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Assessing Habitat Quality Using Population Fitness Parameters:

A Remote Sensing/GIS-Based Habitat-Explicit
Population Model for Sage Grouse
(*Centrocercus urophasianus*)

by: Frank B. Edelmann
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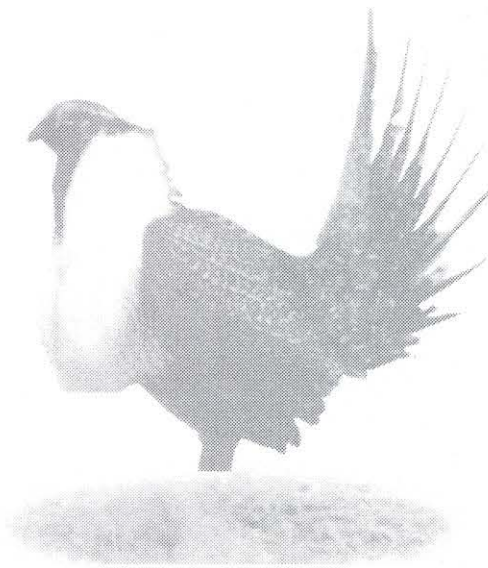
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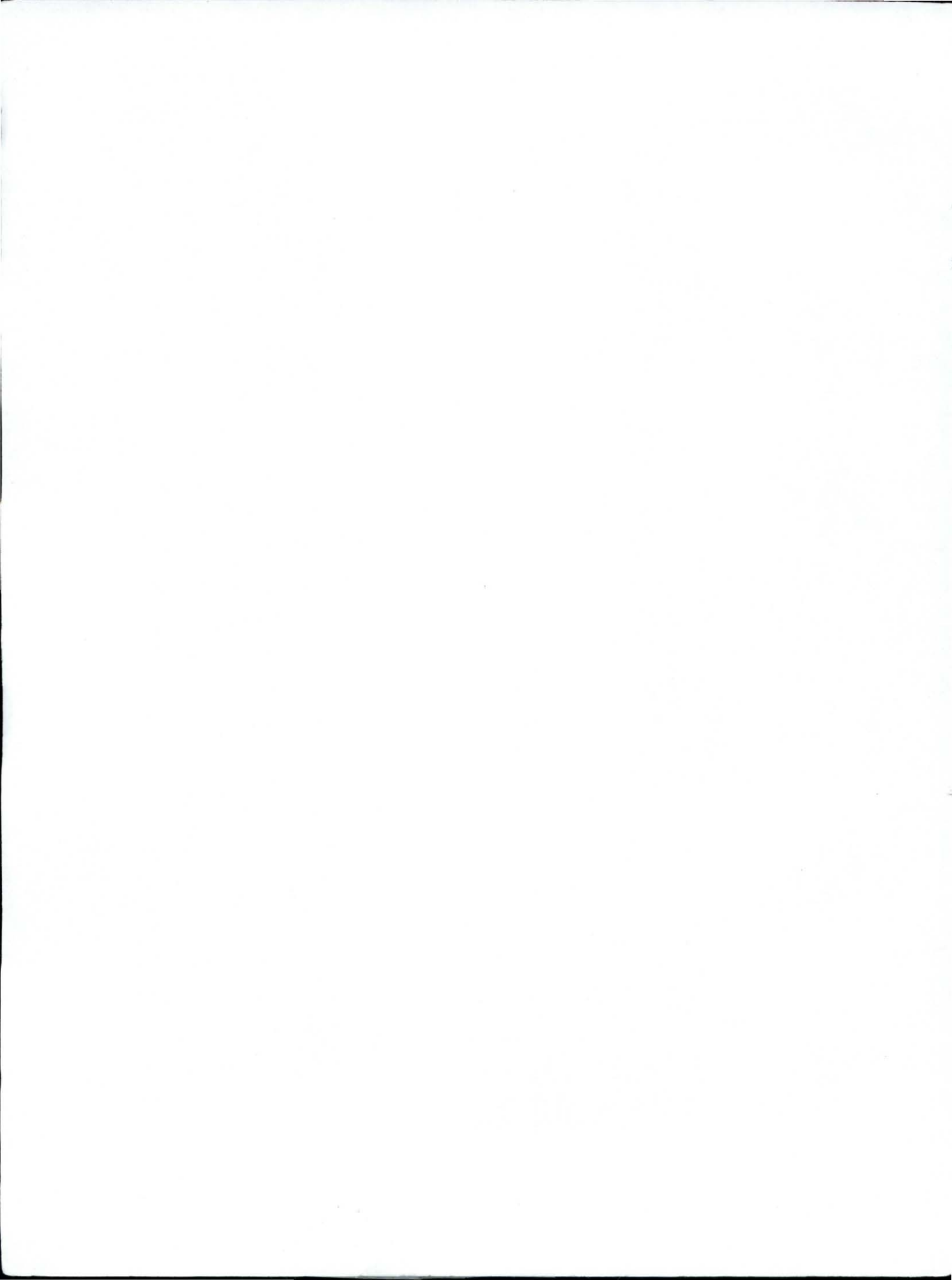
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FORWARD

The habitat evaluation model for sage grouse is part of a continuing partnership between researchers and managers of this important resource. The purpose of the model is to establish a "working hypothesis" for consistent and accurate assessment of habitat quality across all areas currently used by the species. The model is presented as a working hypothesis because many assumptions and formulations have not been validated. Consequently, we believe that validation research should begin simultaneously with management application of the model. If validation research does not proceed in partnership with management application, the accuracy of model predictions will be unknown and therefore of questionable validity. The current trend and status of sage grouse populations dictate that models such as the one presented here be validated immediately in an adaptive management context. We urge researchers and managers to work closely in designing this research across a broad spectrum of habitats within the species' current distribution. Only then can robust relationships between measures of habitat and population fitness be validated and applied prudently in management.

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ABSTRACT

We developed a Habitat-Explicit Population Model to assess habitat quality for sage grouse (*Centrocercus urophasianus*) at the landscape scale using a Geographic Information System (GIS). The model assesses the suitability of a landscape for supporting a sage grouse population by relating habitat associations with population fitness parameters. The model's response variable is population growth rate [λ] and is based on site-specific habitat conditions. The model contains a population module to predict λ and a habitat module to quantify landscape conditions. We used population simulation modeling to identify that the nesting, brooding, and wintering life stages within the first year-of-life accounted for most variation in λ for sage grouse. Thus, these formed the population module, which is a multiple regression that predicts λ for a landscape from vital rate estimates [i.e., $\lambda = \beta_0 + \beta_1(\text{nesting}) + \beta_2(\text{brooding}) + \beta_3(\text{wintering})$, where $\beta_0 = -0.147406$, $\beta_1 = 0.684623$, $\beta_2 = 0.652698$, $\beta_3 = 0.592451$].

The habitat module is comprised of functional relationships which generate the vital rates used in the population module. Functional relationships relate site-specific habitat measurements to each life stage in the population module and predict the corresponding vital rates. Using previously reported data on habitat selection by sage grouse, we constructed the habitat module with variables that were: 1) associated with the 3 life stages in the population module, 2) measurable using satellite imagery, and 3) hypothesized to account for most variation in λ . Of 14 initial habitat variables considered, we retained: 1) sagebrush canopy cover, 2) sagebrush height, 3) herbaceous cover, and 4) slope. Each variable was included in the modeling of each life-stage component, except herbaceous cover, which was not included in the wintering component. Functional relationships were constructed using previously published information and professional judgement.

The model is applied in seven steps:

- Step 1.* define analysis area
- Step 2.* obtain landsat TM digital imagery for analysis area
- Step 3.* classify digital imagery and describe habitat in the analysis area
- Step 4.* build GIS database and assign site specific habitat values
- Step 5.* calculate vital rates from habitat values using the habitat module
- Step 6.* predict λ for the analysis area using the population module, and
- Step 7.* evaluate suitability of the habitat.

Evaluation of habitat suitability is both quantitative and qualitative. Quantitatively, if λ is ≥ 1.0 (i.e. indicative of a stable to increasing population), the habitat is considered suitable. Whereas, if λ is < 1.0 (a decreasing population), the habitat is unsuitable. The model can be used to assess habitat quality at many spatial scales. Descriptive statistics can be calculated to aid qualitative interpretation of model predictions at each scale. However, the model is unvalidated and research is needed to test model predictions and assumptions. Research should occur simultaneously with initial applications of the model in management.

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INTRODUCTION

Quantitative evaluation of wildlife habitat has emerged as an important component of land management planning (Hobbs and Hanley 1990). Natural resource managers are increasingly expected to predict the consequences of habitat alterations (Verner *et al* 1986). The need to evaluate habitats will likely continue to increase because state and federal legislation requires that environmental impacts, including alterations of habitat, be assessed (Krohn 1992). Central to habitat evaluation are models that define the functional relations between species and their habitats (Krohn and Salwasser 1982, Hobbs and Hanley 1990).

Biologists have traditionally guided species conservation and management using models that relate life history requirements with habitat associations. A common approach is to model wildlife-habitat relations by linking known habitat use patterns with maps of existing vegetation, thereby identifying the spatial extent of important habitat features. These models transcend a variety of scales and purposes, from species-specific Habitat Suitability Index (HSI) models, multiple-species wildlife-habitat matrices, to spatially explicit descriptions of animal distributions (Edwards *et al* 1995). Verner *et al* (1986), Morrison *et al* (1992), and Anderson and Gutzwiller (1994) outline many approaches traditionally used for modeling wildlife habitat.

CURRENT KNOWLEDGE

Habitat Suitability Index models which follow Habitat Evaluation Procedures (HEP) are used widely to assess habitat quality for a variety of wildlife. Habitat suitability is a numerical index that represents the capacity of a given habitat to support a selected wildlife species (U.S. Dept. Inter. 1980, 1981). For HEP purposes, HSI models are used to estimate habitat condition in an area compared with a standard that represents the optimum condition for the species of concern (U.S. Dept. Inter. 1980). The HSI model assumes a direct linear relation between the HSI value and carrying capacity, and generally relates habitat characteristics to carrying capacity via population density. Criticisms of HSI models are threefold: 1) reliance on structural characteristics of habitat as surrogates for mechanisms that influence habitat quality, 2) use of density as the indicator of a habitat's ability to support a species, and 3) no indication on the HSI scale when the habitat can sustain a population (Kellner *et al* 1992).

Because of these criticisms, Kellner *et al* (1992) proposed that habitat suitability should be evaluated based on population demography with the comparison standard being a population's growth rate [λ]. In this case, the suitability of habitat depends on its potential to support a viable population [$E(\lambda) \geq 1$] over an appropriate ecological period. Habitat quality would be measured as the expected value of λ [$E(\lambda)$] (Kellner *et al* 1992). These and conclusions of Van Horne (1983) suggest that habitat quality should be defined in terms of

survival and reproduction which ultimately determine λ , rather than population density, which may not be correlated with habitat suitability or quality (e.g. habitat sinks; Van Horne 1983, Pulliam and Danielson 1991).

We believe that assessing the quality of habitat based on population fitness parameters has not been explored or considered thoroughly. Spatially-explicit population models (SEPMs) currently offer the most promise (Dunning *et al* 1995, Turner *et al* 1995). However, SEPMs require parameterization that reflects mechanistic understanding of processes affecting population abundance and distribution over a landscape. Data needed for SEPMs are available for only a few well-studied species. Although we believe this approach is ideal, the lack of basic, spatially-explicit demographic information for many species limits the application of SEPMs.

As a result, we developed a model for wildlife-habitat relationships that bridges crude HSIs and more complex SEPMs. Our approach relates habitat quality to population fitness, but does not directly model the processes that determine these relations. We use habitat characteristics that are easily measured, indicators or surrogates to underlying mechanisms, and presumably associated with expressions of vital rates (Murtaugh 1996). Associative data, as opposed to mechanistic processes, comprise most information currently available for many species. Our approach uses a Habitat-Explicit Population Model (HEPM) that is intermediate between an HSI and SEPM.

This approach holds promise for reliably predicting a landscape's ability to support viable populations. Additionally, our modeling effort should stimulate the formulation of hypotheses that result in research directed toward collecting data about underlying ecological processes so that highly detailed mechanistic models may follow (e.g. SEPMs).

MODELING OBJECTIVES

We have three primary objectives for modeling: 1) to explore the biological and environmental processes, landscape heterogeneity, and their sources of variation that must be captured in the structure of an HEPM; 2) to describe the methods and interpretation of an HEPM applied

to a landscape, including assumptions and limitations; and 3) to use an HEPM to model population-habitat relationships for sage grouse as guided by the suggestions of Dobkin (1995). We developed this model to maximize generality so the HEPM would be universally applicable to all sage grouse populations and habitat despite individual population distribution or migratory behavior. Our overriding goal is to provide a working hypothesis for management that can be validated through ongoing research.

CONCEPTS FOR HABITAT-EXPLICIT POPULATION MODELING

The fundamental question biologists often ask when applying habitat evaluation models is, "Will the habitat support a viable population over time?" Although objectives more specific to wildlife management (e.g. identification of habitat components limiting a population and understanding impacts on a population following habitat perturbation) may stimulate use of a habitat model (Turner *et al* 1993), the ultimate question being asked is related to population viability as determined by habitat (U.S. Dept. Inter. 1980, Verner *et al* 1986).

The use of HEPMs as presented here focuses on addressing this question by assessing habitat quality based on combining relationships between population demographics and habitat parameters. Habitat quality is directly assessed by its ability to support a stable or positively increasing population, on average, over an ecologically meaningful period. Hence, developing and applying HEPMs will require even greater quantities of reliable data than currently used methods of habitat assessment. This approach will require estimation of:

- 1) population parameters,
- 2) habitat parameters, and
- 3) the direct mechanistic relations among these parameters.

By contrast, conventional population viability assessment explicitly evaluates the likelihood of population persistence given a variety of stochastic factors primarily related to population parameters and usually only indirectly related to habitat parameters. Habitat suitability models

only estimate habitat condition based on a standard that indirectly represents optimum population conditions representing an unknown carrying capacity.

