multiple studies, it may be cost effective to build a more general model. This would be modified to accommodate geographic variation in habitat use and land use impacts for individual applications.

Model Relationships

After model objectives have been set, the model builder develops hypotheses about the habitat that will be modeled. These hypotheses involve identification of habitat variables and development of assumptions about the functional relationships of habitat variables into a model consistent with the objectives set for the model.

Developing model hypotheses can be simplified by dividing the habitat into components. These components can include seasonal habitats, specific habitats for species life stages (e.g., juveniles, adults), or life requisites (e.g., food, cover). This subdivision may continue through several levels where components are divided into subcomponents to the point that a clear hypothesis can be stated for the lowest level subcomponents, i.e., each subcomponent can be functionally related to one or more measurable habitat variables.

Interspersion of habitat components may be an important model consideration. Many species utilize habitat mosaics, and individual habitat needs may be associated with specific types of vegetation or landform. Therefore, a habitat model may need to include characteristics of more than one vegetation type and incorporate hypotheses about their spatial configuration. To develop the spatial hypotheses efficiently, habitat components may be linked to vegetation type sections of a model (Figure 2). This model structure introduces a set of spatial variables describing the interspersion of habitat components using vegetation types only as abstract measurement units.

A model based on habitat components explicitly describes hypothesized causal relationships between habitat variables and carrying capacity. Basing the model on a component structure allows the wildlife manager to exercise professional

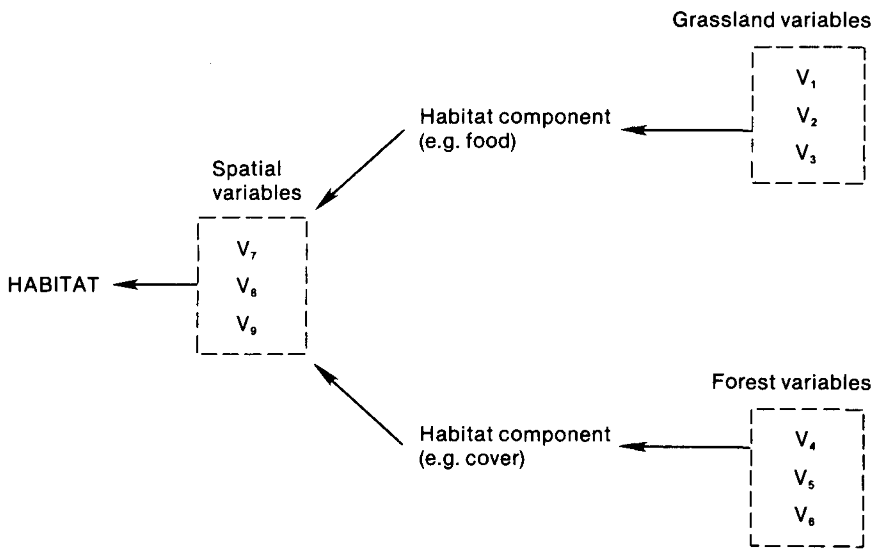

Figure 2. Graphic habitat model, structured around cover type and spatial variables.

opinion in interpretation of model results. The model structure provides a template against which potentially significant habitat variables (not included in the model) can be assessed as possible causes of unreliable model results. Finally, a component structure permits model improvement because individual assumptions can be isolated and tested and functional relationships reformulated as needed.

Unfortunately, there are no guidelines available to help determine a priori which functional relationships are most appropriate for a particular habitat model. However, we believe that clearly stating functional relationships is an extremely important requirement in model building. The use of verbal statements to explain functional relationships may be sufficient in some cases. However, even seemingly simple habitat relationships often are difficult to define clearly in words, particularly when the relationships are nonlinear or when there are interactions between two or more variables.

Mathematics is useful as ". . . a precise and subtle language designed to express certain kinds of ideas more briefly, more accurately, and more usefully than ordinary language" (Halmos 1968:386). We recognize that wildlife managers may resist the use of mathematics, at least partly because expressed hypotheses about habitat relationships may be proven incorrect. However, a major value of clearly stated functional relationships is that the process of proving them wrong increases understanding. Mathematical language improves the credibility of habitat models by making the repeated formulation, testing, and reformulation of hypotheses more rigorous.

Model Evaluation

Model evaluation is identical to hypothesis testing (Holling 1978). In modeling terms, this means understanding the model's behavior to the point that one may anticipate when the model is most likely to be unreliable. Models, as simplifications of real systems, contain less information than the systems they represent and will therefore always be unreliable to some degree. The degree of unreliability will vary with the situation; therefore, the evaluation process should be directed at understanding model behavior throughout the anticipated range of application. Evaluation should be an integral part of *model building,* not an a posteriori endeavor. Model evaluation can be described in two phases: (1) verification, which is directed toward evaluating how well the model matches the model builder's perceptions; and (2) validation, which is directed toward determining how well the model builder's perceptions match reality.

Verification. "To verify" means to determine or prove the truth of something. During this stage of evaluation, we are concerned with whether or not the habitat model and its components behave as the model builder intended and if this behavior conforms to currently accepted biological theory and operational feasibility.

One way to verify habitat models is through the use of sample data sets. Data sets used in the verification exercise should originate from existing habitats used by the species of interest. The sample data are assigned to model variables, and the resulting model behavior compared to the hypothesized response. This exercise can be used to identify logic flaws in the modeler's perceptions as reflected in model design (Halfon 1979).

