

Evaluating Performance of Regional Wildlife Habitat Models: Implications to Resource Planning

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Wildlife management and policy decisions are increasingly being made at the regional, national and international level. Much of the motivation for extending the geographic context of resource planning comes from U.S. federal laws that require resource managing agencies to examine the potential impacts from land resource use on wildlife resources. Several regional approaches have demonstrated the feasibility of using extant resource inventories in developing wildlife habitat models. While testing for feasibility is a logical first step in the development of large-scale resource response models, resource planners need to know if these methods provide information that is useful in the decision-making process. This study has taken the next step of quantifying model performance as a means of characterizing the uncertainty in model predictions. Discriminant function analysis was used to relate the composition of land use and land cover within counties of the south-eastern United States to abundance and presence/absence classes of white-tailed deer, wild turkey and red-cockaded woodpecker. We evaluated model performance by examining: (1) classification accuracy of the model as a whole; and (2) the error and precision of the classification rules comprising the models. Although all models were found to perform significantly better than a random model, the performance criteria indicated that significant improvements in the models could be realized. Sources of model uncertainty are reviewed, and suggestions for how to control for that uncertainty are discussed as a future research need.

Keywords: discriminant analysis, habitat models, regional resource planning, validation, wildlife.

1. Introduction

Those ecosystems that support diverse, and often competing, uses of natural resources are increasingly coming under anthropogenic influence in the form of more intensive management. Human-related disturbances have become so extensive that their effect must be evaluated on a macroscale in order to capture the cumulative effects of local activities. In the context of wildlife resource management, Sanderson *et al.* (1979)

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recommended that future research focus on large-scale trends and generalized prediction models that offer a prescriptive capacity in the resource decision-making environment.

In the decade ensuing Sanderson's recommendation, a profusion of habitat-based planning models was developed to meet the demand for analyses that evaluated the likely impacts of land and resource management on animal habitat (Berry, 1986). While the development of these models did much to interject wildlife considerations into multiple resource planning decisions, there is now concern that model development has exceeded testing of model performance (see Verner *et al.*, 1986). Despite claims that "[w]e know how to verify species-habitat relationships models" (Salwasser and Samson, 1985, p. 319), few tests of the relation between habitat and population performance have been attempted (Morris, 1987), or at least published. In addition, most of these models were developed to address local-scale resource impact questions—limited applied research has been directed at developing planning tools for regional or landscape-level analysis.

Although large-scale analysis of wildlife distribution and abundance in a resource planning context is not prevalent, several investigators have developed approaches that have been successfully applied at the regional level (Sheffield, 1981; Brooks, 1984; Klopatek and Kitchings, 1985). The critical question addressed by these past efforts has been: can extant data sources and analysis methods be used to relate regional patterns of wildlife distribution and abundance to land use and land cover patterns? A second, and equally important question, is: how reliable is the approach and does it offer tenable predictions of wildlife resource response to changing land management and land use patterns? As with local-scale models, part of the difficulty in answering this latter question is the sparsity of data for validation purposes (Schamberger and O'Neil, 1986)—a constraint that is compounded when dealing with regional-level models developed for long-term resource planning. This constraint notwithstanding, there is an obligation to evaluate rigorously the reliability of models to the extent possible.

The objective of this paper is to evaluate the performance of regional models that were developed to analyse wildlife response to changes in land use and timber management in the southern United States (USDA, Forest Service, 1988). These models predict the distribution of wildlife abundance classes based on land use and land cover characteristics. Although feasibility was demonstrated and common measures of model error indicated that these wildlife models fit the data reasonably well (Flather *et al.*, 1989; Joyce *et al.*, 1990), there is a need for more rigorous testing that will lead to quantification of model uncertainty for incorporation into the resource planning process.

2. Methods

Regional habitat models, patterned after Klopatek and Kitchings (1985), were developed using discriminant function analysis to establish statistical relationships between land use and land cover types and abundance classes of white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*) and red-cockaded woodpecker (*Picooides borealis*). Although the focus of this paper is on evaluating model performance, a brief description of the methods associated with model development is provided. A more detailed discussion of model development and application can be found in Flather (1988), Flather *et al.* (1989) and Joyce *et al.* (1990).