By attempting to assess the "expected growth rate" [$E(\lambda)$] of a population through a habitat-based model, we assume habitat directly determines the likelihood of a population's persistence. This can be justified because, although many factors affect survival and reproduction of individuals in a population, all wildlife populations ultimately depend on habitat for existence (Holt and Talbot 1978; Soule 1986, 1987).

The primary assumptions of our modeling approach are:

- 1) population vital rates account for a significant portion of the variation observable in population growth (λ);
- 2) vital rates and corresponding life stages are clearly associated with quality of discrete habitats;
- 3) habitat quality is quantifiable and accounts for most of the variation observed in vital rates and thus in λ ;
- 4) the spatial orientation and geometry of habitat patches do not affect habitat quality; and
- 5) microhabitat characteristics and landscape heterogeneity can be quantified successfully and efficiently over large areas using remote sensing and GIS techniques.

It is unlikely that these assumptions could be met completely for the many life history processes and habitat selection patterns exhibited by a species. Moreover, it is unlikely that enough information is available to evaluate these assumptions for all but a handful of species. Regardless, we believe linking population parameters with environmental factors establishes the appropriate mechanistic framework for evaluating habitat quality. It also fosters a set of questions that should be answered before we can adequately evaluate the roles of the many factors and their interactions that contribute to how populations and vital rate parameters fluctuate through time and space.

A HABITAT-EXPLICIT POPULATION MODEL FOR SAGE GROUSE

We constructed an HEPM for sage grouse to illustrate the development and application of our modeling approach. We identified vital rates most associated with λ (*i.e.* population module), and modeled relations between these vital rates and their corresponding habitat components (*i.e.* habitat module: egg survival with nesting habitat, chick survival with brood habitat, and juvenile survival with wintering habitat). The goal was to develop a habitat model with universal applicability for assessing sage grouse habitat quality.

Currently, only preliminary habitat models exist for sage grouse (*e.g.* Anonymous1, Anonymous2, McCollough, Stiehl 1994a). Further and to our knowledge, no sage grouse HSI model specifically addresses the criticism of HSI models or attempts to model habitat characteristics with vital rates directly (*i.e.* an HEPM). A habitat model with population growth as the standard would address these criticisms and theoretically improve the assessment of habitat quality. This could lead to better habitat assessments whether the objectives be mitigation, population translocation, or habitat improvement.

Our HEPM for sage grouse and an example application are presented in the next section. Detailed descriptions of the concepts, methods, and results used to develop this model appear in Appendices 1 and 2.

Application of the Sage Grouse HEPM

The conceptual process by which habitat suitability can be determined for sage grouse was demonstrated on a hypothetical analysis area (Figure 1a-d). The reader should review this figure before continuing.

Step 1. Define Analysis Area—The analysis area should be permanently delineated so that both individual and cumulative effects of management activities can be evaluated both spatially and temporally (Thomas *et al* 1988). The area should be defined by the biology of the sage grouse population(s) in question, encompassing all seasonal use areas and travel or migration corridors. Boundaries should be

established to encompass an individual population or multiple populations within a fairly contiguous shrub-steppe environment. Because this model is intended to evaluate habitat at the landscape level, an analysis area as large as 10,000 km² (1-million ha) or greater would be reasonable assuming it is biologically meaningful.

Once defined, the evaluation area becomes the permanent base on which sage grouse habitat suitability is determined and management alternatives are evaluated. Boundaries should not be altered as part of an analysis. Alterations could cause significant changes in model results (Thomas *et al* 1988), particularly with respect to cumulative impacts, making temporal analyses difficult if not impossible. However, sub-analyses within the larger analysis area remain possible. In fact, the impacts of management actions (such as grazing, prescribed fires, and seeding) may best be evaluated at smaller scales (*e.g.* individual treatment areas). Overall effects of such actions on sage grouse habitat suitability (*i.e.* impact on the entire analysis area) must then be evaluated for the cumulative effects of management actions on sage grouse-habitat management objectives.

The application of analyses to the entire area and subsets and interpretation of results must be considered carefully, depending on objectives. We suggest this technique can be applied at a variety of scales (1. single scale, 2. multi-scale, hierarchical analysis, or 3. individual sub-analyses). For example, a set of objectives may require that sub-analysis areas be defined and analyzed based on size and shape of typical seasonal home ranges. The entire analysis area would be defined as the set of year-around home ranges for some minimally acceptable size population of sage grouse. However, we caution that as with most ecological analyses, results of this model may be sensitive to scale decisions. Hence, analysis scales used must be biologically meaningful based on specific questions and objectives to be addressed.

Step 2. Obtain Landsat TM Imagery and DEM's for Analysis Area—Landsat Thematic Mapper (TM) and Digital Elevation Model (DEM) are used to characterize the habitat in the

analysis area. Thematic Mapper data are typically marketed as individual scenes by the EOSAT Corporation (4300 Forbes Blvd., Lanham, MD 20706, (800) 344-9933), the sole vendor and copyright holder of the imagery. Data are available for limited dates; the 7-band image consists of 512 rows by 512 columns (Verbyla 1995:10). We recommend obtaining a late spring (May or June) or early summer (July) TM scene for the analysis. These periods roughly coincide with sage grouse nesting, hatch of first clutches, early brood-rearing, and peak herbaceous cover values in most parts of their range.

Digital Elevation Models are available at most regional U.S. Geological Service (USGS) offices. The DEMs are used to build the topography layers of aspect, elevation, and slope in the GIS, and are available in a variety of formats (*e.g.* 7.5 minute, 15 minute, 30 by 60 minute, and 1 degree). The 7.5-minute DEM data correspond to USGS 7.5-minute topographic quadrangle maps and have a cell resolution of 30 m.

Step 3. Classify Digital Imagery—We recommend that the methods of Homer (1990) and Homer *et al* (1993) be used to classify shrub-steppe vegetation using TM imagery. A brief overview of the methods follows, however, Homer's research should be consulted for a more detailed review.

Homer *et al* (1993) used Earth Resource Data Analysis System (ERDAS) software to process and analyze the Landsat data, create the GIS, and digitize other ancillary data. ARC/INFO software could be used if ERDAS is unavailable. Initially, they subset the analysis area from the raw Landsat digital data and retained Band 2 [visible green (0.52-0.60 μm)], Band 3 [visible red (0.63-0.69 μm)], Band 4 [near infrared (0.76-0.90 μm)], and Band 5 [mid-infrared (1.55-1.75 μm)] for analysis.

Next, unsupervised classification with sequential clustering and minimum distance classifying algorithms was used to identify spectral classes. The unsupervised classification removes human classifying error by allowing analytical clustering of classes based on band brightness value alone. Near infrared high altitude aerial photography (NHAP, scale 1:60,000), orthophotoquad maps, knowledge of the area, and band signature and scatter plots

were used to identify the vegetation associated with each of the spectral classes. Field verification sites were then ground-truthed to assess the accuracy of spectral classification and to refine the spectral classes. Centroid hierarchical clustering using TM class brightness means combined with field-collected class vegetation means determined the final spectral classes.

Step 4. Build GIS Database and Assign Habitat Values—After classification of the digital imagery, a GIS is used to create the vegetation and topography data layers and build the necessary equations and functional relationships (refer to Step 6) for calculating λ . A class mean attribute value for sagebrush canopy cover (%), sagebrush height (cm), herbaceous cover (%), and slope (%) is assigned to each pixel in the analysis area.

The following two steps (5 and 6) outline the process for determining habitat suitability. The process is illustrated using a 4-pixel (2 x 2) example from a hypothetical analysis area (Figure 2a-d).

Step 5. Calculate Vital Rates from Habitat Values—A vital rate value is calculated for each pixel in the analysis area using the habitat module. First, a vital rate value is determined for each habitat variable (*i.e.* sagebrush cover, sagebrush height, herbaceous cover, and slope) within each life stage (*i.e.* NEST, BROOD, WINTER) using the appropriate functional relationship (Figures 3a-d, 4a-d, and 5a-c). Then, these vital rates are integrated using the geometric mean to obtain one overall vital rate value for each of the three life stages (Figure 2c).

Step 6. Calculate λ —The $E(\lambda)$ of the observed habitat conditions is predicted for each pixel in the analysis area using the population module. The geometric mean of vital rates for each life stage component is entered into the multiple linear regression equation:

$$E(\lambda) = \beta_0 + \beta_1 (\text{NEST}) + \beta_2 (\text{BROOD}) + \beta_3 (\text{WINTER}),$$

where $\beta_0 = -0.147406$, $\beta_1 = 0.684623$, $\beta_2 = 0.652698$, $\beta_3 = 0.592451$ (Figure 2d). This process is repeated for each pixel in the analysis area. Once λ has been calculated for each pixel, a probability distribution of $E(\lambda)$ is built.

This probability distribution is used as the basis for evaluating the overall suitability of the analysis area for sage grouse.

Step 7. Evaluate Suitability of Habitat—Evaluation of habitat suitability is both quantitative and qualitative. Because habitat suitability is defined in the model as a binomial, a 1-tailed 1-sample *t*-test can be used quantitatively to test the hypotheses that the observed distribution of λ is greater or less than 1.0 (*i.e.* $H_0: \lambda \geq 1.0$, $H_1: \lambda < 1.0$). The significance level (α) for this test is left to the discretion of the investigator, but should be chosen based on: 1) the relative consequences of committing a Type I or a Type II error, 2) determination of replicate observations, and 3) concern of spatial dependence among replicates. If the central tendency of the distribution of $E(\lambda)$ is ≥ 1.0 , the habitat is considered suitable (Figure 6a). Whereas, if the central tendency of $E(\lambda)$ is < 1.0 , the habitat is unsuitable (Figure 6b). Because λ is predicted for each cell in the analysis area, it is possible to use the GIS to query the data base and identify cells with $\lambda < 1.0$. These cells can then be qualitatively categorized and ranked by their predicted value of λ to produce a coded map identifying areas most in need of habitat improvement.

Inferences about the status of a population based on habitat suitability should not be made without demographic data. Although the habitat is apparently suitable [*i.e.* $E(\lambda)$ is ≥ 1.0], a population could be declining due to stochastic events (*e.g.* heavy precipitation or snow storms during nesting or immediately following hatching) or other non-habitat factors (*e.g.* pesticides, predation). Also, habitat suitability should be evaluated over multiple years (*e.g.* 3-5 yrs) because of yearly fluctuations in both habitat and non-habitat factors and the long-lived nature of sage grouse. Demographic data should be collected simultaneously with habitat evaluation before altering management actions specifically designed to affect population vital rates. Also, habitat quality, as predicted by this model, would represent the average value $E(\lambda)$ for a population occurring in that landscape over an appropriate ecological period (Kellner *et al* 1992). Such a population would undoubtedly experience population fluctuations (positive and negative growth) through time.

Advantages and Limitations of the Model

Our HEPM for sage grouse integrates landscape data on habitat with demographic data to analyze habitat suitability, and can be used to evaluate management options and human impacts on habitat. This model has several advantages over traditional approaches to assessing habitat suitability. Advantages include:

- evaluation of large areas of habitat can be accomplished without regard to land ownership or jurisdictional boundaries; assessments are therefore cost efficient as to time, effort, and monetary expense per hectare evaluated;
- digital satellite imagery can be readily used to qualitatively (*i.e.* visually) and quantitatively (*i.e.* change detection) document and monitor temporal and spatial change in the abundance and distribution of vegetation cover types;
- the potential impact various land management actions might have on the distribution and abundance of a wildlife population can be evaluated;
- conservation and management efforts are focused on the life stages that contribute most to population growth;
- important management questions can be addressed through an adaptive management approach.

Although our model has several advantages over more traditional habitat evaluation methods, it is not without limitations. These include:

- initial cost to classify satellite imagery, build the GIS database, and validate the model is high;
- habitat variables and model resolution (*i.e.* pixel size) are constrained by current remote sensing technology;
- the model is not currently spatially explicit (*i.e.* assumes all habitat patches are of equivalent quality despite spatial orientation), nor does it account for non-habitat factors that may influence population growth;

- the model is not scaled to 1.0 and therefore not compatible with U.S. Department of the Interior's HEP;
- firm recommendations cannot currently be provided as to the appropriate analysis scale(s).

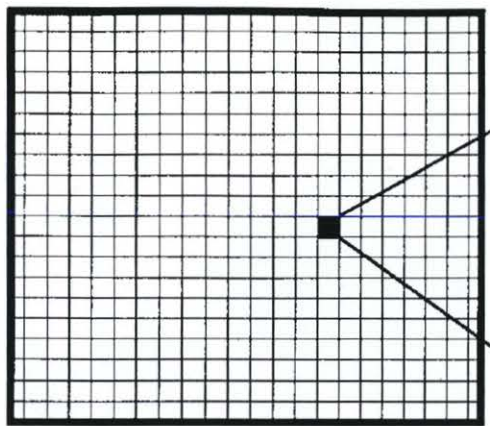
MODEL VALIDATION

Despite limitations, we believe the conceptual basis of the sage grouse HEPM is sound. This model has promise for objectively and quantitatively evaluating habitat quality and for directing conservation efforts of sage grouse. The remote sensing/GIS application allows expanded research of landscape level wildlife-habitat relationships and habitat quality. A GIS model also gives managers a rapid and efficient means of assessing influences of alternative management strategies over large areas. In addition, we believe the model has potential applications for a variety of species, particularly those that are habitat specialists.

The validity of both the population and habitat modules of the HEPM must be tested before widespread use is appropriate. The validation process should address the model's 1) appropriateness, 2) objectives, 3) structure, 4) utility, 5) completeness, and 6) accuracy and reliability. Morrison *et al* (1992) provide a list of criteria useful for validating wildlife-habitat relationship models.

The process of validation should follow the hypothetico-deductive method (Ratti and Garton 1994) and include a rigorous experimental design with treatments, controls, and multiple study sites (*i.e.* geographic areas) with varying densities of sage grouse. The process should also evaluate the validity of model assumptions, the different mathematical means of combining habitat variables, and testing of competing or alternative models (Bunnell 1989). Finally, the process should address probabilities of committing Type I and II Errors when applying this model for making management decisions.

