

EVALUATING POPULATION-HABITAT MODELS USING ECOLOGICAL THEORY

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Passage of the Forest and Rangeland Renewable Resources Planning Act (P.L. 93-378) (RPA), as amended by the National Forest Management Act (P.L. 94-588), requires the U.S.D.A., Forest Service (FS) to develop and conduct periodic national assessments of renewable natural resources on forests and rangelands. Such assessments report the current and expected status of natural resources, and propose alternative opportunities with associated ecological, economic, and social impacts (Hoekstra et al. 1979).

The appraisals of wildlife resources require the ability to forecast consequences of human-induced environmental changes accurately, relative to both national and forest-level management planning. Models relating wildlife populations to habitat have been developed. The FS must develop, modify, and recommend assessment methods for wildlife, and needs a basis for evaluating these methods. A synthesis of existing ecological knowledge and theory into a framework for evaluating these models can function as that basis.

In terms of FS assessment goals, a synthesis should expediently identify ecological weaknesses and limitations in models and provide a mechanism for proposing recommendations and research hypotheses. Accordingly, this paper reviews and organizes ecological theory relevant to predicting changes in wildlife populations (see Flather 1982), and illustrates the utility of this framework in a case example by evaluating the Pattern Recognition Method (PATREC) (Williams et al. 1977). Specifically, we define reasons for selecting PATREC, describe the method, review ecological theory, and evaluate PATREC's use.

CRITERIA FOR SELECTION

Population models can be classified as either energy-flow models, population-parameter models, or habitat-evaluation models. We analyzed these 3 approaches with respect to their potential for meeting assessment goals.

Energy-flow models are restrictive because the data requirements and knowledge necessary to construct them are not available for most wildlife species. Population-parameter models currently are limited because data are difficult to obtain and applications do not address population response to land management actions. Habitat evaluations, however, attempt to establish a direct link between a population and the habitat to be altered. In addition, existing habitat data bases will support regional analyses. Thus, we chose habitat-based modeling as a starting point for research on techniques for national assessments.

We then rated specific habitat-evaluation models based on objectivity and cost of data, ability to directly estimate population levels rather than habitat quality, and capability to predict changes in wildlife populations from alternative land-management activities. In addition to PATREC, some of the other models considered (Hawkes et al. 1983) included those developed by Willis (1975), Hawes and Hudson (1976), Boyce (1977), U.S. Army Corps of Engineers (1980), and U.S. Department of the Interior (1980b). PATREC best met the criteria and warranted further consideration in terms of ecological theory.

PATTERN RECOGNITION AND PATREC

Pattern recognition generally refers to a process with the objective of assigning obser-

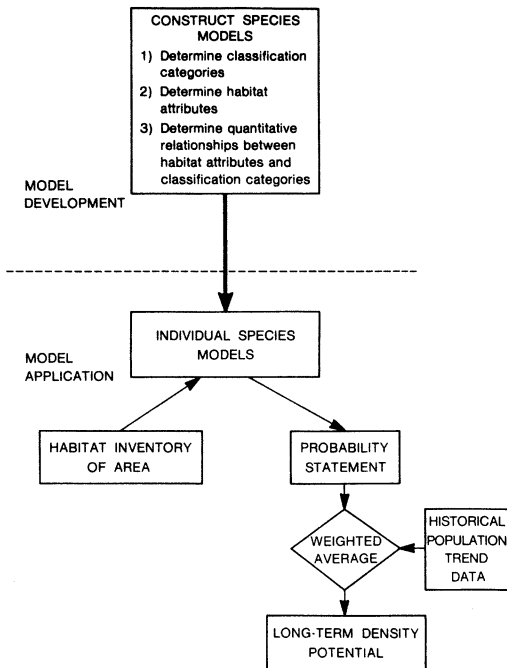


Fig. 1. Diagrammatic representation of the PATREC process.

valuations to classes based upon a set of common attributes (Tou and Gonzalez 1974). PATREC is only 1 method that could be used in the assignment process. Application has focused on classifying landscape patterns as wildlife habitat by examining relationships among population-level classes and habitat characteristics (Williams et al. 1977, Seitz et al. 1982). Each class has a nonexclusive but characteristic set of habitat attributes that define a pattern. The attributes can be used to categorize additional unclassified units. PATREC uses Bayesian statistical inference (an alternative to classical statistical inference), which employs both objective data from samples and the scientist's subjective judgment (Spurr and Bonini 1973) to categorize patterns.