2.1. LAND BASE AND WILDLIFE DATA SOURCES

The study area was a 12-state region in the south-eastern United States (Figure 1). Extant regional inventories of land base characteristics were used to compile county-level descriptions of land use and land cover. Estimates of land area by land use and forestland descriptors (Table 1) were available from the National Resources Inventory (USDA, Soil Conservation Service, 1987) and regional timber inventories from the Forest Inventory and Analysis units (USDA, Forest Service, 1985). To control for differences in total county area, all land base variables were expressed as a proportion of a given county, thereby providing a compositional description of the county. Configurational measures of the county land base (e.g. size, shape and distribution of land types) were not available from these data.

Selection of wildlife species to model was contingent on the availability of region-wide information on species distribution and abundance; however, an effort was made to select species of regional management importance. Abundance data for white-tailed deer and wild turkey were obtained from the South-eastern Co-operative Wildlife Disease Study, University of Georgia. Maps depicting the distribution of abundance classes were used to categorize each county into one of three classes: low, moderate or high densities. The red-cockaded woodpecker is sensitive to timber management practices (Lennartz and McClure, 1979) and receives special protection and management consideration under the Endangered Species Act (Public Law 93-205). This bird lives in a social group called a clan which is made up of 2–9 birds with one breeding pair (Hooper *et al.*, 1980). Several cavity trees are used by the clan for roosting and nesting, and these sites define a colony. A search of the literature provided information on the distribution of active colonies across the South (Jackson, 1978; James *et al.*, 1981; Baker, 1982; Carter *et al.*, 1983; Wood and Wenner, 1983). State wildlife agencies, Forest Service biologists and state Natural Heritage Programs were also contacted for county-level estimates of active colonies.

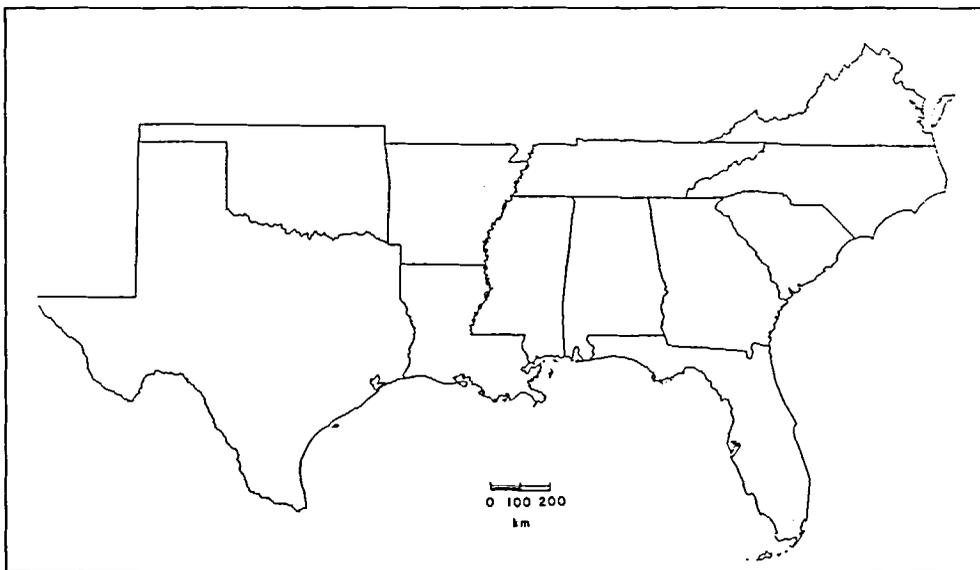


Figure 1. Map of the 12-state region in the south-eastern United States where wildlife habitat models were developed.

TABLE 1. Land use and land cover types used to develop wildlife models

Variable	Definitions (expressed as proportion of total county land area)
TOTCRP	Total cropland acreage calculated by summing area estimates for row crops, close grown crops, horticultural crops, unplanted cropland and other cropland
TOTPAST	Total pastureland and rangeland acreage calculated by summing area estimates for pasture, range and rotation hay and pasture
HUMAN	Total acreage associated with human development calculated by summing area estimates for urbanland, roads, railroads, strip mines and farm structures
NP	Total acreage estimates of natural pine
PP	Total acreage estimates of planted pine
OP	Total acreage estimates of oak-pine
UH	Total acreage estimates of upland hardwood
LH	Total acreage estimates of lowland hardwood
AGE1	Age Class 1† area across all forest types (except PP)
AGE2	Age Class 2‡ area across all forest types (except PP)
AGE3	Age Class 3§ area across all forest types (except PP)
HWAGE1	Age Class 1 area across hardwood types
HWAGE2	Age Class 2 area across hardwood types
HWAGE3	Age Class 3 area across hardwood types
PNAGE1	Age Class 1 area across pine types (except PP)
PNAGE2	Age Class 2 area across pine types (except PP)
PNAGE3	Age Class 3 area across pine types (except PP)

† Age Class 1: 0–20 years.