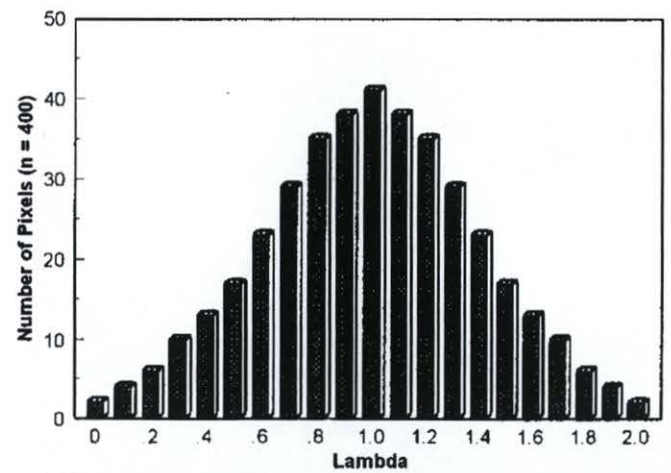
Figures & Tables



(a) Hypothetical analysis area. Each cell represents a 30 m x 30 m pixel.

NEST =	N1. Sagebrush Cover	= N1	$= (N1 \cdot N2 \cdot N3 \cdot N4)^{1/4}$
	N2. Sagebrush Height	= N2	
	N3. Herbaceous Cover	= N3	
	N4. Slope	= N4	
BROOD =	B1. Sagebrush Cover	= B1	$= (B1 \cdot B2 \cdot B3 \cdot B4)^{1/4}$
	B2. Sagebrush Height	= B2	
	B3. Herbaceous Cover	= B3	
	B4. Slope	= B4	
WINTER =	W1. Sagebrush Cover	= W1	$= (W1 \cdot W2 \cdot W3)^{1/3}$
	W2. Sagebrush Height	= W2	
	W3. Slope	= W3	

(b) Based on Landsat TM data, each pixel in the analysis area was assigned a value for sagebrush cover and height, herbaceous cover, and slope. A vital rate was then derived for each habitat variable (N1...W3) within each life stage using the appropriate functional relationship graph (Figures 2-4). These biological vital rates were then integrated into a mathematical formula via the geometric mean.

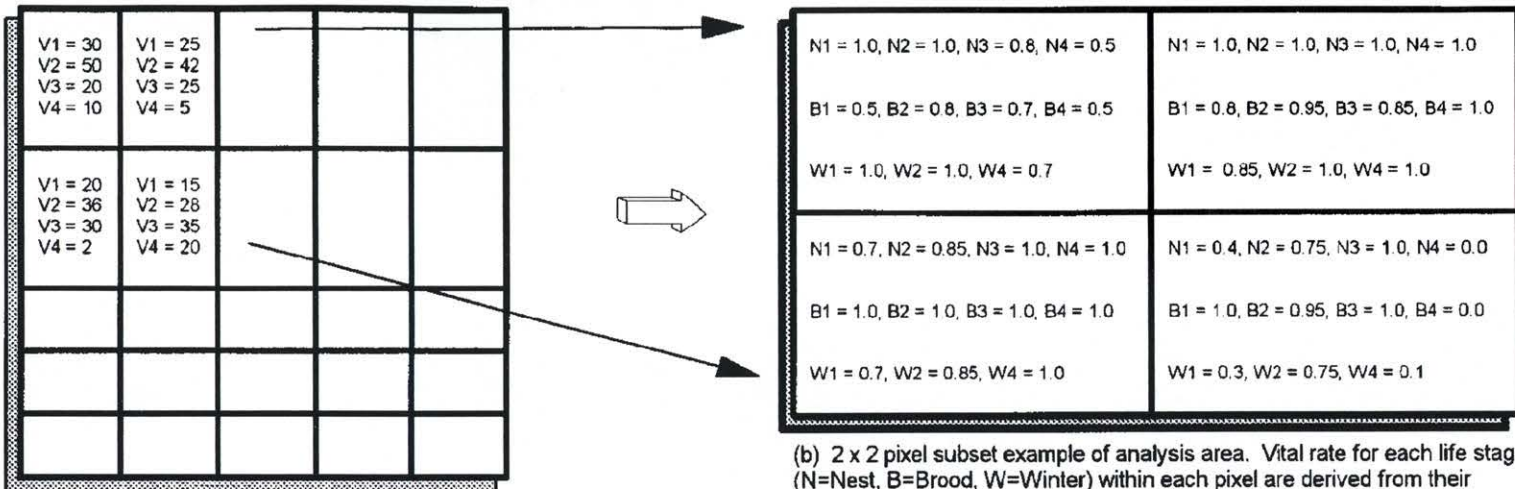


(d) The probability distribution of lambda (here a hypothetical normal distribution) for the analysis area is then used to evaluate the overall habitat suitability of the analysis area.

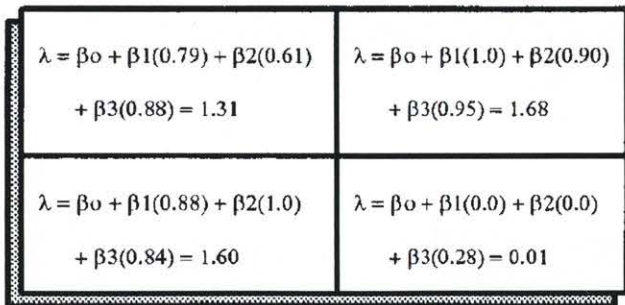
$$\text{Lambda } (\lambda) = \beta_0 + \beta_1(\text{NEST}) + \beta_2(\text{BROOD}) + \beta_3(\text{WINTER})$$

(c) The combined geometric mean probability for NEST, BROOD, and WINTER was then put into the regression equation from the population module to calculate a lambda for that pixel. This process was repeated for each pixel in the analysis area and a probability distribution of lambda was constructed.

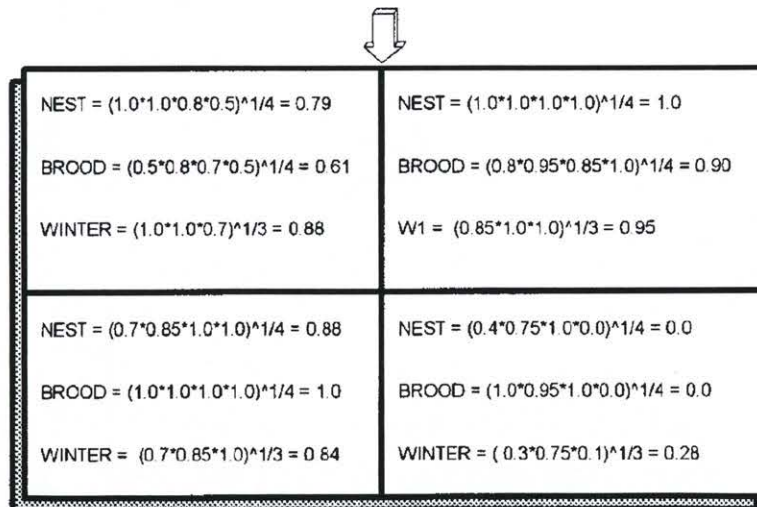
Figure 1. The conceptual process by which habitat suitability was determined for sage grouse on a hypothetical analysis area.



(b) 2 x 2 pixel subset example of analysis area. Vital rate for each life stage (N=Nest, B=Brood, W=Winter) within each pixel are derived from their corresponding functional relationship graphs (Fig. 2-4). N1...N4, B1...B4, and W1...W4 correspond to values derived from V1...V4.

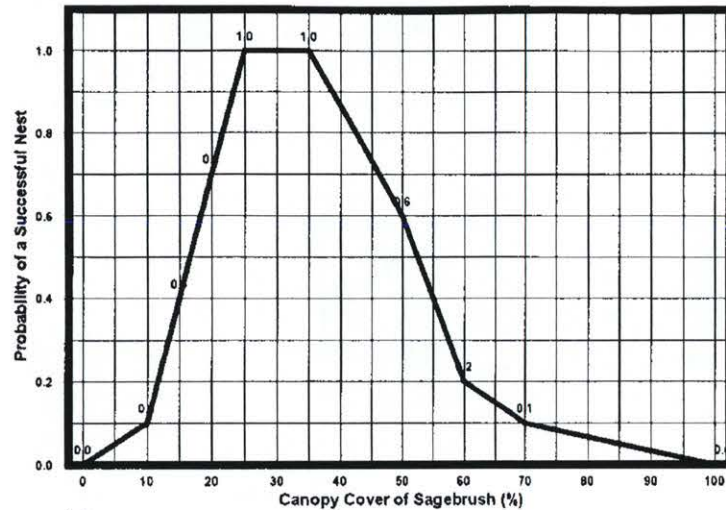


(d) Geometric mean of vital rates for each life stage are then entered into a multiple linear regression to calculate λ for each pixel (coefficient $\beta_0 = -0.14$, $\beta_1 = 0.68$, $\beta_2 = 0.65$, and $\beta_3 = 0.59$).

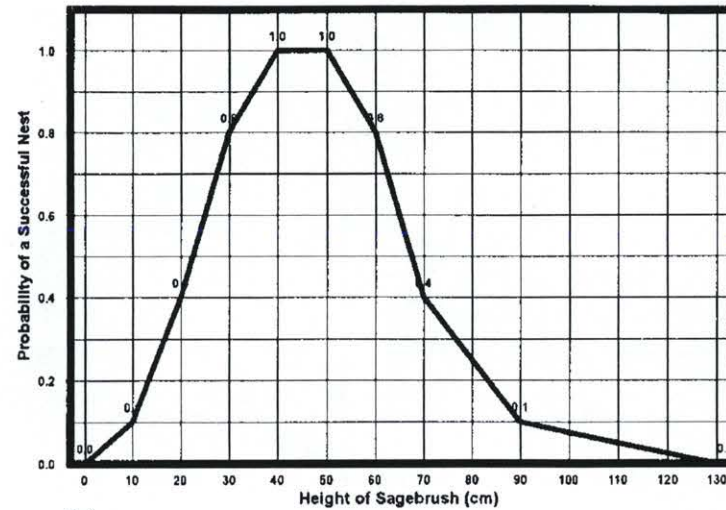


(c) Integration of vital rate values for Nest, Brood, and Winter into a geometric mean probability.

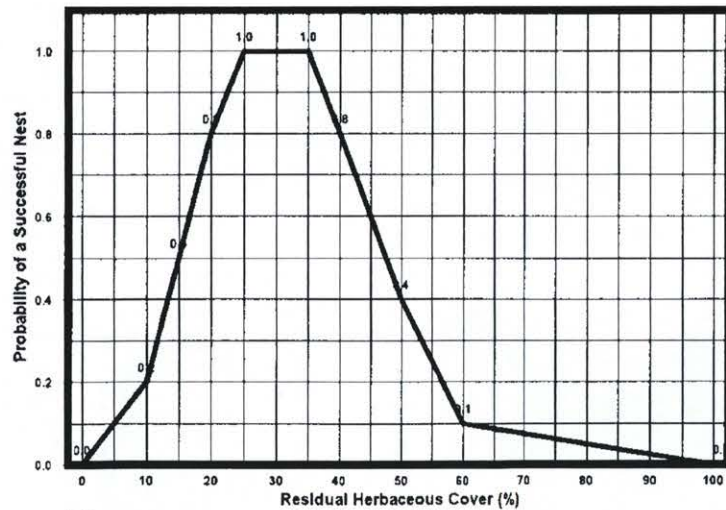
Figure 2. Detailed example of the process by which λ was calculated for a hypothetical 2 x 2-pixel analysis area.



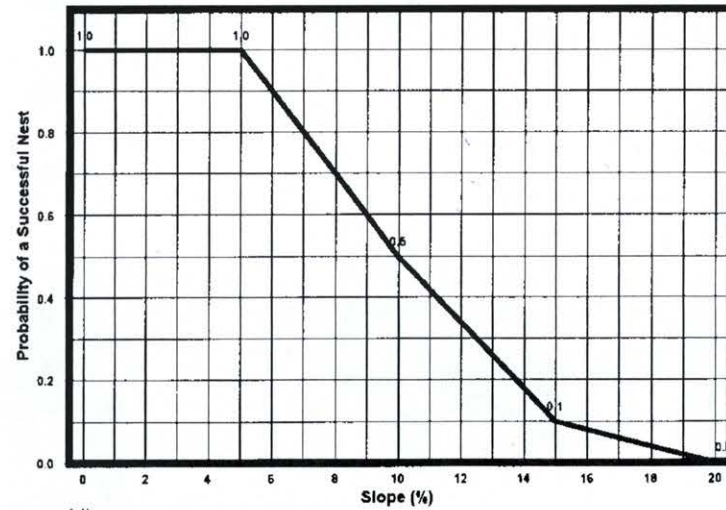
(a)



(b)

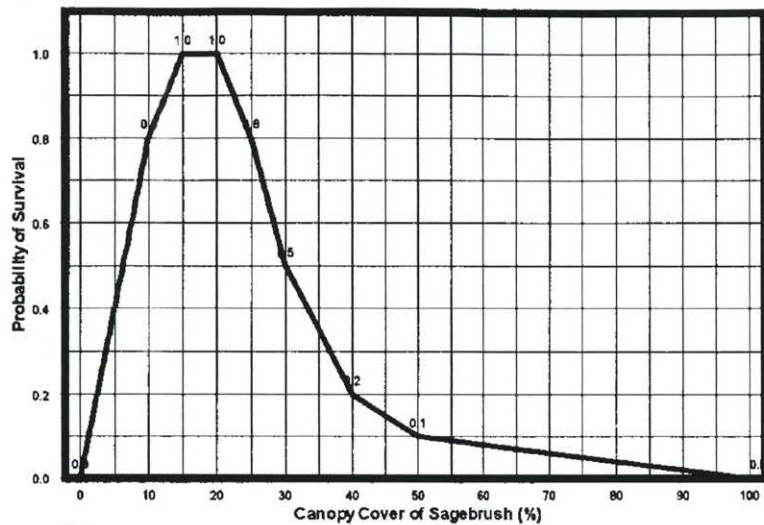


(c)