The PATREC classification process comprises 2 steps: model development and model application (Fig. 1). Development involves

constructing individual species models by determining:

1. The population-level classes based on user objectives. (Is the user interested in predicting presence/absence, or relative population levels?)
2. A list of habitat attributes believed to be important in differentiating the population-level classes chosen.
3. The quantitative relationship between habitat attributes and population-level classes (interpreted as a frequency of occurrence of each habitat attribute within each population class).

Points 2 and 3 are accomplished through expert opinion, literature search, or empirical investigation. Application involves the collection of habitat data, which are compared with the information in the species model to make a probability statement about the ability of an area to support a population. Population estimates are desirable for national assessments; PATREC can provide such estimates by calculating an expected value (Spurr and Bonini 1973). Historical population trends are used to estimate the average abundance characteristic of each population-level class. These values are multiplied by their associated probabilities and summed to estimate the long-term density potential (Kling 1980).

PATREC provides a probability that an area can support user-defined population classes, which can be converted to a long-term population average for comparisons among areas. A more comprehensive review of PATREC can be found in Williams et al. (1977) and Kling (1980).

ECOLOGICAL THEORY IN EVALUATIONS

The Conceptual Model

Theory provides a logical framework for analyzing problems and improving existing assessment techniques. Techniques for nation-

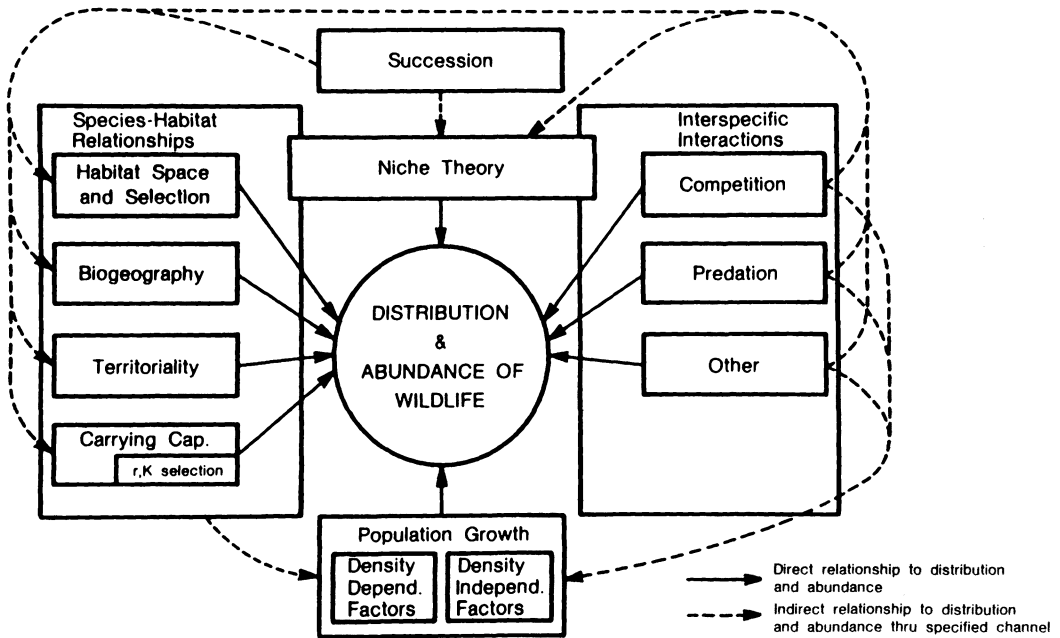


Fig. 2. Conceptual model relating distribution and abundance to areas of ecological theory.

al wildlife assessments must be able to withstand critical evaluation based on ecological theory; however, ecologists disagree which theories support evaluations of this type. For this reason, the framework that we propose is tentative. Our hypothesized model depicts 5 interrelated areas of ecological thought deemed important in evaluations of habitat-based population models (Fig. 2).