‡ Age Class 2: 21–50 years.

§ Age Class 3: 50+ years.

2.2 MODEL DEVELOPMENT

Discriminant function analysis (Johnson and Wichern, 1984) was used to generate classification rules that predict deer and turkey abundance class membership, or red-cockaded woodpecker colony presence/absence based on land base predictor variables. Counties served as the observational unit and, therefore, the set of objects to be classified by the discriminant models.

Deer and turkey models were developed for six physiographic strata (mountain, piedmont, eastern coastal plain, mid-south coastal plain, Mississippi Valley, and western coastal plain and highlands). The stratification was based on the Soil Conservation Service's Major Land Resource Area (USDA, Soil Conservation Service, 1981). The red-cockaded woodpecker analysis was restricted to the coastal plain region of the South—the primary range of the species. Separate models were developed for the south-east region (Virginia, North Carolina, South Carolina, Georgia and Florida) and south-central region (Alabama, Tennessee, Mississippi, Louisiana, Arkansas and eastern Texas and Oklahoma).

Two assumptions critical to discriminant analysis are multivariate normally distributed predictor variables, and similar covariance structure between classification groups (Johnson and Wichern, 1984). The assumption of multivariate normality is difficult to test directly. In practice, one has to be satisfied with subjecting each variable to univariate tests of normality (Habbema and Hermans, 1977). All land base variables were transformed ($\arcsin \sqrt{x}$) prior to statistical analysis to more closely approximate a normal distribution. Significant deviation from normality of the transformed variables resulted in elimination of that variable from further consideration in model develop-

ment. The covariance structure of our data was significantly different among abundance classes and, therefore, resulted in classification rules based on quadratic discriminant functions rather than linear functions (see Williams, 1983).

2.3. EVALUATING MODEL PERFORMANCE

The most desirable test of any statistical model would be to apply the model to independent data with known outcomes. Prediction errors can be estimated directly under these circumstances. However, the difficulty in obtaining region-wide estimates of wildlife population status poses very limiting constraints on the availability of independent data sets with which to conduct such tests. This constraint forces reliance on the data available for model development to assess model performance. Two measures of discriminant model performance were examined: (1) classification accuracy; and (2) the error and precision of the classification rules that comprise the models.

2.3.1. Classification accuracy

A commonly used estimate of classification accuracy with discriminant analysis is the resubstitution estimator (Snapinn and Knoke, 1989). The resubstitution estimate of error is based on the proportion of misclassified observations in the sample used to build the discriminant function. However, resubstitution estimates of error are known to be optimistically low, leading to inflated confidence in model performance (Breiman *et al.*, 1984).

An alternative is to employ a simple resampling plan such that classification accuracy is based on observations that did not contribute to the estimate of model coefficients. Cross-validation is a procedure that estimates error over the sample data set, not allowing each observation into the construction of the classification rule for its prediction (Efron and Gong, 1983). This resampling approach has been shown to be much less biased in its estimation of classification accuracy than resubstitution estimates (Snapinn and Knoke, 1989).

Both cross-validation and resubstitution estimates of classification accuracy were calculated. The difference between the two estimates provided an indication of the over-optimism that can be attributed to models that are evaluated only superficially.

2.3.2. Error and precision of the classification rules

The classification rules generated by discriminant analysis assign an observation to a class based on posterior probabilities that are conditioned on an observed vector of predictor variables. An observation is predicted to be a member of that class with the greatest estimated posterior probability.

The cross-validation analysis calculates \hat{P}_{ij} , which is the estimated posterior probability that observation i belongs to the j th class when observation i is held out from the estimate of the classification rule. Because class membership is known for each observation in the data set, we have *a priori*:

$$P_{ij} = \begin{cases} 1 & \text{if observation } i \text{ belongs to class } j \\ 0 & \text{otherwise.} \end{cases}$$

A discriminant function model with no uncertainty in its prediction would correctly predict class membership with $\hat{P}_{ij} = P_{ij}$. In practice, however, \hat{P}_{ij} is often not equal to P_{ij} . A correct classification is still realized if the maximum \hat{P}_{ij} , across classes, is associated with the class where $P_{ij} = 1$. Consider a simple case where two discriminant models (A and B) have been developed to classify observations into one of two classes. If the posterior probabilities for a hypothetical observation i known to come from class 2 were calculated as:

	Model A	Model B
P_{i1}	0.49	0.10
P_{i2}	0.51	0.90

then both models would correctly classify the observation as being a member of class 2. Yet model A is clearly less certain in its prediction than model B. Information concerning model performance would be lost if evaluation was based solely on classification accuracy.