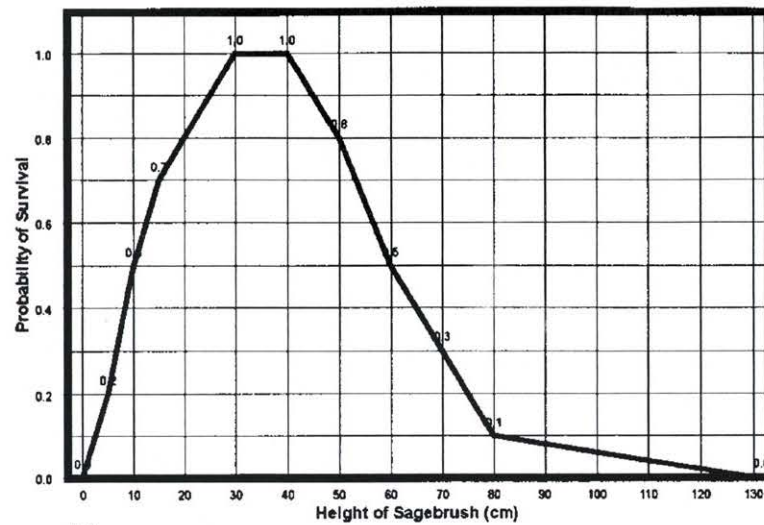


(d)

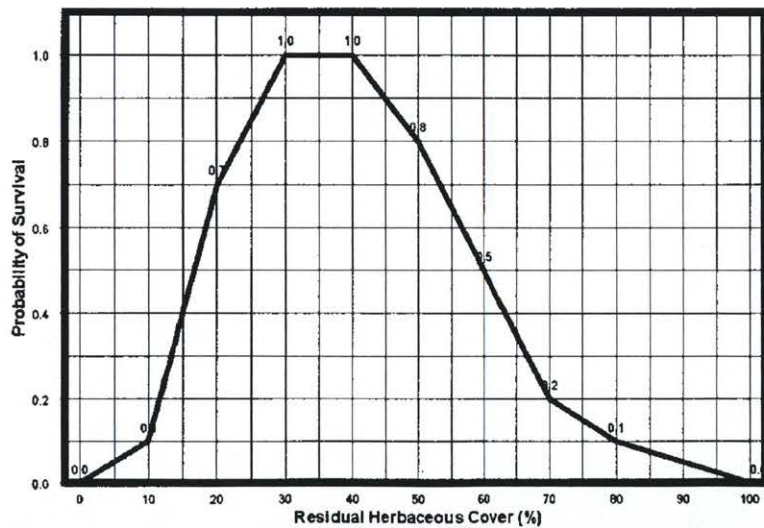
Figure 3. Hypothesized functional relationships between characteristics of sage grouse nesting habitat and probability of a successful nest.



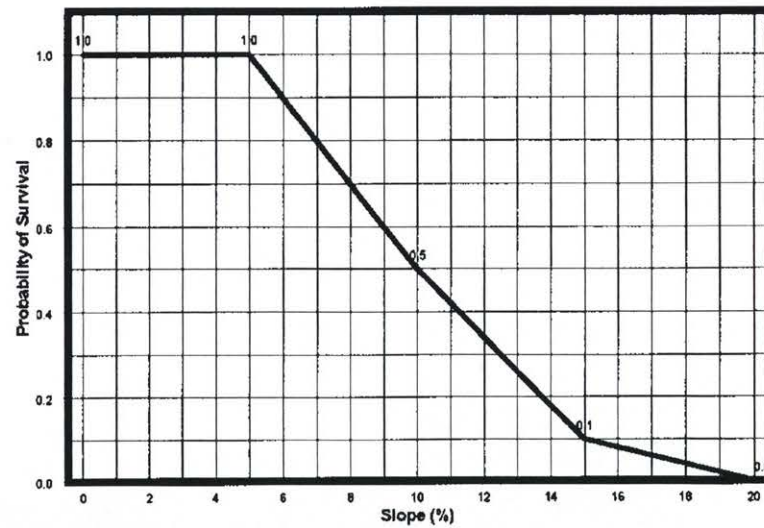
(a)



(b)

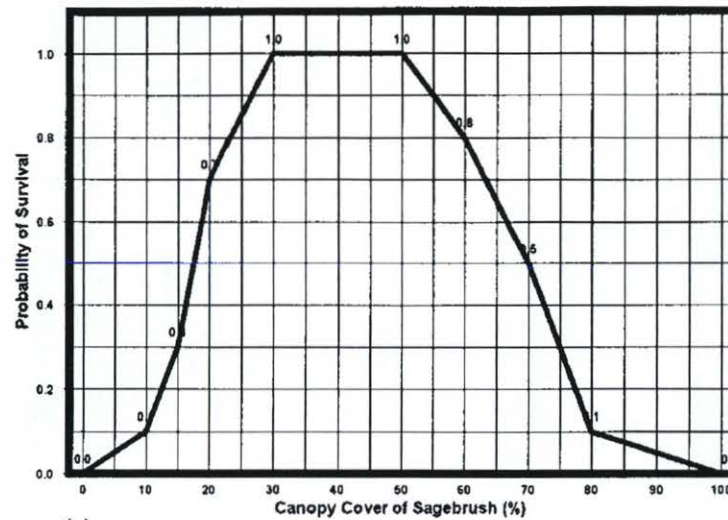


(c)

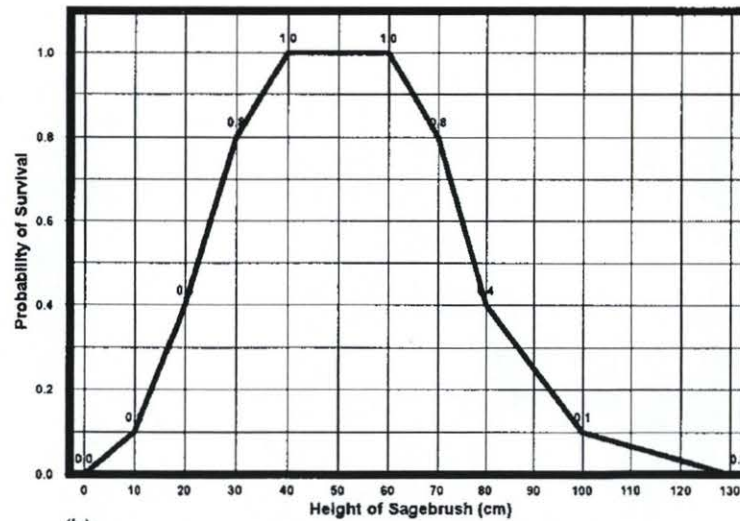


(d)

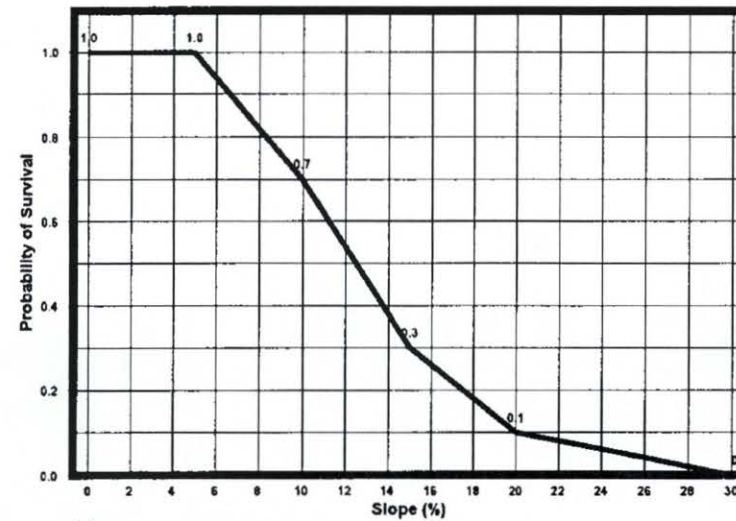
Figure 4. Hypothesized functional relationships between characteristics of sage grouse brood-rearing habitat and probability of survival during the brooding period.



(a)

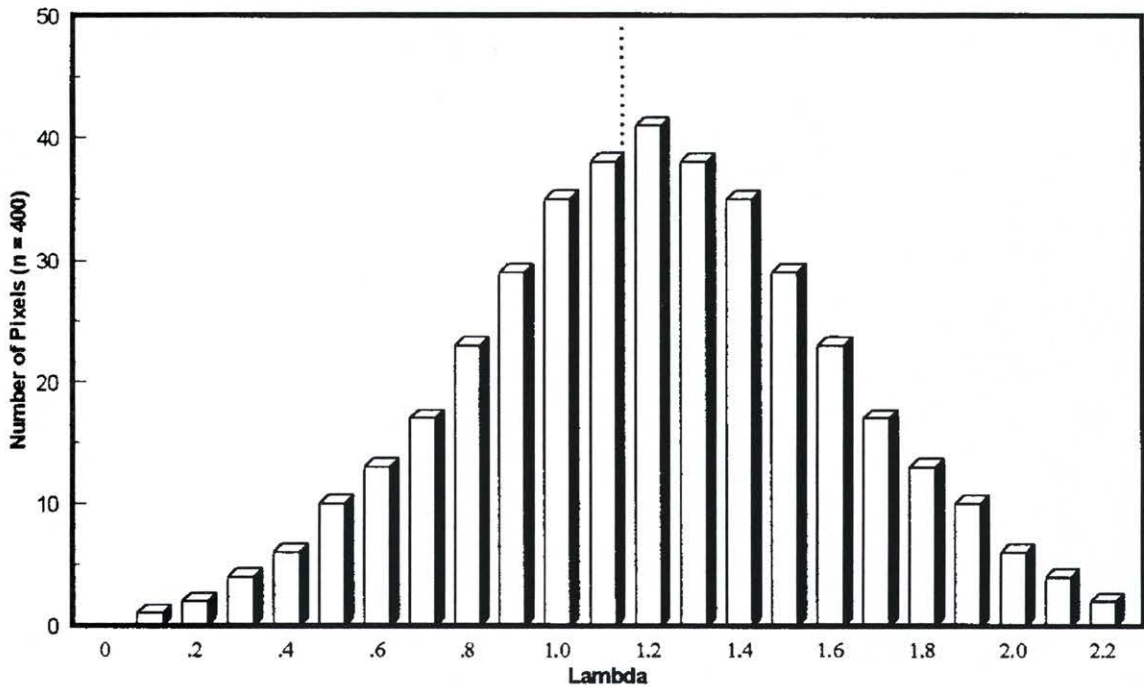


(b)

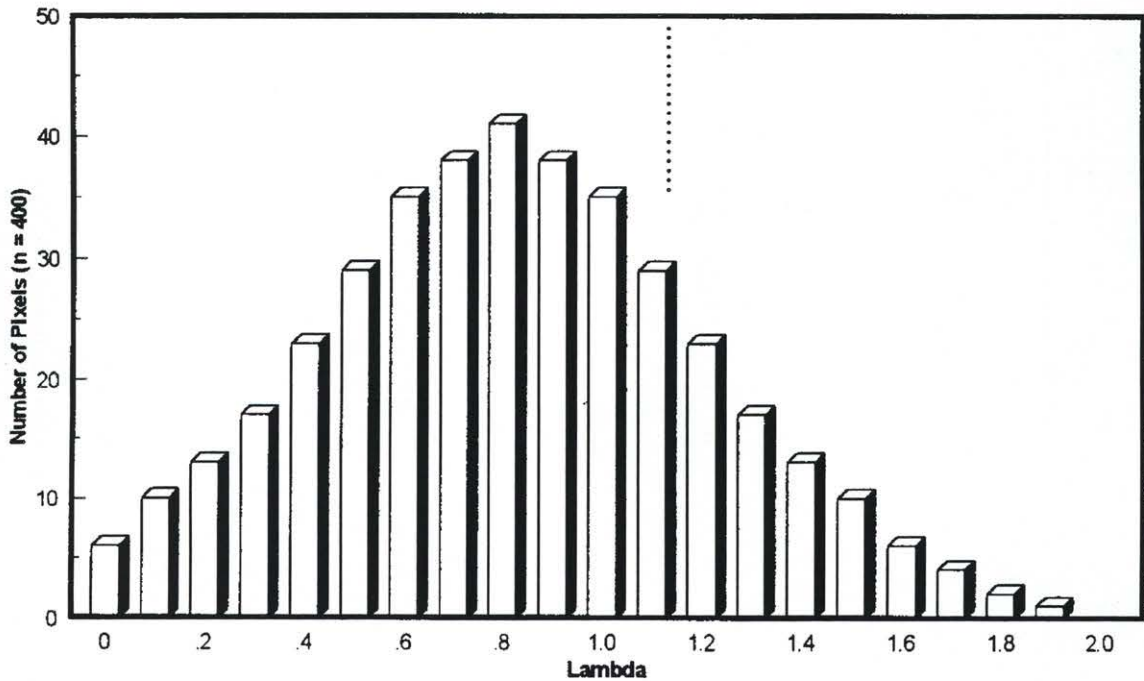


(c)

Figure 5. Hypothesized functional relationships between characteristics of sage grouse winter habitat and probability of juvenile survival during the wintering period.



(a) Assuming that the mean of the distribution is significantly > 1.0 , the prediction would be that the habitat is suitable (dotted line indicates threshold of suitability).



(b) Assuming that the mean of the distribution is significantly < 1.0 , the prediction would be that the habitat is unsuitable (dotted line indicates threshold of suitability).

Figure 6. Illustration of two possible outcomes of a habitat suitability analysis for sage grouse on a hypothetical analysis area.

Table 1. Literature sources used to develop functional relationship graphs between sage grouse success/survival and characteristics of their seasonal habitats. Letter(s) indicate whether source provided information on nest (N), brood (B), or winter (W) habitat for the variable in question.

Source	Grass Cover	Grass Height	Forb Cover	Forb Height	Herbaceous Cover	Sagebrush Cover	Sagebrush Height	Composition of Big Sagegrush	Shrub Cover	Shrub Height	Visual Obstruction	Bare Ground	Slope	Aspect
Autenrieth (1986)	N					NBW	NW						W	W
Barnett and Crawford (1994)	N		N		N	N						N		
Beck (1977)									W	W			W	W
Colenso et al. (1980)						N	N							
Connelly (1982)									W	W				
Connelly et al. (1991)	N	N			N									
Drut (1993)	B		B		B				B					
Dunn and Braun (1986)			B			B	B		B					
Eng and Schladweiler (1972)						W	W		W					
Fischer (1994)	N	N	N				N		N					
Gill (1965)							N						N	
Gray (1967)	N		N		N	N			N			N		
Gregg (1992)	N		N		NB				N					
Gregg et al. (1994)			N											
Hanf et al. (1994)	N	N	N		N				N					
Hayden-Wing et al. (1985; in Rothwell 1993)										N				
Hofmann (1991)						N								

Table 1. Con't.