Species-Habitat Relationships.—The specific areas of ecological theory that support the concept of species-habitat relationships include habitat space and selection, island biogeography, territoriality, and carrying capacity. In addition, the principle of carrying capacity must be considered together with life history strategies, including the concept of *r*-vs. *K*-selection (MacArthur and Wilson 1967).

Habitat space and habitat selection, although different concepts, are inseparable in our conceptual framework. Habitat space is described empirically by those structural characteristics of a land area that relate to the

spatial distribution of a species, and is the product of the behavioral process of habitat selection. Habitat selection principles assume that it is adaptive for an animal to select a specific site over another. Theoretically, natural selection favors those individuals that select better habitats, resulting in a correlation between preference for a given patch type and fitness within it (Pianka 1974:104). Consequently, density decreases from areas of more suitable habitat to areas of less suitable habitat (Andrewartha and Birch 1954, Wynne-Edwards 1962). Although this pattern appears to hold in general (Partridge 1978), the relationship between density and habitat suitability should be examined carefully. VanHorne (1983) suggested consideration be given to season of critical habitat use (e.g., winter range), time lags, and intraspecific interactions that temporarily may result in higher densities in lower quality habitat as subdominants are forced out of optimal habitat.

Island biogeography also has implications to

species-habitat relationships. This theory focuses primarily on community dynamics and the influence of island size, shape, and proximity on species richness. Application to nature reserve design has been fraught with controversy over the appropriate strategy (a single large reserve vs. several small reserves) for the preservation of species (Diamond 1975b, Simberloff and Abele 1976, 1982, Gilpin and Diamond 1980, Kindlmann 1983). Notwithstanding this controversy, island biogeography has applicability to the management of individual species. Diamond (1975b), Fritz (1979), and Samson (1980) have used principles of island biogeography to determine minimum area requirements for individual populations. Such investigations indicate that the size and distribution of habitat patches must be considered when explaining the distribution and abundance of species.

Other areas of ecological theory relevant to species-habitat relationships include territoriality, carrying capacity, and *r*- and *K*-selection. Territoriality is a complex of behavioral mechanisms, part of which function to minimize overexploitation of resources by permitting some individuals to have a sufficient resource base to survive and reproduce. Density dependence associated with territorial behavior is logically linked to carrying capacity, a broader concept of population limits in any given habitat. Mathematically, carrying capacity is defined by the upper population limit where the growth rate is equal to zero. However, biological interpretation is complex because of confusing terminology and use (Giles 1978), and confounding concepts such as *r*- and *K*-selection.

Species which are *r*-selected have high reproductive rates, reduced competitive ability (Pianka 1970, Horn 1978), and rarely reach an equilibrium density. Populations usually are below carrying capacity (Krebs 1978), but can overshoot the resources (Elseth and Baumgardner 1981). Populations of *r*-selected organisms tend to be regulated more by density-independent mortality factors (Pianka 1970).

In contrast, populations of *K*-selected organisms occur at or near carrying capacity. Population size tends to be constant over time and less influenced by density-independent mortality factors (Pianka 1970). Selection has favored more efficient use of resources, high competitive ability, and lower reproductive rates (Pianka 1970, Horn 1978). These *r* vs. *K* comparisons represent the extremes of this continuum.

Population Growth.—Population growth is a second major area of ecological theory involving intrinsic factors that regulate abundance. The logistic equation is a commonly cited mathematical expression of restricted growth, and is the basis upon which many sophisticated models have been built. Population growth is species specific for a particular environment (Johnson 1977) and is perceived as a product of 2 opposing forces: the biotic potential of the species and density-dependent or independent environmental limitations (Elseth and Baumgardner 1981).