In order to quantify the uncertainty associated with the classification rule's calculation of posterior probabilities we defined:

$$E_{ij} = P_{ij} - \hat{P}_{ij} \quad (i = 1, \dots, n \text{ observations}, j = 1, \dots, k \text{ classes})$$

as an estimate of the error associated with the posterior probabilities, and:

$$\text{Var}[E_{0,j}] \quad (i = 1, \dots, k)$$

as an estimate of classification function precision.

3. Results

3.1. HABITAT ASSOCIATIONS

A total of 14 discriminant models was developed. The variables selected and resubstitution estimates of classification accuracy are provided in Table 2. White-tailed deer, a habitat generalist, was the least specific in its land type associations. In general, deer abundance was negatively correlated with human-related land uses; cropland had a negative influence on deer abundance in areas already dominated by agricultural land use; cropland had a positive influence in strata dominated by forest cover, presumably due to the increased land type diversity; and higher deer abundance was associated with early forest successional stages. Lower wild turkey abundance was consistently associated with increased acreage in cropland and human-related land uses; increased area in natural forest types and older age classes of forest tended to be associated with higher turkey abundance. Red-cockaded woodpecker, a habitat specialist, was primarily dependent upon large acreage in natural pine stands and old age classes of natural pine and oak-pine. Increased acreage in upland hardwood and cropland was associated with the absence of active red-cockaded woodpecker colonies. These empirically determined habitat associations were consistent with reported life history information and expert review of the models (see Flather *et al.*, 1989; Flather, 1988).

3.2. EVALUATING CLASSIFICATION ACCURACY

The resubstitution estimates of model error shown in Table 2 indicated that the models fit the data reasonably well. Classification accuracies ranged from 87% to 73% across strata, with region-wide estimates of 79%, 82% and 80% for deer, turkey and red-cockaded woodpecker, respectively. In addition, the geographic distribution of the errors across the study region did not indicate a spatial bias in misclassification (Figure 2).

Cross-validation estimates of prediction error indicate a deterioration in model accuracy for white-tailed deer and wild turkey when compared with the resubstitution estimates (Table 3). Region-wide estimates of prediction accuracy for deer and turkey were 19% and 15% less under cross-validation. Cross-validation estimates of accuracy for the red-cockaded woodpecker were only 4% less than resubstitution estimates.

The deterioration in accuracy observed with deer and turkey when we compared resubstitution and cross-validation estimates of classification accuracy was disproportionate across the abundance classes. Accuracy deteriorated to a much greater degree within the high abundance classes. Given that a county supported a high density of deer or turkey, the proportion of counties correctly classified under cross-validation declined by 30–40% when compared with resubstitution estimates.

Despite the absence of impressive classification accuracy, the discriminant models for all species performed significantly better ($P < 0.001$, kappa statistic) than a random classification function (Titus *et al.*, 1984; Cohen, 1968). The kappa statistic, which measures the improvement of a discriminant model over chance, indicated that these regional wildlife models performed 36%, 41% and 50% better than a random classification rule for white-tailed deer, wild turkey and red-cockaded woodpecker, respectively.

3.3. EVALUATING ERROR AND PRECISION OF CLASSIFICATION RULES

Precision estimates based on all observations in the data set ($E_{0,j}$) suggested that the models were performing well. The errors, as measured by $E_{0,j}$, are not significantly different from 0 as indicated by the 95% confidence intervals (Table 4). However, these estimates of precision masked the uncertainty that existed in the discriminant models. This masking occurred for two reasons. First, errors where $P_{ij} = 1$ tend to cancel errors where $P_{ij} = 0$. The second reason was an idiosyncrasy of the deer and turkey data related to the following conditions: (1) sample sizes were not equal across abundance classes (low abundance had many more observations than high abundance), and (2) misclassification tends to occur in adjacent classes. Therefore, the high abundance class ($E_{0,3}$) will have a low mean error because of the unlikely probability of misclassifying low abundance counties as high abundance counties.