Source	Grass Cover	Grass Height	Forb Cover	Forb Height	Herba- ceous Cover	Sage- brush Cover	Sage- brush Height	Composi- tion of Big Sagegrush	Shrub Cover	Shrub Height	Visual Obstruc- tion	Bare Ground	Slope	Aspect
Homer (1990)									W	W			W	W
Hulet et al. (1986)					N			N	N	N				
Hupp and Braun (1989)													W	W
Jarvis (1974)													N	N
Klebenow (1968)					N			N				B		
Klebenow (1969)	NB		NB		B	NB	N		NB			N		
Klott and Lindzey (1990)	B		B		B	B	B		B	B		B		
Klott et al. (1993)	NB	NB	NB						NB	NB	NB	NB		
Martin (1970)	B		B		B	B	B							
Martin (1976; in Rothwell 1993)									B					
Martin (1990)	B		B		B	B			B			B		
May (1970)							N						N	N
Musil et al. (1994)	N	N	N		N	N			N	N		N	N	
Nelson (1955)							N							
Patterson (1952)							N							
Petersen (1980)							N						N	N
Peterson (1970)			B			B	B							
Poley (1969)							N						N	
Pyrah (1970; in Gregg 1992)	N													

Table 1. Con't.

Source	Grass Cover	Grass Height	Forb Cover	Forb Height	Herbaceous Cover	Sagebrush Cover	Sagebrush Height	Composition of Big Sagebrush	Shrub Cover	Shrub Height	Visual Obstruction	Bare Ground	Slope	Aspect
Rasmussen and Griner (1938; in Gregg 1992)						N	N							
Ritchie et al. (1994)					N									
Robertson (1991)						W		W	W	W				
Rothenmaier (1979)						N	N							
Savage (1969)	B		B		B	B	B		B			B		
Schlatterer (1960)														N
Schoenberg (1982)			NB			NBW	NBW						NBW	NBW
Schroeder (1995)	NBW	NBW	NBW	NBW	NBW	NBW		NBW	NBW	NBW	NBW	NBW	NBW	NBW
Sime (1991)	N		N		N		N		N					
Smith and Klott (1995)	NB	NB	NB		NB				NB	NB		NB		
Sveum (1995)	NB	NB	NB		NB			NB	NB	NB		NB		
Wakkinen (1990)	N	N	N		N	N	N		N			N	N	
Wallestad (1971)	B		B			B	B		B					
Wallestad (1975)						W								
Wallestad and Pyrah (1974)						N	N							
Wallestad and Schladweiler (1974)									N					

Table 2. Results of regression analysis used to develop the predictive model relating $E(\lambda)$ to habitat characteristics based on vital rates associated with characteristics based on vital rates associated with sage grouse life states for a habitat-explicit population model.

Regression Results Analysis of Variance								
Source	DF	Sum of Squares	Mean Square Error	F-value	P > F			
Model	3	18.9961	6.33204	1953.3920	0.0001			
Error	996	3.2286	0.0032					
Total	999	22.2247						
Parameter Estimates								
Parameter	DF	Estimated Coefficient	Standardized Coefficient	SE	t-value H_0 : Parameter=0	P > t	Partial r^2	Model R^2
β_0	1	-0.147406	0.0000	0.0230578	-6.393	0.0001		
β_1	1	0.684623	0.75978542	0.0108883	62.877	0.0001	0.5601	0.5601
β_2	1	0.652698	0.50210379	0.0157008	41.571	0.0001	0.2542	0.8144
β_3	1	0.592451	0.20095700	0.0356248	16.630	0.0001	0.0403	0.8547



APPENDIX 1. Concepts and Rationale for Building a Habitat-Explicit Population Model for Sage Grouse

Several concepts were addressed while developing the Habitat-Explicit Population Model (HEPM) for sage grouse. The following is a discussion describing these concepts and their influence on the underlying premises that define the development, application, and interpretation of HEPMs.

DEFINING HABITAT QUALITY

To assess habitat, we first need to define habitat and its contribution to the observed vital rates of a population, and thus the population growth rate [λ]. More specifically, we need to define "habitat quality" and its measurement scale. We define habitat quality as a binomial: habitat is suitable or unsuitable. Although potentially occupied, unsuitable habitat [*i.e.* $E(\lambda) < 1.0$] is incapable of supporting a self-sustaining population over an ecologically meaningful period (*i.e.* sink or suboptimal habitat). Whereas, suitable habitat [*i.e.* $E(\lambda) \geq 1.0$] can support a viable population over time (Pulliam 1988, Pulliam and Danielson 1991, Kellner *et al* 1992). Therefore, our definition of habitat quality is intertwined with the population parameters a particular habitat may be expected to support.

Habitat quality is a much easier idea to comprehend than to describe rigorously. Of primary difficulty is quantifying the dynamic 4-dimensional (*i.e.* 3-dimensional space and 1-dimensional time) nature of resource availability on the landscape and other environmental conditions. This includes quantifying landscape heterogeneity, spatially and temporally, with respect to variation in fitness parameters expressed in populations occupying that landscape (Pulliam 1988, Pulliam and Danielson 1991). Modeling effects of habitat changes on populations over time is especially difficult (Dunning *et al* 1995). The quality of any space in the environment can also vary among segments of a species or population with respect to specific life stage requirements (*e.g.* nesting, brood-rearing, or wintering) or activities (*e.g.* roosting, foraging, or escaping).

Additionally, habitat patches do not exist in a vacuum (patches are considered homogenous within some observable boundary). The juxtaposition of patches and the changes in patterns with time and scale can also be important for determining habitat quality. This is especially important for mobile species with specialized habitat requirements for distinct life stages (Levin 1992, Pulliam 1988, Pulliam *et al* 1992). Thus, the quality of a habitat patch may depend on (or be correlated with) the quality of an adjacent patch or the distance among patches that provide adequate requirements for subsequent life stages (*e.g.* distance between wintering and nesting habitat; Legendre 1993).

Where do biologists get information for modeling the covariation between landscapes and population parameters that reflect habitat quality? Empirical research on a species' habitat selection as it relates to fitness would be most useful in determining habitat requirements and defining variations in quality. However, we typically lack empirical data on fitness consequences associated with habitat selection patterns (Warner 1992). This information is needed to develop a thorough definition of habitat quality as it relates to all factors that affect a population's long-term viability (Gilpin and Soule 1986, Akcakaya 1992).

Lacking empirical data, we can develop models that assess a population's prognosis with estimates of habitat quality by filling information gaps with ecological theory (*e.g.* foraging theory: Mangel and Clark 1986, Stephens and Krebs 1986). Currently, habitat selection data comprises most of the information available that relates environmental characteristics to a wildlife species' fitness. Habitat selection is defined here as the nonrandom exploitation of a resource or group of resources encountered in the environment (temporally and spatially) by an individual. Nonrandom use also implies an understanding of the environment that the organism occupies such that it can expect some rate-of-encounter for the resource of interest, at least spatially (Manly *et al* 1993). Therefore, selection for specific habitat characteristics

implies a level of importance in a resource's quality for meeting an animal's requirements for survival and reproduction.

However, few habitat selection studies directly quantify relations between selection and fitness consequences. Hence, models constructed with population-habitat relationships are generally "hypothesized" from incomplete data and must be applied with extreme caution until rigorously validated.

SOURCES OF VARIATION

Our modeling approach relates observable patterns in the landscape to resulting population vital rates (Cantrell and Cosner 1991, Dutilleul 1993), assuming habitat patterns associated with greater population growth are of higher quality. However, both landscapes and resulting population vital rates can vary greatly. To detect factors important for explaining relations between landscapes and populations, we must first identify sources of variation for both. Our approach focuses on explaining covariation between habitat measures and population parameters, keeping in mind that total variation can be nested or partitioned differently according to scale (Levin 1992, Palmer 1992).

These sources of variation can be separated into internal and external factors, which we operationalize as non-habitat and habitat parameters, respectively. Habitat selection is an example of an internal factor because it is inherent to an individual regardless of how the patterns may have developed (*e.g.* genetic or learned behavior; Morrison *et al* 1992). The environment that an individual encounters is external and includes biotic and abiotic factors. Population fitness parameters are expressions of interactions between internal factors (*e.g.* energetic requirements, habitat selection patterns, demographic stochasticity, density dependence, and social behavior) and external factors (*e.g.* physical environment, predator community, inter- and intraspecific competition, and environmental stochasticity) that individuals encounter while traveling through space and time. Thus the conceptual model for the probability of persistence over time is indexed by population growth rate as:

$$\lambda = f(\text{habitat parameters}) + f(\text{non-habitat parameters}) + f(\text{habitat} \times \text{non-habitat parameters}) + e.$$

Little empirical information is available for directly linking the effects of non-habitat parameters to fitness parameters. Therefore we do not specifically attempt to explain these sources of variation by modeling non-habitat parameters in an HEPM. Instead, we assume these non-habitat factors generally account for relatively less of the variation in λ than do habitat parameters.

We also recognize the importance of interactions between habitat and non-habitat factors (*e.g.* survival affected by the interaction of hiding cover and predator density) for determining a population's observed λ . Interactions are even more difficult to quantify and understand, especially if nonlinear, because specific information is required for all interacting factors. We assume interactions most likely occur, but that increasing habitat quality mitigates the negative effects of non-habitat parameters. For example, we assume that the probability of nest success is ultimately determined by quality and quantity of hiding cover regardless of community composition and densities of potential nest predators.

Although we de-emphasize many factors in an attempt to justify focusing on habitat in predicting a population's growth rate, we recognize the importance of non-habitat factors. Those factors not parameterized (*i.e.* non-habitat and interaction parameters) can contribute to unexplained variation in λ and account for discrepancies between predicted and observed values (*e.g.* during validation attempts). However, as parameter estimates for non-habitat factors become available, they could be included in our modeling approach, and thus improve predictions.

Other sources of error between predicted and observed λ s could be due to poor estimates of functional relations between habitat parameters and vital rates, sampling variation in empirical data, and environmental and demographic stochasticity. Moreover, many ecological relationships may have nonlinear or synergistic responses. As a result, the usual linear statistical approaches to understanding and

predicting these relations (e.g. linear regression, linear discriminant analysis, analysis of variance, log linear modeling, and logit modeling) may produce unreliable models (Brennan *et al* 1986, Gutzwiller and Anderson 1986).

Although we focus our modeling efforts on functional habitat parameters, these account for only a portion of the variation that ultimately determine the expression of population fitness parameters. Many other factors can influence fitness over time (e.g. predator density, climate, and exploitation). However, habitat may be thought of as the common denominator for all factors because in its absence, all other factors, including the population itself, will be absent.

MODEL STRUCTURE

Because a population's growth rate is the best measure of long-term viability (excluding significant immigration and emigration), we replaced the arbitrary scale (0.0-1.0) used for many habitat evaluation approaches (e.g. HSI models and Habitat Effectiveness Models) with the biologically interpretable scale of λ (Ricklefs 1979, Kellner *et al* 1992, Noon and Sauer 1992). Accordingly, the response variable and prediction scale of an HEPM would be λ (accounting for contributions of survival and reproduction to the observed λ ; Pulliam 1988, Kellner *et al* 1992).

Because of criticisms by Van Horne (1983) and according to Kellner *et al* (1992), we propose using suitability and quality definitions that relate to the potential of a habitat to support a viable population. Habitat quality, and thus expected population viability, would be defined as an $E(\lambda) \geq 1.0$. Therefore, suitability would have a dichotomous definition with habitat being either able to support a viable population or unable to support a viable population. A habitat score ≥ 1.0 would indicate suitable habitat of varying quality, whereas a score of < 1.0 would indicate unsuitable habitat.

The structure of an HEPM also differs from most other approaches by having two predictive modules, a population module and a habitat module. The population module is a means of relating population vital rates (e.g. nest success, brood survival, and adult survival) to $E(\lambda)$. Those vital rates useful for predicting a population's λ

are retained in the population module as module components. Components may often be related to discrete segments of a species' life history, such as life stages. Partitioning the total variation between vital rates and habitat variables by life stages should help eliminate variation in predictions. More important, the vital rates modeled must account for a large portion of the population's resulting growth rate.

Each component in the population module must have a corresponding component in the habitat module that can be sampled from the landscape. Thus, the habitat module is constructed of functional relationships (empirical or hypothetical) that relate physical, temporal, and spatial habitat characteristics to population component vital rates. As with the population module, highly accurate predictions can result only if habitat characteristics modeled account for large proportions of the variation observed in corresponding vital rates.

Any of several methods can be used to investigate, develop, and model relationships between vital rates and λ , and between habitat characteristics and vital rates. For example, population growth models may be acceptable that are individual-based, life-stage-based, age-based, or population-based. Methods selected will depend on available data, on population and habitat components of interest, and on the scale at which predictions will be applied. Two factors are key for accurate prediction with an HEPM. First, the life stages parameterized (*i.e.* vital rates) must account for significant portions of the variation in λ , and second, habitat factors related to these life stages must account for significant portions of the variation that the vital rate estimates. The approach used must conform to the life history strategy of the species of concern and the response variable should be some measure of population growth (e.g. λ). Also, assumptions of the method used must be considered so that predictions of the resulting model are most likely to be reliable.

Habitat quality is predicted using the population module parameterized with vital rates predicted from the habitat module. Habitats associated with relatively high survival and reproduction are considered higher quality.

Predictions of habitat quality are functions of relations between habitat characteristics and associated vital rates, and relationships between these vital rates and the $E(\lambda)$ that landscape may support (Kellner *et al* 1992). For accurate predictions, habitat components and corresponding vital rates should be clearly associated, discrete, measurable, and account for significant proportions of λ (*e.g.* nest sites and nest success, or roosting sites and winter survival). The habitat specialist may be most appropriate for this approach, with its more easily understood habitat requirements, often limited distribution, and observable fitness consequences, *e.g.* sage grouse and sagebrush (*Artemisia* spp.) habitats.