Interspecific Interactions.—Habitat analyses rarely consider interspecific interactions. The influences of these interactions on animal distribution and abundance are sometimes evident (Abramsky et al. 1979, Williams and Batzli 1979a, b), yet at other times appear to be nonexistent (Rotenberry and Wiens 1980). In addition, the actual effect can be direct (interference competition or consumption of prey) or indirect (altering species-habitat relationships). Consequently, interspecific interactions are difficult to represent accurately in a habitat model.

Niche Theory.—Niche is described by the range of all physical and biological variables that, in combination, permit a species to exist (Pianka 1981). Hutchinson (1957) viewed a niche as an abstract space defined by many dimensions, with each dimension corresponding to some requisite for the species.

Niche theory is depicted in Fig. 2 as a "bridge" between species-habitat relationships and interspecific interactions. This relationship is a manifestation of the 2 conceptual

components of a niche—the fundamental niche and realized niche (Hutchinson 1957). The former considers the animal-environment interactions in isolation; the latter considers the actual amount of resource space used by an organism as restricted by an interacting community. Theoretically, knowledge of both is required to predict distributional and abundance changes resulting from community disturbance.

Succession.—Succession relates to the dynamic nature of the biotic community rather than directly to the abundance or distribution of populations. The theoretical development and traditional arguments concerning the mechanisms of succession are important to our framework only as they relate to the predictability of the process.

Clements (1916) perceived succession as a regular sequence of seral stages that culminates in a climax community reflective of the regional climate. However, many observations do not support such orderliness. Several alternative views have been proposed to account for variation in seral stage sequence and composition of climax communities. The alternatives view plant communities as gradients rather than discrete units of association, with succession being a function of species growth, survival, and dispersal capability (Gleason 1926, Whittaker 1953, Drury and Nisbet 1973); and thus predictable within probability limits (Johnson 1977). This predictability of the succession process (when in conjunction with theories of habitat space, habitat selection, and niche), is valuable in establishing the relationship between changes in species composition and abundance and changes in vegetation.

A CASE EXAMPLE EVALUATION: PATREC

National wildlife assessments need the capability to predict effects of alternative management activities on wildlife resources. Evaluation involves appraising the utility of a model in attaining a goal; success being judged

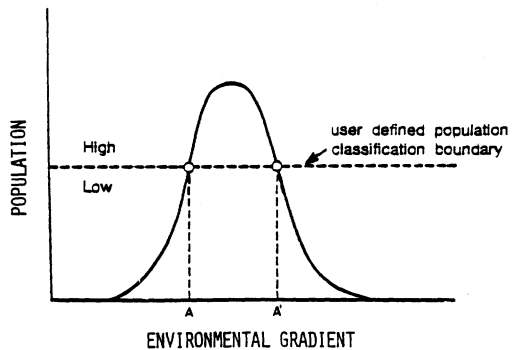


Fig. 3. Hypothetical representation of an environmental gradient of a habitat variable in PATREC.

against established standards (Suchman 1967: 37). The standard we use is ecological theory; the conceptual framework (Fig. 2) we propose for evaluating predictive models is our hypothesis of relevant ecological theory. We examine the implicit ecological assumptions made by the developers of PATREC and evaluate them against the described theory.

Evaluation of PATREC Assumptions

The ecological literature offers theoretical and empirical support for the PATREC methodology. This support stems from concepts expounded in habitat space, habitat selection, and niche theory; all evident in our interpretation of PATREC's basic ecological premise.

Premise 1.—Animal distribution and abundance can be explained and predicted by environmental descriptors of a particular unit of land.

This assumption is founded on the theory that a species' ability to survive and reproduce can be characterized by a unique set of environmental attributes at a given level of ecological generalization.

The various habitat attributes that comprise a PATREC species-habitat model represent the environmental gradients important in delineating the population-level classes on the ground. Figure 3 depicts this theoretical relationship for a single habitat variable. The intercepts defined by the population classifi-

cation boundary represent the range of values (A-A') for that variable that differentiate between areas of high and low population levels.

Premise 2.—Distributional abundance patterns can be assessed solely through species-habitat considerations.