To get a more refined assessment of the precision on the classification functions, E was estimated for each class given that an observation came from that class ($E_{j,j}$). Under conditional estimates of E , P_{ij} is fixed at 1.0 and hypothesis tests for $E = 0$ are not appropriate. Alternatively, we defined three regions on $E_{j,j}$ that related to the relative uncertainty that can be attributed to the classification rules. The first region, where $E_{j,j} > [(k-1)/k]$, for k classes, indicates that the model cannot distinguish class j from the other classes. The second region is defined as:

$$0.5 \leq E_{j,j} \leq \left(\frac{k-1}{k} \right)$$

TABLE 2. Variables selected and the resubstitution estimates of classification accuracy for each physiographic stratum for white-tailed deer, wild turkey and red-cockaded woodpecker

Species	Stratum					
	Mountain	Piedmont	Eastern coastal plain	Mid-south coastal plain	Miss. valley	Western coastal plains/highlands
White-tailed deer	TOTCRP NP UH AGE1 AGE2 AGE3	TOTCRP TOTPAST HUMAN NP PP UH HWAGE1 HWAGE2	TOTPAST HUMAN NP PP OP UH AGE1 AGE2	HUMAN NP PP OP UH AGE1 AGE2	TOTCRP LH HWAGE1 HWAGE2 HWAGE3	TOTCRP TOTPAST HUMAN OP UH HWAGE1 HWAGE2
Classification accuracy (resubstitution)	79	78	77	84	73	85