ISSUES OF SCALE

Determining the scale at which habitat is described and evaluated is critical for all stages of habitat-explicit population modeling (*e.g.* collecting field data, developing functional relationships, model structuring, and model implementation). Previously, habitat descriptions for modeling wildlife-habitat interactions generally followed some vegetation classification scheme or habitat typing (U.S. Dept. Inter. 1980, Scott *et al* 1993). Classification conventionally resulted from delineation of habitat patches based on visually perceived landscape boundaries. For example, habitat was usually categorized at a single macro-scale through cover-type mapping (*i.e.* vegetational, geographical, and geological characteristics; U.S. Dept. Inter. 1980). This approach has the risk of defining human-perceived boundaries as opposed to real and multiple boundaries most likely to be perceived by an organism (Levin 1992, Host *et al* 1996). This resolution may or may not describe characteristics important for a species' habitat selection and associated fitness parameters.

Although habitat patches are usually considered discrete, homogenous units, habitat characteristics may often be more accurately described as a continuum or gradient (Palmer 1992, Host *et al* 1996). Describing habitat with continuously measured variables should capture more information about a landscape, whether simply describing that landscape, investigating population-habitat relationships, or predicting

habitat quality with an HEPM. Also, to understand the internal and external processes that determine a population's persistence over time, the first step is understanding the many scales of heterogeneity and variability in landscapes that provide the resources necessary for organisms to survive and reproduce. Accurate predictions about population phenomena across ranges of variation pivot on mechanistic understandings of these processes that may operate at many scales (Levin 1992). Hence the finer the resolution of description, the better opportunity we have to identify boundaries and features that organisms perceive in the landscape when making resource selection choices that ultimately determine their fitness (Pulliam 1988).

A population's use of a landscape may be predictable if we have knowledge of the availability and distribution of resources for a population to exploit (*i.e.* the spatial variability, heterogeneity, and geometry of resources across a landscape; Palmer 1992, Dunning *et al* 1995). We may also be able to predict accurately the expected habitat quality of that landscape at a finite point in time if we understand the effects of: 1) scale on resource selection, 2) resource availability and selection on population survival and reproduction, and 3) fitness parameters on population growth and persistence. Finally, future habitat quality may be predicted if the landscape's trajectory is known or modeled (Hansen *et al* 1992, Urban *et al* 1992, Hansen *et al* 1993).

Detailed spatially-related environmental descriptions (*i.e.* small scale sampling units) are more likely to capture scales and boundaries that animals perceive in their environment. Many processes affecting ecological organization probably also operate across a range of spatial and temporal scales (Levin 1992). Detailed habitat descriptions would facilitate equally detailed investigations of habitat-vital rate interactions and processes for constructing an HEPM. However, it may be difficult to describe habitat availability over large areas with spatially-referenced and continuously measured variables without some categorization of the landscape. Development of a feasible sampling scale is necessary to quantify available habitat adequately and capture the multiple scales at

which individuals of a population perceive their environment (Levin 1992).

For development, implementation, and validation of an HEPM, we suggest collecting habitat information and thus describing landscapes at the smallest scale feasible. Measuring continuous variables in small areas and integrating them into landscape descriptions may allow more detailed descriptions of the environment's multivariate, continuous nature. This would also allow investigation of processes across many scales. Therefore, the landscape of interest should be completely gridded with equal-sized cells of the smallest dimensions feasible. Each cell could be spatially referenced and assigned values for each variable, preferably on a continuous scale, in the habitat module. Cells become homogenous-within "habitat patches." As the sampling unit (*i.e.* grid cell) decreases in area, descriptions of variables may more closely approximate the continuum on which they exist. Information collected at a micro-resolution also permits assessment at macro-resolutions, and any number of intermediate resolutions using different methods of cell aggregation. When considering validation of an HEPM, micro-scale information would also allow application of the model at many resolutions, and tests of accuracy and robustness across multiple scales.

REMOTE SENSING AND GIS FOR HEPMS

Recent developments in remote sensing and Geographical Information Systems (GIS) have provided the means to apply the detailed information of wildlife-microhabitat relationships to landscapes (Breininger *et al* 1991, Scott *et al* 1993). Satellite remote sensing makes it relatively easy to describe and monitor temporal changes across landscapes (Hegyí and Walker 1991, Green and Cosentino 1996). Methods to rapidly delineate and quantify critical habitat features on large spatial scales are needed to implement an HEPM model efficiently and to facilitate resulting habitat management (Homer 1990). Therefore, we recommend HEPMs be developed and implemented using remote sensing and GIS techniques.

Remote sensing and GIS, which allow evaluation of wildlife-habitat relations at many

scales and over large areas, were used increasingly more during the last decade (Cannon *et al* 1982, Leckenby *et al* 1985, Davis and DeLain 1986, Lancia *et al* 1986, Donovan *et al* 1987, Gagliuso 1991, Pereira and Itami 1991, Clark *et al* 1993, Homer *et al* 1993, Turner *et al* 1993, Gustafson *et al* 1994, Roseberry *et al* 1994, Duncan *et al* 1995). These methods can also be used to construct and test spatially-explicit habitat models (Holt *et al* 1995) designed to understand processes that influence wildlife populations (Dutilleul 1993, Conroy *et al* 1995).

Satellite imagery is a powerful tool for quantifying habitat because of the large area covered, detail of information, consistency of spectral response, and frequent revisit time of satellites (Green and Cosentino 1996). The Landsat Thematic Mapper (TM) is one form of remote sensing that has several advantages over traditional methods (*e.g.* interpretation of aerial photos) for quantifying habitat:

- 1) it is generally cost effective for analyzing habitat over large areas,
- 2) allows for rapid qualitative and quantitative spatial assessment,
- 3) allows incorporation of ancillary digital data to aid in vegetation classification and model development,
- 4) can be used in temporal analysis to document and monitor habitat change, and
- 5) allows habitat to be monitored at a fine scale (Homer 1990, Miller and Conroy 1990, Congalton 1991, Choung 1992, Verbyla 1995, Green and Cosentino 1996).

Recently collected TM data are available for most of the United States from the Earth Observation Satellite Company (EOSAT; Scott *et al* 1993, Koeln *et al* 1994).

Commonly, TM imagery is used to identify and map general cover types (*e.g.* cropland, range, or forest) and evaluate wildlife food availability and potential habitat associations for species of interest (Homer 1990). Previous approaches, however, have generally focused on associating broad cover types to wildlife habitat and have not evaluated the possibility of using TM data to associate fine-scale structural and compositional attributes of wildlife habitat

(Homer *et al* 1993). We propose using TM data to identify vegetation cover types and to define their structure based on measures such as vegetation height, density, and species composition. The framework of a GIS can be used to

add ancillary data (*e.g.* slope and aspect) that will enhance the TM classification process and provide a more powerful modeling tool. Our proposed approach relies extensively on the work of Homer (1990) and Homer *et al* (1993).

APPENDIX 2. Methods, Results, and Discussion for Building a Habitat-Explicit Population Model for Sage Grouse

The following describes the methods we used to build the Habitat-Explicit Population Model (HEPM) for sage grouse, the results of these methods, and a discussion of the results. Methods follow from the conceptual approach described in Appendix 1, and results that apply to the application of the sage grouse HEPM are presented in the main text. Additional discussion and interpretation of the model's results are also presented in the main text.

METHODS

We used empirical and simulated data, and hypothesized relationships based on ecological theory and professional judgement to develop an HEPM for sage grouse. Life stages with vital rates that accounted for the most variability in the population growth rate [λ] were selected as variables for the population module (Edelmann *et al* 1997). Life stages were selected from analyses of empirical and simulated data from across the range of sage grouse. These life stages also were included in the habitat module. Then "hypothesized" functional relationships were generated to relate topographic and vegetational characteristics to vital rates associated with each life stage in the population module. Functional relationships were constructed with guidance from empirical data, ecological theory, and professional judgement.

We then predicted habitat quality for a defined landscape using the population module, parameterized with the vital rates predicted from the habitat module. Predictions of habitat quality are functions of relations between habitat measurements and associated vital rates, and relationships between these vital rates and the growth rate that habitat may be expected [$E(\lambda)$] to support.

Population Module

Determining Life Stage Importance for Sage Grouse—We used the methods of Wisdom and Mills (1997) to identify the relative importance of sage grouse life stages to population growth as specifically applied by Edelmann

et al (1997). Results of this report were used to develop the population module of our sage grouse HEPM (report is available from K.P. Reese).

Modeling Life Stage Importance—Those vital rates associated with life stages accounting for most of the variation in λ as identified by Edelmann *et al* (1997) were then modeled using least-squares multiple regression (Zar 1984, Ott 1988, SAS Inst., Inc. 1988). Regression coefficients expressed the relative contribution of life-stage vital rates (*i.e.* predictor variables) for predicting the population's finite rate of increase (λ , the response variable). The resulting linear regression function comprised the population module of the HEPM:

$$\lambda_i = \beta_0 + \beta_1(\text{life stage}_{1i}) + \beta_2(\text{life stage}_{2i}) + \dots + \beta_n(\text{life stage}_{ni}) + e_i$$

Habitat Module

Life-Stage Components—Prediction functions were constructed by relating habitat variables considered important for predicting life-stage vital rates to the life stage components in the population module. Individual sets of habitat functions were developed for each life stage in the population module. That is, each life-stage component (*e.g.* nesting, brooding) comprising the population module also occurred in the habitat module. Each life-stage component of the habitat module was then built with 3–4 habitat variables that provided the best prediction of that corresponding population vital rate (*e.g.* egg survival). Predicted vital rates for each life-stage component incorporated in the population module, were used to parameterize the population module from which λ was calculated.

Habitat Variables—As with the population module, many approaches to quantifying the habitat module may be acceptable depending on objectives, life history strategies, and data available. We selected habitat variables that characterized the current knowledge of habitat selection by sage grouse at both macro- and micro-habitat levels of resolution. But little information is available that relates habitat

characteristics to expressions of vital rates. When explicit information was not available, we constructed hypothesized habitat/vital rate functions based on professional judgement augmented by ecological theory. Based on review of available literature, variables reported to be important to sage grouse ecology were considered for modeling. Candidate variables were:

- sagebrush cover (%)
- sagebrush height
- composition of big sagebrush (%),
- total shrub cover (%)
- total shrub height (cm)
- grass cover (%)
- grass height (cm)
- forb cover (%)
- forb height (cm)
- total herbaceous cover (%)
- visual obstruction (dm)
- bare ground (%)
- slope (%)
- aspect (degrees)

Spatial Variables—We investigated spatial variables depicting movement rates and distances, juxtaposition of habitats specific to life requisites, and interspersions of different cover types for inclusion in the habitat module. Information on sage grouse movements however, was highly variable. No data relating movement patterns to fitness parameters were available to guide the development of functional relationships. This being the case, we did not account for habitat juxtaposition in the sage grouse HEPM with spatial variables. If spatial data become available, the structure of our model would approach that of a spatially-explicit population model, providing more accurate and detailed predictions for conservation management (Conroy *et al* 1995, Dunning *et al* 1995).

Functional Relationships—We reviewed 52 documents on sage grouse research conducted between 1938 and 1995. These included state and federal agency reports, university theses and dissertations, and journal articles. Peer reviewed literature was given greater consideration than other sources. However, because of a general lack of information, all relevant literature was considered when formulating functional relationships (Table 1).

Functional relationships are only explicit hypotheses based on the best available information about species-habitat relationships and are not intended to be statements of proven cause and effect. As such, they have a high degree of scientific uncertainty, reflecting the fact that our prediction of species response to environmental conditions is not perfect. Uncertainty may occur because: 1) the system is naturally variable and complex, and thus difficult to predict; 2) the process of estimating model parameters entails error; 3) models used to generate predictions are in some sense invalid; or 4) the scientific question being asked is ambiguous or incorrect (Morrison *et al* 1992:228).

We used reported data to guide placement of minimum, optimal, and maximum values for the relationships between vital rates and habitat characteristics. The slope or curve of the functions between these points was largely hypothesized because little information was available to delineate them precisely. In cases where an actual vital rate was unavailable (*e.g.* brood survival) we substituted habitat use information in its place. As a result, estimates of variation about these curves were not available or generated.

Integrating Habitat Variables—Additionally, we considered how to combine vital rate predictions for life-stage components that contain ≥ 1 habitat variable. Individual habitat-vital rate functions were constructed for each variable and incorporated into each single life stage component of the habitat module. Hence a life-stage vital rate was estimated with each functional relationship developed for that life stage. These multiple estimates must be combined to provide a single vital rate prediction that can be used to parameterize that life-stage component in the multiple regression prediction model of the population module.

Six mathematical methods of defining relations between model variables and suitability of the habitat are commonly accepted: 1) minimum function, 2) additive function, 3) multiplicative function, 4) power functions, 5) arithmetic mean, and 6) geometric mean (U.S. Dept. Inter. 1980, Stiehl 1994b). No standard equation can be considered "best" for a given situation, but some can be defended more easily based on logic and the biological attributes of the species

in question. Empirically established relationships would have been preferred if data were available.

The geometric mean or compensatory function (which assumes interaction among and between variables) is appropriate when zero suitability for any variable(s) will result in an overall value of zero. Optimum conditions exist only if all values are one. If any value is zero, the result of the function is zero. A low value (other than zero) for 1 variable will be partially compensated for by higher values of the other interacting variables. With respect to our model, we believe that sage grouse respond primarily to habitat variables with relatively low ranges in values, with secondary compensation provided by variables with higher ranges. Therefore, we selected the geometric mean to combine multiple functional relationships into single vital rate estimates in the habitat module. This was the best quantification of the relation among two or more variables and habitat quality for sage grouse.