Interspecific relationships are not included explicitly in PATREC models. This may be due to the difficulty in defining and quantifying these interactions and a lack of data. Problems associated with this supposition have been recognized (Kling 1980:34) but addressed inadequately through assumptions that errors can be reduced by careful interpretation and acknowledgment of the influence that competition, predation, and disease play in regulating numbers.

Errors in PATREC predictions associated with interspecific interactions can result from 2 situations. First, seemingly identical habitat can have differences in species composition which may alter the species-habitat relationships. Biogeographical studies have shown that animals colonizing islands with few other species will expand their niches—a phenomenon termed ecological release (MacArthur and Wilson 1967, MacArthur 1972). Williams and Batzli (1979*b*) and Abramsky et al. (1979) observed the same phenomenon following removal of a suspected competitor. In addition, diffuse competition in species-rich habitats could eliminate or exclude a species that would otherwise be an expected member of the faunal community based on the habitat characteristics. This pattern stimulated the development of community assemblage rules (Diamond 1975*a*, Haefner 1981).

A second error stems from situations in which predation limits a population. In such cases, the distribution or abundance of a population may be more a function of predation than the resource base (May 1977, Nelson and Mech 1981).

As currently applied, PATREC models do not consider competitor or predator interactions. Thus, the association patterns between

a species and its habitat may not be consistent because of variation in the animal community.

Intraspecific interactions can also invalidate Premise 2. Territorial behavior may result in higher density in suboptimal habitat by forcing individuals to move from optimal habitat during highly productive years (VanHorne 1983). Conversely, during years of low populations only optimal habitat will be occupied (Partridge 1978). Because such fluctuations may be independent of changes in habitat characteristics (e.g., survivorship in wintering areas), abundance patterns may not be explainable on the basis of habitat related variables.

A corollary of Premise 2 is derived from general pattern recognition principles. Because PATREC is based on perception and recognition of habitat patterns, it presumes:

Premise 3.—Similar patterns or configurations of habitat will reflect similar patterns of abundance, resulting in a consistent and accurate classification of sites according to their ability to support populations.

Descriptions of species habitat requirements are based on observations made in the context of the entire faunal community. The observed habitat space occupied by the organism has been influenced by other coexisting populations. Consequently, PATREC's habitat pattern characterization for a species is an estimate of that species' realized niche. According to niche theory, however, a realized niche is not a unique entity like its fundamental counterpart. Rather, it is dependent upon faunal composition. Therefore, shifts in the realized niche are expected to mirror changes in composition of a community. Because PATREC has yet to incorporate variables that capture variation in interacting fauna, deviations from predicted population patterns may be expected.

A final premise concerns the use of expected value (Spurr and Bonini 1973) in translating probabilities associated with discrete rel-

ative population classes into a statement of average, long-term potential abundance.

Premise 4.—The average population associated with each relative population class defines a potential equilibrium level. These averages represent long-term potential abundance. Therefore, if habitat conditions remain relatively static, the mean population level should be constant. Although not explicitly stated, this premise assumes that observed populations are at or near carrying capacity.

The developers of PATREC recognized that wildlife populations fluctuate, and thus used average population levels to estimate equilibrium levels. The principles of carrying capacity and r - and K -selection, however, suggest that calculation of populations based on an assumed equilibrium level may be applicable only to certain species.

The opportunistic strategy and variable populations characteristic of r -selected organisms suggest that populations of these species tend to be independent of the upper resource limits of a particular habitat. Consequently, modeling of such wildlife populations through habitat relationships is difficult. On the other hand, the characteristics of K -selected species suggest a stronger relationship between abundance and quantities of their resource base. Although populations of species falling closer to K on the r - K continuum may be predicted more consistently in habitat-based modeling, they are ironically less sensitive to short-term habitat changes.