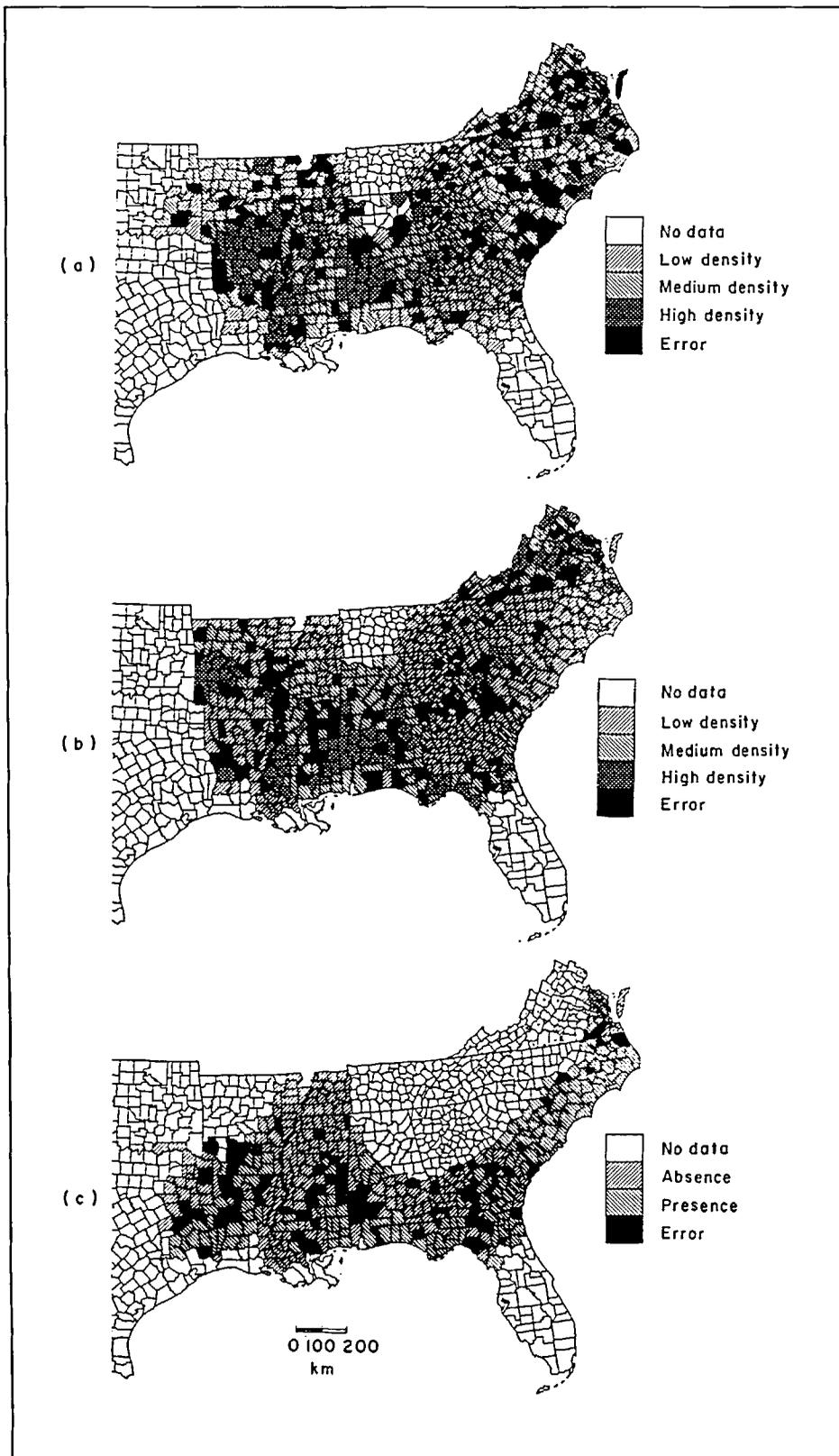


Figure 2. Distribution and abundance maps for: (a) white-tailed deer; (b) wild turkey; and (c) red-cockaded woodpecker. Counties misclassified by model under resubstitution are indicated as errors.

TABLE 3. Region-wide classification matrices depicting the number (%) of countries from each density class (rows) and predicted density class (columns) under resubstitution and cross-validation for white-tailed deer, wild turkey and red-cockaded woodpecker models

		Resubstitution			Cross-validation		
		White-tailed deer			White-tailed deer		
		To class			To class		
From class	Low	Low	Moderate	High	Low	Moderate	High
	Moderate	246 (79)	53 (17)	14 (4)	214 (68)	75 (24)	24 (8)
	High	49 (15)	246 (78)	22 (7)	95 (30)	189 (60)	33 (10)
		8 (6)	18 (13)	116 (82)	31 (22)	50 (35)	61 (43)
		Proportion correct classification: 0.79			Proportion correct classification: 0.60		
		Wild turkey			Wild turkey		
		To class			To class		
From class	Low	Low	Moderate	High	Low	Moderate	High
	Moderate	388 (90)	28 (6)	17 (4)	362 (84)	49 (11)	22 (5)
	High	53 (26)	135 (67)	15 (7)	86 (42)	87 (43)	30 (15)
		15 (12)	12 (9)	103 (79)	34 (26)	33 (25)	63 (48)
		Proportion correct classification: 0.82			Proportion correct classification: 0.67		
		Red-cockaded woodpecker			Red-cockaded woodpecker		
		To class			To class		
From class	Presence	Presence	Absence		Presence	Absence	
	Absence	236 (79)	62 (21)		225 (76)	73 (24)	
		34 (18)	156 (82)		46 (24)	144 (76)	
		Proportion correct classification: 0.80			Proportion correct classification: 0.76		

TABLE 4. Region-wide statistics on error and precision of the classification rules for white-tailed deer, wild turkey and red-cockaded woodpecker models based on cross-validation (for deer and turkey: 1 = low, 2 = moderate, 3 = high; for red-cockaded woodpecker: 1 = absent, 2 = present)

Species	E	N	\bar{X}	s	s_x	95% CI	
						Lower	Upper
White-tailed deer	$E_{0,1}$	772	-0.0203	0.4535	0.0163	-0.0522	0.0116
	$E_{0,2}$	772	0.0026	0.4828	0.0174	-0.0315	0.0367
	$E_{0,3}$	772	0.0177	0.3662	0.0132	-0.0082	0.0436
	$E_{1 1}$	313	0.3707	0.3338	0.0189	0.3336	0.4077
	$E_{2 2}$	317	0.4363	0.3334	0.0187	0.3996	0.4729
Wild turkey	$E_{3 3}$	142	0.5897	0.3556	0.0298	0.5313	0.6481
	$E_{0,1}$	766	-0.0192	0.4196	0.0152	-0.0490	0.0106
	$E_{0,2}$	766	0.0004	0.4444	0.0161	-0.0311	0.0319
	$E_{0,3}$	766	0.0188	0.3456	0.0125	-0.0057	0.0433
	$E_{1 1}$	433	0.2392	0.2775	0.0133	0.2131	0.2653
Red-cockaded woodpecker	$E_{2 2}$	203	0.5872	0.3149	0.0221	0.5439	0.6305
	$E_{3 3}$	130	0.5825	0.3553	0.0311	0.5215	0.6434
	$E_{0,1}$	488	0.0284	0.4143	0.0188	-0.0084	0.0652
	$E_{0,2}$	488	-0.0284	0.4143	0.0188	-0.0652	0.0084
	$E_{1 1}$	298	0.2783	0.2882	0.0167	0.2456	0.3110
	$E_{2 2}$	190	0.3636	0.2427	0.0176	0.3291	0.3981

and characterizes the situation where the model is uncertain in its assignment of class membership because the posterior probabilities may be nearly equal between two or more classes. We interpreted this region as one of ambiguous classification. Values of $E_{ij} < 0.5$ provides evidence for an unambiguous classification function and defines the third region of model uncertainty.