RESULTS

Population Module

Results are taken from Edelman *et al* (1997). Survival during the first year of life accounted for >84% of the variation in λ based on our analyses. This encompassed the vital rates of egg survival, chick survival, and juvenile survival. We regressed λ on these vital rates to build the predictive model for the population module (Table 2). The population module constructed for predicting λ based on vital rates comprising the first year of life for sage grouse follows:

$$E(\lambda) = -0.147406 + 0.684623(\text{egg survival}) + 0.652698(\text{chick survival}) + 0.592451(\text{juvenile survival}).$$

Habitat Module

Life Stage Components—Sage grouse habitat components of nesting, brood-rearing, and wintering, which correspond respectively to egg survival, chick survival, and juvenile survival, comprise the habitat module. Habitats required for these life stages are called hereafter NEST,

BROOD, and WINTER. These life-stage components accounted for most of the variation in growth rates in the population module analysis. These life stages also have relatively discrete habitat components that have been described and/or quantified with respect to our selection criteria. For the most part, fitness consequences have not been determined for the habitat selection patterns described, with the notable exceptions of nest success and nest site selection.

Habitat Variables—Of the initial 14 habitat variables considered for inclusion in the model, we chose to retain four: 1) sagebrush canopy cover, 2) sagebrush height, 3) herbaceous cover, and 4) slope. All selected variables are included in the modeling of NEST, BROOD, and WINTER. The exception is herbaceous cover, which is not included in the WINTER component. These variables were selected because they have repeatedly been important in studies of sage grouse habitat selection and they can be classified from Landsat TM data (Homer 1990). Slope was retained to eliminate habitats unsuitable for sage grouse.

Additional variables thought to be important to habitat selection by sage grouse were considered for inclusion in the model, however these structural characteristics cannot currently be classified accurately from satellite imagery and were thus excluded. The most notable exclusions were grass height and cover, and forb cover. These structural characteristics are important for nesting and brooding habitat (Martin 1990, Connelly *et al* 1991, Greg 1992, Fischer 1994) and are at least partially included in the model through correlations with the surrogate variable "herbaceous cover." If or when technology is available to remotely sense grass height and separate grass and forb cover, these variables should be considered for inclusion in the habitat module.

Functional Relationships—The hypothesized functional relationships between sage grouse vital rates and associated habitat variables for each life stage component were constructed graphically. These relationships were for NEST (Figure 3a-d), BROOD (Figure 4a-d), and WINTER (Figure 5a-c) life stages, as shown in the main text.

DISCUSSION

Although effects of habitat selection on nesting and brooding have been investigated, little information is currently available relating habitat parameters to fitness parameters. Moreover, vital rates have seldom been estimated for sage grouse populations, which is why simulated data were required in our analyses. Functional relationships between habitat used during nesting and brooding and corresponding fitness consequences should be assessed before reliable methods for effectively evaluating sage grouse habitats can be developed (e.g. Habitat Suitability Models; U.S. Dept. Inter. 1981, Van Horne 1983, Kellner *et al* 1992), or management actions prescribed with high probabilities of success (Braun *et al* 1977).

The following is a discussion of the critical assumptions as they pertained to the development of the sage grouse HEPM.

Assumption 1: *Population vital rates modeled account for a significant portion of the variation in λ .* Using empirical data, we demonstrated that the first year of life of female sage grouse accounted for the largest proportional influence on population growth. The vital rates modeled (egg survival, chick survival, and juvenile survival) accounted for approximately 84% of the variation observed in λ , showing that this assumption was valid.

Assumption 2: *Vital rates and corresponding life stages are clearly associated with quality of discrete habitat requirements.* This assumption states that habitat requirements are discrete for each life stage modeled and that vital rates within those life stages are dependent upon habitat quality. Based on what is known about sage grouse biology, the vital rates modeled appear to be associated with relatively definable habitat requirements (i.e. egg survival and nesting habitat, chick survival and brood-rearing habitat, and juvenile survival and winter habitat). However, minimal data exist to link vital rates with habitat quality. This is especially true for chick survival and brood-rearing habitat. Until further data becomes available, this assumption largely exists as a working hypothesis requiring rigorous validation.

Assumption 3: *Habitat quality is quantifiable and accounts for most of the variation observed in vital rates and thus in population*

growth. This assumption is likely invalid for many wildlife species. In fact, most HSI or habitat models that predict species presence, population density, or species richness from environmental characteristics capture only a portion (typically $\leq 50\%$) of the variation in those species' parameters (Morrison *et al* 1992). This does not mean that habitat is unimportant; it is usually critical. It does mean that we may be limited in our ability to manage habitat alone and expect with a high confidence that the population will show a direct response. Our predictive ability may be enhanced when modeling a habitat specialist such as sage grouse. In such cases, greater probability exists that habitat will account for most of the variation in population growth.

Assumption 4: *The spatial orientation and geometry of habitat patches do not affect habitat suitability.* This assumption is probably not entirely valid because most wildlife species require a minimum size, juxtaposition, and interspersion of cover types before the habitat is used or occupied. Fragmentation or natural landscape heterogeneity and variability may make some habitat patches less suitable or even unsuitable based on size and spatial orientation to adjacent habitat patches (Palmer 1992, Turner *et al* 1993). We believe the predictive power of this model would be greatly enhanced if it were spatially explicit. However, little is known currently about the spatial characteristics of sage grouse habitat requirements as they relate to population vital rates. Consequently, insufficient data are available to model these complex spatial relations.

Assumption 5: *Microhabitat characteristics and landscape heterogeneity can be quantified successfully and efficiently over large areas using remote sensing and GIS techniques.* Essentially all but one of the habitat variables (% herbaceous cover) parameterized in this model have been classified successfully using Landsat TM imagery and ancillary data (Homer *et al* 1993). Homer *et al* (1993) did not classify herbaceous cover because they modeled sage grouse *wintering* habitat. However nothing has suggested that the classification of this variable would pose additional problems. With advances in technology we hope to incorporate additional variables (e.g. forb cover and height of herbaceous cover) that could increase the predictive power of this model.

LITERATURE CITED

- Akcakaya, H. R. 1992. Population viability analysis and risk assessment. Pages 148-157 in D. R. McCullough and R. H. Barrett, eds. *Wildlife 2001: populations*. Elsevier Applied Sci., New York, NY.
- Anderson, S. H., and K. J. Gutzwiller. 1994. Habitat evaluation methods. Pages 592-622 in T. A. Bookhout, ed. *Research and management techniques for wildlife and habitats*, 5th ed. The Wild. Soc., Bethesda, MD. 740pp.
- Anonymous1. Unknown.
- Anonymous2. Unknown. Analysis procedure for identifying and evaluation of sage grouse habitat.
- Autenreith, R. E. 1986. Sage grouse. Pages 763-779 in A. S. Eno, R. L. DiSilvestro, and W. J. Chandler, eds. *Audubon wildlife review 1986*. The Natl. Audubon Soc., New York, NY. 1094pp.
- Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. *J. Range Manage.* 47:114-118.
- Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection in winter. *J. Wildl. Manage.* 41:18-26.
- Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. *Wildl. Soc. Bull.* 5:99-106.
- Breiner, D. R., M. J. Provanca, and R. B. Smith. 1991. Mapping Florida scrub jay habitat for purposes of land-use management. *Photogrammetric Eng. and Remote Sensing* 57:1467-1474.
- Brennan, L. A., W. M. Block, and R. J. Gutierrez. 1986. The use of multivariate statistics for developing habitat suitability index models. Pages 177-182 in J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. Univ. Wisconsin Press, Madison.
- Bunnell, F. L. 1989. *Alchemy and uncertainty: what good are models?* U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. PNW-GTR-232. 27pp.
- Cannon, R. W., F. L. Knopf, and L. R. Pettinger. 1982. Use of landsat data to evaluate lesser prairie-chicken habitat in western Oklahoma. *J. Wildl. Manage.* 46:915-922.
- Cantrell, R. S., and C. Cosner. 1991. The effects of spatial heterogeneity in population dynamics. *J. Math. Biol.* 29:315-338.
- Choung, S. H. 1992. Wetland change detection using landsat-5 thematic mapper data in Jackson Hole, Wyoming. Ph.D. Diss., Univ. Idaho, Moscow. 230pp.
- Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. *J. Wildl. Manage.* 57:519-525.
- Colenso, B. E., M. S. Boyce, and J. Tate, Jr. 1980. Developing criteria for reclamation of sage grouse habitat on a surface coal mine in northeastern Wyoming. Pages 27-31 in *The Mitigation Symposium: A national workshop on mitigating losses of fish and wildlife habitats*. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. RM-65.
- Congalton, R. G. 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sens. Environ.* 37:35-46.
- Connelly, J.W., Jr. 1982. An ecological study of sage grouse in southeastern Idaho. Ph.D. Diss., Washington State Univ., Pullman. 84pp.
- Connelly, J.W., Jr., W.L. Wakkinen, A.D. Apa, and K.P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. *J. Wildl. Manage.* 55:521-524.
- Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecol. Applic.* 5:17-19.
- Davis, L. S., and L. I. DeLain. 1986. Linking wildlife-habitat analysis to forest planning with ECOSYM. Pages 361-369 in J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. Univ. Wisconsin Press, Madison.
- Dobkin, D. S. 1995. Management and conservation of sage grouse, denominative species for the ecological health of shrub steppe ecosystems. U.S. Dep. Inter., Bur. Land Manage., Portland, OR (BLM/OR/WA/PL-95/037+1792). 26pp.

- Donovan, M. L., D. L. Rabe, and C. E. Olson, Jr. 1987. Use of geographic information systems to develop habitat suitability models. *Wildl. Soc. Bull.* 15:574-579.
- Drut, M. S. 1993. Habitat use and selection by sage grouse broods in southeastern Oregon. M.S. Thesis, Oregon State Univ., Corvallis. 44pp.
- Duncan, B. W., D. R. Breininger, P. A. Schmalzer, and V. L. Larson. 1995. Validating a Florida scrub jay habitat suitability model, using demography data on Kennedy space center. *Photogrammetric Eng. and Remote Sensing* 61:1361-1370.
- Dunn, P. O., and C. E. Braun. 1986. Summer habitat use by adult female and juvenile sage grouse. *J. Wildl. Manage.* 50:228-235.
- Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecol. Applic.* 5:3-11.
- Dutilleul, P. 1993. Spatial heterogeneity and the design of ecological field experiments. *Ecology* 74:1646-1658.
- Edelmann, F. B., M. J. Wisdom, K. P. Reese, and J. W. Connelly. 1997. Contribution of sage grouse life stages to population growth. Unpubl. rep., Dep. Fish and Wildl. Resour., Univ. Idaho, Moscow. 17pp.
- Edwards, T. C., C. G. Homer, S. D. Bassett, A. Falconer, R. D. Ramsey, and D. W. Wight. 1995. Utah gap analysis: An environmental information system. Utah Coop. Fish and Wildl. Resour. Unit, Utah State Univ., Logan. Final Project Rep. 95-1. 46pp.
- Eng, R. L., and P. Schladweiler. 1972. Sage grouse winter movements and habitat use in central Montana. *J. Wildl. Manage.* 36:141-146.
- Fischer, R. A. 1994. The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho. Ph.D. Diss., Univ. Idaho, Moscow. 150pp.
- Gagliuso, R. A. 1991. Remote sensing and GIS technologies: An example of integration in the analysis of cougar habitat utilization in southwest Oregon. Pages 323-329 in M. Heit, and A. Shortreid, eds. *GIS applications in natural resources*. GIS World, Inc., Fort Collins, CO. 381pp.
- Gill, R. B. 1965. Distribution and abundance of a population of sage grouse in North Park, Colorado. M.S. Thesis, Colorado State Univ., Fort Collins. 185pp.
- Gilpin, M. E., and M. E. Soule'. 1986. Minimum viable populations: processes of species extinction. Pages 19-33 in M. E. Soule', ed. *Conservation biology: The science of scarcity and diversity*. Sinauer Assoc., Sunderland, MA.
- Gray, G. M. 1967. An ecological study of sage grouse broods with reference to nesting, movements, food habits, and sagebrush strip spraying in the Medicine Lodge Drainage, Clark County, Idaho. M.S. Thesis, Univ. Idaho, Moscow. 200pp.
- Green, K., and B. Cosentino. 1996. Using satellite imagery to detect and monitor forest change. *Geo Info Systems*, February, pp. 22-30.
- Gregg, M. A. 1992. Use and selection of nesting habitat by sage grouse in Oregon. M.S. Thesis, Oregon State Univ, Corvallis. 46pp.
- Gregg, M.A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. *J. Wildl. Manage.* 58:162-166.
- Gustafson, E. J., G. R. Parker, and S. E. Backs. 1994. Evaluating spatial pattern of wildlife habitat: A case study of the wild turkey. *Am. Midl. Nat.* 131:24-33.
- Gutzwiller, K. J., and S. H. Anderson. 1986. Improving vertebrate-habitat regression models. Pages 161-164 in J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates*. Univ. Wisconsin Press, Madison.
- Hanf, J. M., P. A. Schmidt, and E. B. Groshens. 1994. Sage grouse in the high desert of central Oregon: results of a study, 1988-1993. U.S. Dep. Inter., Bur. Land Manage., Prineville, OR (BLM/OR/WA/PT-95/002-4120.7, Series P-SG-01). 56pp.
- Hansen, A. J., D. L. Urban, and B. Marks. 1992. Avian community dynamics: the interplay of human landscape trajectories and species life histories. Pages 170-195 in A. J. Hansen and F. di Castri, eds. *Landscape boundaries: consequences for biological diversity and ecological flows*. Springer-Verlag, New York, NY.