Verification can be expanded into what is often referred to as a sensitivity analysis where the emphasis is on identification of those variables, or functional relationships, that most critically affect model output. This is usually accomplished by manipulating input values of a selected variable(s) over a wide range of possibilities, while maintaining other variables constant. This identifies variables to which the model is very sensitive and alerts the model builder to variables that will require a precise field measurement.

The final stage of model verification should include a field application to make sure that model variables can be satisfactorily measured. The most critical variables in terms of model behavior are measured with the appropriate techniques to determine if the required accuracy level can be obtained under field conditions. The field sites used should contain enough variety so that all of the measurement techniques required for model variables can be applied and evaluated. As a result of these field exercises, the model builder can develop a list of variables and measurement techniques that are theoretically and operationally acceptable.

Validation. Validation is an attempt to determine the degree of agreement between model behavior (i.e., its output) and the real situation it was designed to mimic. "To validate" may be a misleading phrase; we tend to agree with Holling (1978) and others, that, like hypothesis testing, the actual process involves efforts directed more at invalidation, or understanding a model's degree of unreliability.

Validation efforts usually involve evaluation of the model's outputs against some standard of comparison. The standard should be a data set that was not included or consulted during model development. Identification of a standard is not an easy task. A seemingly obvious choice, both from a theoretical and operational standpoint, would be densities of populations using the habitats of interest. This inclination is reflected in recent studies: ". . . the system whose habitat ratings consistently correspond more closely to relative abundance values would be the most accurate" (Whelan et al. 1979:400), and "The real test . . . is whether the scores reflect animal abundance or wildlife usage of the habitat" (Baskett et al. 1980:146). However, there are several factors that should be considered when attempting to validate a habitat model with animal abundance data.

Attempts to validate a model heavily laden with assumptions (i.e., untested hypotheses) will have a high likelihood of ending in failure and/or frustration. This is because no insight is gained about the conditions under which the individual assumptions are likely to be invalid, thereby resulting in unrealistic model behavior. The best recourse is to design a set of validation efforts directed toward individual model assumptions before attempting to evaluate behavior of the entire model.

The ultimate objective of the validation process is a comparison of overall model behavior to observed animal abundance. However, the goal of validation *is not* to determine if a model can explain variations in any animal abundance data set. Most models can be adjusted to fit a given data set, but the adjusted model may not be reliable when exposed to new conditions such as a major land use change (Holling 1978). Therefore the validation process should be conducted on sites that emulate actual land-use changes similar, if not identical, to those of interest. This can be accomplished by comparing estimates of animal abundance on altered sites against those of unaltered sites. Such comparisons should give some indication as to the reliability of model projections under conditions of actual use. If projections do not correspond well with observed conditions, then model hypotheses can be reformulated based on the information gained.

The population abundance data set also must meet other criteria. The data must represent a long enough time span such that there is some confidence in the data as a measure of population limits. Moreover, the abundance data need be no more rigorous than the acceptance level set for model outputs (i.e., precision and accuracy as defined by model objectives). For models with unitless outputs, highly precise and accurate population density data are not required. Other types of abundance data, such as frequency of use (the proportion of years a habitat is occupied) and similar indices of habitat occupancy, may be adequate standards against which to judge model behavior.

In situations where validation is not or cannot be currently attempted, the overall model performance will remain unknown in terms of both acceptance and ideal goals. However, if the model meets a lower acceptance level that permits use, then a long-term monitoring plan can be initiated to facilitate the validation process. Attaining the goal of more precisely defining the causal relationships that influence animal abundance requires a long-term commitment of time and resources. Monitoring of land-use changes over an extended period to determine how well the habitat model predicts changes in population limits should be accompanied by an effort to reformulate cause and effect relationships in the model. Such monitoring efforts are not commonly included in the land-use planning process.

Finally, validation should not be used to reject one particular model because it fails to meet a pre-set acceptance level. Validation efforts should be used to select the "best" of two or more models for a particular application. When carried to completion, validation involves rejection and reformulation of alternative hypotheses with the ultimate selection of the most practical model for a land use application.

Discussion

This paper has emphasized the limitations of habitat models for land use planning. This emphasis was intentional because we believe that habitat models are often used for purposes other than those intended. When they fail to perform at ideal levels, they are often considered unreliable and useless, and therefore discarded. This situation occurs most frequently when habitat models that are based on simple variable sets and numerous assumptions are employed as predictors of actual animal abundance without first adequately testing the assumptions. Animal densities at any one time are the expression of previous environmental influences regulating birth rates, death rates, or both. Unless habitat models include all variables which causally explain such influences, precise correspondence between output and observed populations should not be expected for most species.

Current attempts to operationally define habitat with models are often viewed with skepticism: "Even to attempt to standardize something so complex as an evaluation of natural populations will strike many biologists as ludicrous" (Graber and Graber 1976:2). Such feelings are understandable; science deals in facts, and facts require time to acquire. However, wildlife scientists must be cognizant of the wildlife manager's need to be able to deal in values. "To say we don't know enough is to take refuge behind a half-truth and ignore the fact the decisions will be made regardless of the amount of information available . . . it is far better to examine available knowledge, combine it with expert opinion on how the system operates, and makes predictions about the consequences of alternative management actions" (Thomas 1979:preface).

Habitat models that do not precisely mimic animal abundance are not without value for land-use planning. They provide a format for the systematic use of habitat requirement information in making value judgements about the effects of different management options. The operational acceptance of the model will be dependent on the user's decisions about whether or not the model is useful in facilitating land use decisions. We can attain this level of acceptance through improved communications between model builders and users, directed at realistic operational objectives.

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