The results from this analysis indicate that classification function uncertainty varies across species and abundance classes (Table 4). The deer and turkey classification functions were less precise with moderate and, in particular, high abundance classes. The mean values for $E_{3|3}$ fell within the region of ambiguous classification, and the 95% confidence interval nearly included the value 0.667 (the upper limit of this region for the three-class problem). Therefore, the deer and turkey models had difficulty recognizing counties known to support high densities of these species. Conversely, the red-cockaded woodpecker models had mean values for E_{ij} which were significantly less than 0.5 ($P < 0.05$), indicating an unambiguous classifier, with somewhat greater uncertainty associated with predicting presence of active colonies.

The foregoing tests assumed normally distributed conditional errors. Application of the Kolmogorov-Smirnov test (Conover, 1971) rejected the null hypothesis of normally distributed conditional errors in all cases ($P < 0.001$). While statistics such as t are robust to departures from normality (Larsen and Marx, 1981), our conclusions regarding patterns in model performance would be strengthened if also observed under distribution-free criteria.

Cumulative distribution plots (Figure 3) of the conditional errors further support the observation that the deer and turkey models are having the most difficulty in distinguishing the high abundance class. For deer and turkey, only about 40% of the values for $E_{3|3}$ fell within the region of unambiguous classification (i.e. $E_{3|3} < 0.5$). Application of the sign test (Conover, 1971) revealed that the median of $E_{3|3}$ for both species was not significantly ($P > 0.05$) different from 0.667, the upper limit of the ambiguous classifica-

tion region. Conversely, nearly 75% of the conditional errors for the red-cockaded woodpecker model fell within the region of unambiguous classification (Figure 3), with medians shown to be significantly less than 0.5 (sign test, $P < 0.001$).

4. Discussion

Species-habitat relationship models have taken on many forms (see Hawkes *et al.*, 1983; Verner *et al.*, 1986). Their fundamental basis, however, is the same: wildlife distribution and abundance is assumed to be intrinsically tied to habitat, and therefore habitat characteristics can be used to make inferences regarding wildlife population levels (or other indicators of population status). Despite the availability and variety of habitat-based modeling approaches, most have been developed and applied at the site-specific level, and arbitrary application of a site-level model to a region as a whole is not recommended (Risser *et al.*, 1984).

Motivated primarily by recent U.S. legislation, several researchers have developed regional approaches to wildlife habitat modeling. Brooks (1984) developed multivariate relationships between breeding bird abundance and land use and forestland characteristics in an examination of bird community patterns. Klopatek and Kitchings (1985) used a similar methodology to relate abundance classes of selected birds and mammals to areal estimates of Küchler potential natural vegetation types within counties.

Although these regional approaches represent advancements in the area of regional evaluation of resource management, limited attempts have been made to estimate rigorously actual model prediction errors. Brooks (1984) reported resubstitution estimates of prediction error, while Klopatek and Kitchings (1985) did not provide an indication of model performance. Without adequate assessments of model performance, it is difficult objectively to incorporate the uncertainty in model predictions into the decision-making process. Ignoring the error makes it impossible to determine the significance of predicted wildlife response, thus increasing the risk of making a faulty, or at least untenable, planning decision.

Our analysis has shown that while feasibility is no longer of concern, considerable uncertainty in empirically-defined regional habitat relationships can exist. Although all