Three additional points from our evaluation are not related directly to any assumptions inherent in PATREC. The first is the interpretation of the expected value estimate as a potential population level. Potential population has been defined as habitat capability without regard for limiting effect from other species (U.S. Dep. Inter. 1980a). Such an interpretation is an intuitively attractive concept, but one that is difficult to measure and confounds testing of model predictions. For example, construction of PATREC models considers in-

terspecific influences implicitly because differences in population classes can be attributed to variation in the habitat and faunal community. The result is an inaccurate representation of true population potential. Testing of predictions is also difficult because overestimates can be rationalized based on semantic differences between potential and actual populations. Such rationalization may preclude critical examination of the ecological reasons for these discrepancies. Techniques that predict potential populations as described here ultimately must be tested against what actually can be observed.

The second point concerns the lack of direct consideration of successional changes in vegetation. To accomplish the assessment mandate of predicting the effects of future habitat conditions, PATREC must be linked to other models, such as timber-inventory projection models (Alig et al. 1984), to account for successional changes. Otherwise, the temporal changes of PATREC variables will require subjective decisions.

A third point concerns the influence of geographic scale on population-habitat models such as PATREC. Current applications of PATREC, and habitat models in general, have been site specific. However, national assessments necessitate evaluations of wildlife habitat over larger areas that are regional in extent. At this level of ecological generalization, some ecological concepts (e.g., selection of habitat at a particular site, territorial behavior) become less important in the modeling exercise. The modeler must be aware of scale as it will influence the relative value of each component comprising the proposed ecological framework in explaining distributional and abundance patterns.

CONCLUSIONS AND RECOMMENDATIONS

In his empirical examination of PATREC, Kling (1980) found a lack of consistency in its

ability to evaluate wildlife habitat. One possible explanation for inconsistent predictions is violation of ecological theory. We used a theoretical framework considering species-habitat relationships, population growth, interspecific interactions, niche, and succession to evaluate the premises inherent in PATREC. Our evaluation represents a preliminary step in analyzing the limitations of PATREC and has been more heuristic than definitive. Recommendations and research needed to improve habitat-based models such as PATREC include:

1. Making a concerted effort to examine the influence of interspecific interactions on model predictions of distribution and abundance. The explanatory power of interspecific interactions is unknown. If interspecific interactions are significant, then competitors and predators may be treated as a composite rather than by examining interactions among all species. Diversity within a guild could be indicative of competition (Pianka 1981). The additional influence of human predation could be incorporated through relative measures of hunting pressure.
2. Categorizing species to minimize error associated with omission of species interactions as model components. This categorization could be based on the theory of *r*- and *K*-selection. Southwood (1981:42) concluded that *K*-strategists are less likely to be influenced by other species in the establishment of equilibria levels. Conversely, species intermediate on the *r*-*K* continuum are likely to reach an equilibrium level midway on the population growth curve because of competition or predation. Although all species must be considered to satisfy legal mandates, focusing habitat modeling efforts on species which are less affected by other organisms may offer an interim methodology while techniques that explicitly include both habitat and species
3. Defining habitat variables the same as land-base and resource variables used in inventory projection models, including both habitat variables that are measured directly and those calculated from resource inventories. The temporal relationships in inventory projection models would be incorporated explicitly by habitat-based models. Accomplishing this task requires concurrent research on the utility of existing resource inventory variables in habitat-based modeling of wildlife populations. Wildlife habitat variables are measured in resource inventories (McClure et al. 1979), however, critical evaluation of these variables from the standpoint of ecological theory is needed. In addition, application of resource inventory variables in habitat-based models will help define the inventory information necessary for an accurate and efficient representation of wildlife resources.

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LANDSAT APPLICATION TO ELK HABITAT MANAGEMENT IN NORTHEAST OREGON

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Planning regulations promulgated in response to the Forest and Rangeland Renewable Resources Planning Act (RPA) of 1974 and the National Forest Management Act (NFMA) of 1976 require inventory and monitoring of wildlife habitat (Legislative Affairs Staff 1983). Forest managers have the respon-

sibility of addressing public issues and concerns in a changing world, and new procedures may be required to meet these added responsibilities.

After characteristics for elk (*Cervus elaphus*) habitat were defined for the Blue Mountains of Oregon and Washington (Black et al.