- Hansen, A.J., S. L. Garman, B. Marks, and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecol. Applic.* 3:481-496.
- Hayden-Wing, L., L. D. Constan, J. Hull, M. Jackson, and T. Segerstrom. 1985. Movement patterns and habitat affinities of a sage grouse population in northeastern Wyoming. *Proc. Issues and technology in the management of impacted western wildlife.* Thorne Ecol. Inst., Boulder, CO. 1:207-226.
- Hegyi, F., and P. Walker. 1991. Multi-resource inventories with air- and space-borne digital remote sensing, GIS and video imaging: Tomorrow's vision, a reality today. Pages 315-317 in M. Heit, and A. Shortreid, eds. *GIS applications in natural resources.* GIS World, Inc., Fort Collins, CO.
- Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? *J. Wildl. Manage.* 54:515-522.
- Hofmann, L. A. 1991. The western sage grouse (*Centrocercus urophasianus phaios*) on the Yakima training center in central Washington: A case study of a declining species and the military. M.S. Thesis, Central Washington Univ., Ellensburg. 189pp.
- Holt, R. D., S. W. Pacala, T. W. Smith, and J. Liu. 1995. Linking contemporary vegetation models with spatially explicit animal population models. *Ecol. Applic.* 5:20-27.
- Holt, S. J., and L. M. Talbot. 1978. New principles for the conservation of wild living resources. *Wildlife Monogr.* 59.
- Homer, C.G. 1990. Use of Landsat TM data in a GIS to model sage grouse winter habitat. M.S. Thesis, Utah State Univ., Logan. 26pp.
- Homer, C.G., T.C. Edwards, R. D. Ramsey, K. P. Price. 1993. Use of remote sensing methods in modeling sage grouse winter habitat. *Wildl. Soc. Bull.* 57:78-84.
- Host, G. E., P. L. Polzer, D. J. Mladenoff, M. A. White, and T. R. Crow. 1996. A quantitative approach to developing regional ecosystem classifications. *Ecol. Appl.* 6:608-618.
- Hulet, B. V., J. T. Flinders, J. S. Green, and R. B. Murray. 1986. Seasonal movements and habitat selection of sage grouse in southern Idaho. Pages 168-175 in E. D. McArthur and B. L. Welch, compilers. *Proc. Symposium on the biology of Artemisia and Chrysothamnus.* U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. INT-200.
- Hupp, J. W., and C. E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. *J. Wildl. Manage.* 53:823-829.
- Jarvis, J. M. 1974. Sage grouse population studies on the Parker Mountain in south-central Utah. Utah dep. Fish and Game, Fed. Aid Job Comp. Report W-65-R, Job C-1.
- Kellner, C. J., J. D. Brawn, and J. R. Karr. 1992. What is habitat suitability and how should it be measured? Pages 476-488 in D. R. McCullough and R. H. Barrett, eds. *Wildlife 2001: populations.* Elsevier Applied Sci., New York, NY.
- Klebenow, D. A. 1968. The nesting and brood habitat of sage grouse. M.S. Thesis, Univ. Idaho, Moscow. 61pp.
- Klebenow, D.A. 1969. Sage grouse nesting and brood habitat in Idaho. *J. Wildl. Manage.* 33:649-661.
- Klott, J. H., and F. G. Lindzey. 1990. Brood habitats of sympatric sage grouse and Columbian sharp-tailed grouse in Wyoming. *J. Wildl. Manage.* 54:84-88.
- Klott, J.H., R.B. Smith, and C. Vullo. 1993. Sage grouse habitat use in the Brown's bench area of south-central Idaho. *Idaho Bur. Land Manage. Tech. Bull.* 93- 4. 14pp.
- Koeln, G. T., L. M. Cowardin, and L. L. Strong. 1994. Geographic information systems. Pages 540-566 in T. A. Bookhout, ed. *Research and management techniques for wildlife and habitats*, 5th ed. The Wildl. Soc., Bethesda, MD.
- Krohn, W. B. 1992. Sequence of habitat occupancy and abandonment: potential standards for testing habitat models. *Wildl. Soc. Bull.* 20:441-444.
- Krohn, W.B., and H. Salwasser. 1982. Opening remarks: habitat classification assessments for fish and wildlife. *Trans. North Am. Wildl. and Nat. Resour. Conf.* 47:33-34.
- Lancia, R. A., D. A. Adams, and E. M. Lunk. 1986. Temporal and spatial aspects of species-habitat models. Pages 65-69 in J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* Univ. Wisconsin Press, Madison.
- Leckenby, D. A., D. L. Isaacson, and S. R. Thomas. 1985. Landsat application to elk habitat management in northeast Oregon. *Wildl. Soc. Bull.* 13:130-134.

- Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? *Ecology* 74:1659-1673.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. *Ecology* 67:1127-1138.
- Manly, F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, U.K. 177pp.
- Martin, N. S. 1970. Sagebrush control related to habitat and sage grouse occurrence. *J. Wildl. Manage.* 34:313-320.
- Martin, N.S. 1976. Life history and habitat requirements of sage grouse in relation to sagebrush treatment. *Proc. West. Assoc. State Game and Fish Comm.* 56:289-294.
- Martin, R. C. 1990. Sage grouse responses to wildfire in spring and summer habitats. M.S. Thesis, Univ. Idaho, Moscow. 36pp.
- May, T. A. 1970. Effects of sagebrush control on distribution and abundance of sage grouse. Colorado Dep. Game, Fish, and Parks, Job Compl. Rep. W-37-R-23, Work Plan 3, Job 8a, pp. 115-138.
- McCullough, S. A. (Date unknown). Habitat suitability model: sage grouse eco-regions 3111 and 3112. U.S. Dep. Inter., Fish and Wildl. Ser., Ecological Services, Fort Collins, CO. 11pp.
- Miller, K. V., and M. J. Conroy. 1990. SPOT satellite imagery for mapping Kirklands' warbler wintering habitat in the Bahamas. *Wildl. Soc. Bull.* 18:252-257.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. Univ. Wisconsin Press, Madison. 343pp.
- Murtaugh, P.A. 1996. The statistical evaluation of ecological indication. *Ecol. Applic.* 6:132-139.
- Musil, D. D., K. P. Reese, and J. W. Connelly. 1994. Nesting and summer habitat use by translocated sage grouse (*Centrocercus urophasianus*) in central Idaho. *Great Basin Nat.* 54:228-233.
- Nelson, O.C. 1955. A field study of the sage grouse in southeastern Oregon with special reference to reproduction and survival. M.S. Thesis, Oregon State Coll., Corvallis. 113pp.
- Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 in D. R. McCullough and R. Barrett, eds. *Wildlife 2001: populations*. Elsevier Applied Sci., New York, NY.
- Ott, L. 1988. An introduction to statistical methods and data analysis. PWS-Kent Publi. Co., Boston, MA. 834pp.
- Palmer, M. W. 1992. The coexistence of species in fractal landscapes. *Am. Nat.* 139:375-397.
- Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books, Inc., Denver, CO. 341pp.
- Pereira, J.M.C., and R.M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: A study of the Mt. Graham red squirrel. *Photogrammetric Eng. and Remote Sensing* 57:1475-1486.
- Petersen, B. E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. M.S. Thesis, Colorado State Univ., Fort Collins. 86pp.
- Peterson, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. *J. Wildl. Manage.* 34:147-155.
- Poley, B. 1969. Effects of sagebrush control on distribution and abundance of sage grouse. Colorado Dep. Game, Fish, and Parks, Job Compl. Rep. W-37-R-22, Work Plan 3, Job 8a, pp. 61-86.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *Am. Nat.* 137:652-661.
- Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.* 137:50-66.
- Pulliam, H.R., J.B. Dunning, and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecol. Applic.* 2:165-177.
- Pyrah, D. B. 1970. Effects of chemical and mechanical sagebrush control on sage grouse. Pages 54-56 in E. F. Schlatterer and D. B. Pyrah, eds. *Ecological effects of chemical and mechanical sagebrush control*. Mont. Dept. Fish and Game.
- Rasmussen, D. I., and L. A. Griner. 1938. Life history and management studies of the sage grouse in Utah, with special reference to nesting and feeding habits. *Trans. North Am. Wildl. Conf.* 3:852-864.

- Ratti, J. T., and E. O. Garton. 1994. Research and experimental design. Pages 1-23 in T. A. Bookhout, ed. Research and management techniques for wildlife and habitats, 5th ed. The Wildl. Soc., Bethesda, MD.
- Ritchie, M. E., M. L. Wolfe, and R. Danvir. 1994. Predation of artificial sage grouse nests in treated and untreated sagebrush. *Great Basin Nat.* 54:122-129.
- Ricklefs, R. E. 1979. *Ecology*. 2nd ed. Chiron Press, Inc., New York, NY. 699pp.
- Robertson, M. D. 1991. Winter ecology of migratory sage grouse and associated effects of prescribed fire in southeastern Idaho. M.S. Thesis. Univ. Idaho, Moscow. 88pp.
- Roseberry, J. L., B. J. Richards, and T. P. Hollenhorst. 1994. Assessing the potential impact of Conservation Reserve Program lands on bobwhite habitat using remote sensing, GIS, and habitat modeling. *Photogrammetric Eng. and Remote Sensing* 60:1139-1143.
- Rothmaier, D. 1979. Sage grouse reproductive ecology: Bbreeding season movements, strutting ground attendance and site characteristics, and nesting. M.S. Thesis, Univ. Wyoming, Laramie. 97pp.
- Rothwell, R. 1993. Antelope, sage grouse, and neotropical migrants. Pages 396-401 in D. M. Finch and P. W. Stangel, eds. Status and management of neotropical migratory birds. U.S. Dep. Agric., For. Serv., Gen. Tech. Rep. RM-229.
- SAS Institute, Inc. 1988. SAS/STAT user's guide, release 6.03 ed. SAS Inst. Inc., Cary, NC. 1028pp.
- Savage, D. E. 1969. The relationship of sage grouse to upland meadows in Nevada. Job Completion Rep. W-39-R-9, Job12, Nevada Fish and Game Comm. 101pp.
- Schlatterer, E. F. 1960. Productivity and movements of a population of sage grouse in southeastern Idaho. M.S. Thesis, Univ. Idaho, Moscow. 87pp.
- Schoenberg, T. J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. M.S. Thesis, Colorado State Univ., Fort Collins. 86pp.
- Schroeder, M. A. 1995. Productivity and habitat use of sage grouse in north-central Washington (2/92-11/95). Prog. Rep., W-96-R, Washington Dep. Fish and Wildl. 24pp.
- Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, G. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. C. Edwards, Jr., J. Ulliman, and R. G. Wright. 1993. Gap analysis: A geographic approach to protection of biological diversity. *Wildl. Monogr.* 123. 41pp.
- Sime, C. A. 1991. Sage grouse use of burned, non-burned, and seeded vegetation communities on the Idaho National Engineering Laboratory, Idaho. M.S. Thesis, Montana State Univ., Bozeman. 72pp.
- Smith, R. B., and J. H. Klott. 1995. Seasonal distribution and habitat use of sage grouse in the Brown's bench area of southcentral Idaho. Idaho Dep. of Fish and Game, Jerome. Unpubl. rep.
- Soule', M.E. 1986. Conservation biology: the science of scarcity and diversity. Sinauer Assoc., Sunderland, Mass.
- Soule', M.E. 1987. Viable populations for conservation. Cambridge Univ. Press, Cambridge, U.K.
- Stiehl, R.B. 1994a. Utah single coovertype sage grouse model. U.S. Dep. Inter., Natl. Biol. Survey, Midcont. Ecol. Sci. Cent. Fort Collins, CO. Mimeo. 3pp.
- Stiehl, R.B. 1994b. Habitat evaluation procedures workbook. U.S. Dep. Inter., Natl. Biol. Survey, Midcont. Ecol. Sci. Cent. Fort Collins, CO.
- Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton Univ. Press, Princeton, NJ.
- Sveum, C. M. 1995. Habitat selection by sage grouse hens during the breeding season in south-central Washington. M.S. Thesis, Oregon State Univ., Corvallis, OR. 86pp.
- Thomas, J. W., D. A. Leckenby, M. Henjum, R. J. Pedersen, and L. D. Bryant. 1988. Habitat-effectiveness index for elk on Blue Mountain winter ranges. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. PNW-GTR-218. 28pp.
- Turner, M. G., Y. Wu, W. H. Romme, and L. L. Wallace. 1993. A landscape simulation model of winter foraging by large ungulates. *Ecol. Modeling* 69:163-184.
- Turner, M.G., G.J. Arthaud, R.T. Engstrom, S.J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. *Ecol. Applic.* 5:12-16.

- Urban, D. L., A. J. Hansen, D. O. Wallin, and P. J. Halpin. 1992. Life-history attributes and biodiversity: Scaling implications for global change. Pages 173-195 in O. T. Solbrig, H. M. van Emden, and P. G. van Oordt, eds. Biological diversity and global change. Int. Union of Biol. Sci. Paris, France. Monogr. 8.
- U.S. Department of Interior. 1980. Habitat evaluation procedures: ESM 102. U.S. Dep. Inter., Fish and Wildl. Serv., Div. Ecol. Serv. ESM/80/4. 150pp.
- U.S. Department of Interior. 1981. Standards for the development of habitat suitability models: ESM 103. U.S. Dep. Inter., Fish and Wildl. Serv., Div. Ecol. Serv. ESM/81/1. 150pp.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47:893-901.
- Verbyla, D. L. 1995. Satellite remote sensing of natural resources. CRC Press, Inc., Boca Raton, FL. 198pp.
- Verner, J., M. L. Morrison, and C. J. Ralph. 1986. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* Univ. Wisconsin Press, Madison. 470pp.
- Wakkinen, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage grouse in southeastern Idaho. M.S. Thesis, Univ. Idaho, Moscow. 57pp.
- Wallestad, R.O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. *J. Wildl. Manage.* 35:129-136.
- Wallestad, R.O. 1975. Life history and habitat requirements of sage grouse in central Montana. Montana Dep. Fish and Game, Game Manage. Div., Helena. 66pp.
- Wallestad, R.O., and D.B. Pyrah. 1974. Movements and nesting requirements of sage grouse hens in central Montana. *J. Wildl. Manage.* 38:630-633.
- Wallestad, R.O., and P. Schladweiler. 1974. Breeding season movements and habitat selection of male sage grouse. *J. Wildl. Manage.* 38:634-637.
- Warner, R.E. 1992. Long-term perspectives of upland game bird research in North America. Pages 709-717 in D.R. McCullough and R. H. Barrett, eds. *Wildlife 2001: Populations.* Elsevier Applied Sci., New York, NY.
- Wisdom, M.J., and L.S. Mills. 1997. Using sensitivity analysis to guide population recovery: Prairie-chickens as an example. *J. Wildl. Manage.* 61:302-312.
- Zar, J.H. 1984. *Biostatistical analysis.* Prentice-Hall, Inc., Englewood Cliffs, N.J. 718pp.



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