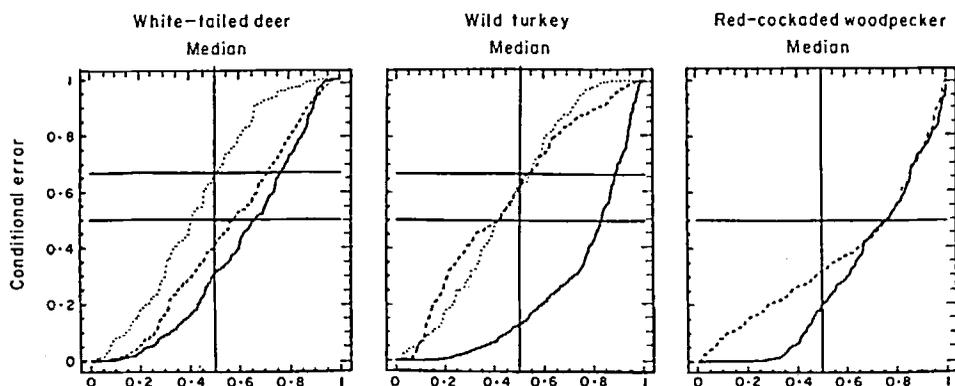


Figure 3. Cumulative distribution plots of conditional error (E_j) for species models. Reference lines for the upper and lower limits for the region of ambiguous classification as defined in the text are provided. —, E_{1j} ; ----, E_{2j} ; ····, E_{3j} .

models provided significantly improved predictions over a random classification function, the prediction errors for deer and turkey were relatively high—misclassification rates of 40% and 33%, respectively. Similarly, conditional precision estimates (E_{ji}) indicated that there is considerable confusion in the assignment of counties to deer and turkey abundance classes. This confusion was also associated with those deer and turkey abundance classes where unambiguous classification was expected, namely the higher abundance classes. A plot of species abundance along an environmental gradient has been described as a Gaussian (bell-shaped) response curve (Gauch and Whittaker, 1972; Meents *et al.*, 1983). A Gaussian curve implies that the low abundance class would be the most difficult class to distinguish, since low abundance is associated with extremes on the environmental gradient and, therefore, with an inherently more variable set of environmental factors. By the same logic, a high abundance class, which is associated with a narrower, and, therefore, less variable set of values along the gradient, should be easier to describe empirically. For these reasons, it was surprising that the models had the most difficulty distinguishing the high density and presence classes.

The uncertainty associated with these regional models raises questions concerning the sources of uncertainty. An obvious source is the data used to generate the empirical habitat relationships. Wildlife distribution and abundance data are difficult to obtain at any geographic scale, which has hindered completion of even basic trend analyses (Flather and Hoekstra, 1989). The wildlife data used in this study are of an undefined accuracy, since they represent a compilation from wildlife biologists rather than from statistically-designed surveys. Although the latter would be desirable, the data used in this study were, to our knowledge, the only region-wide estimates of distribution and abundance for these species available.

Error in the land base inventories also contribute to the uncertainty in the regional models. In order to get a complete description of the land base, multiple inventories with multiple designs and objectives were merged. Because each inventory was conducted independently, a simple merging would not guarantee that a sum across land area types would be consistent with known total county area. Although all estimates were proportionately adjusted to be consistent with total county land area estimates (see Flather *et al.*, 1989), errors associated with merging inventories remain. Such errors could be minimized by a single and complete land area inventory.

A source of uncertainty that is of a more conceptual nature concerns the conversion of the habitat-quality continuum into a discrete form. Given the state of wildlife inventories, it was felt that the precision on the wildlife data would only support models based on habitat-quality classes as represented by abundance and presence/absence categories. While habitat quality may indeed be a continuum, current inventory information may only support categorical analyses. Therefore, we may have to accept less precise classification rules as measured by E_{ji} if classification accuracy remains within acceptable limits.

Finally, the level of uncertainty may also be related to species life history. Although only three species models were developed for this study, there was a clear inverse relationship between habitat specialization and model uncertainty—a similar pattern was also described for birds in shrubsteppe environments (Wiens and Rotenberry, 1981). Whether this is true in general will require examining regional models for many species. The implication is that the scale at which a species perceives its habitat will affect regional habitat model performance and argues for careful selection of species for use in regional resource planning (see Kolasa, 1989).

If regional models of wildlife response to changes in land use and land cover are to

be used effectively in resource planning and policy analysis, then evaluating model performance becomes imperative for two reasons. First, resource planning is inherently multi-resource. If trade-offs among resources are to be analysed objectively then performance estimates are required if levels of confidence are to be assigned to various resource model outputs. One approach may be to weight the information content of any given model inversely to the uncertainty in its predictions. Second, model performance evaluations provide benchmarks against which to explore improvements in each model. This study has provided an initial estimate of the uncertainty in regional habitat models for three species. The more difficult task of partitioning uncertainty among the sources of error (*sensu* Wallach and Goffinet, 1987) and devising ways of controlling for that error, is a subject requiring further research.

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