A rapid approach to modeling species-habitat relationships.

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Abstract

A growing number of species require conservation or management efforts. Success of these activities requires knowledge of the species' occurrence pattern. Species-habitat models developed from GIS data sources are commonly used to predict species occurrence but commonly used data sources are often developed for purposes other than predicting species occurrence and are of inappropriate scale and the techniques used to extract predictor variables are often time consuming and cannot be repeated easily and thus cannot efficiently reflect changing conditions. We used digital orthophotographs and a grid cell classification scheme to develop an efficient technique to extract predictor variables. We combined our classification scheme with a priori hypothesis development using expert knowledge and a previously published habitat suitability index and used an objective model selection procedure to choose candidate models. We were able to classify a large area (57,000 ha) in a fraction of the time that would be required to map vegetation and were able to test models at varying scales using a windowing process. Interpretation of the selected models confirmed existing knowledge of factors important to Florida scrub-jay habitat occupancy. The potential uses and advantages of using a grid cell classification scheme in conjunction with expert knowledge or an HSI and an objective model selection procedure are discussed.

Keywords: Florida scrub-jay; species-habitat model; occupancy; habitat mapping; model selection

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1. Introduction

In the current conservation crisis, many populations are declining due to anthropogenic destruction or alteration of the species' critical habitat (DeGraaf and Rappole 1995, Marzluff and Sallabanks 1998). Many of these species are geographically widespread, despite their habitat specificity, e.g. red-cockaded woodpecker *Picoides borealis* (REF NEEDED). Consequently, a growing number of species require conservation efforts and habitat management over large areas. Central to preserving such declining species is knowledge of the species range/geographic distribution/occurrence pattern and the distribution of suitable habitat (Gibson et al. 2004, Johnson et al. 2004, Noss 1983 as cited in Beard et al. 1999). Species-habitat models are often the only efficient approach to acquiring this information. However, species-habitat models often require predictor variable data be obtained from extensive or inaccessible areas. Thus, many species-habitat models use existing GIS data sources generated for other purposes (e.g. land cover maps, satellite imagery, climatic maps and topographic maps) to expedite or eliminate the need to collect habitat data on the ground (e.g., Irwin 1998, Raphael et al. 1998, Villard et al. 1998, Dettmers and Bart 1999, Shriner et al. 2002, Seoane et al. 2003). Often such data is not collected at an appropriate spatial or temporal scale for the species of interest (Greco et al. 2002, Tobalske 2002).

Even given readily available GIS data, conservation biologists and managers must have sufficient knowledge of the species-habitat relationship (the process being modeled) to relate GIS data sources to important habitat suitability predictors. Theoretically, vegetation features serve as the best predictors of vertebrate habitat occupancy because in many cases habitat selection is thought to operate on vegetation structure (Beard et al. 1999, Cody 1985). However, extracting fine resolution vegetation features (e.g., mapping land cover types) from GIS data sources often requires substantial time and effort (Seoane et al. 2003). This constraint is significant when management decisions based on predictive models are required in short time spans or frequent updates of habitat data are required, as is often the case in conservation planning and management (Fleishman et al. 2001). The need for decision support in conservation efforts often exceeds resources (Fielding and Bell 1997). In some cases workers have avoided mapping detailed vegetation data by using course resolution landscape properties to predict species occurrence (e.g., Fleishman et al. 2001, Mitchel et al. 2001) but this approach will not be appropriate in many cases since models must match the scale of the process being modeled to have the best predictive power (Huston 2002). Consequently, techniques are needed that can quickly generate habitat data of suitable scale over large areas.

We developed a rapid approach to species-habitat modeling in which habitat classification is integrated with an objective model selection procedure. As an efficient alternative to detailed land cover mapping, we classified grid cells by a set of predictive vegetation and landscape variables that are interpreted from high-resolution aerial photographs. The grid cell classification scheme was derived from a set of *a priori* hypotheses (models) developed using existing knowledge. This knowledge was based in part on a modified habitat suitability index, HSI, (Breininger 1992, Breininger et al. 1998, Burgman et al. 2001, Duncan et al.1995). Although HSI are not explicitly designed to predict occurrence they can be useful to generate *a priori* hypotheses for model selection procedures (Van Horne 2002) such as the information-theoretic approach based on Akaikes Information Criterion suggested by Burnham and Anderson (2002). This approach is superior to indiscriminate predictor variable selection based on availability because developing models *a priori* is the only way to effectively confirm genuine effects (Burnham and Anderson 2002). Often investigators focus on prediction and ignore the opportunity to gain insight into the mechanism of habitat selection (Fielding and Bell 1997) but understanding the mechanism that underlies patterns of distribution is essential to conservation and management (Rushton 2004). The combination of expert opinion (or a HSI) and objective model selection can be a valuable step in determining species-habitat relationships (Van Horne 2002).

The focus of this study was to develop an efficient approach to wildlife-habitat modeling that uses rapidly generated and biologically meaningfully habitat data in conjunction with an objective model selection procedure. We demonstrate this approach by developing predictive models of habitat occupancy of the Florida scrub-jay *Aphelocoma coerulescens* population on John F. Kennedy Space Center/Merritt Island National Wildlife Refuge (KSC). The Florida scrub-jay is a threatened species and the population on KSC has the potential to be one of the largest metapopulations of the species (Stith 1999, Stith et al. 1996) and thus is important to conservation of the species. A large amount of scrub-jay habitat on KSC is difficult to access and occupancy of these areas is unknown. Knowledge of occupancy in these remote areas could facilitate adaptive management efforts for this population..

2. Methods

2.1 Field methods

Fieldwork was conducted during March and April of 2000. Presence/absence data for the model was collected by sampling scrub-jay occupancy at random points. Sampling points were overlaid on primary and secondary scrub-jay habitat maps that were previously created using soils data (Breininger et al. 1991). A Trimble GPS unit (Trimble 1996, 1999) was used to navigate to within 2 meters of the points. Florida scrub-jays are permanently territorial birds (Woolfenden and Fitzpatrick 1984) and respond aggressively to playback of conspecific recordings. Using playback of scrub-jay vocalizations on a handheld tape cassette player we thoroughly sampled a 150 meter radius circle around each point to approximate the size of an average scrub-jay territory (Woolfenden & Fitzpatrick 1984). Playback was initiated at the center of the circle followed by playback at points 75 meters from the center point in each of the cardinal directions until scrub-jays were detected or the process was completed. Playback at each point in the sampling area began with a two minute bout of play followed by a minute of silence and then another 2 minute bout of play in the opposite (180 compass degrees) direction. If no jays were seen or heard within the 150 m radius sampling area after playback was conducted at all five points the sampled area was deemed unoccupied.

2.2 GIS/mapping

Mapping of landscape characteristics was done using ArcInfo 7.0 and ArcMap 8.2. Landscape attributes were determined based on 1:24000 color infrared orthophotos taken in spring 2000. First, a grid coverage was created consisting of 10 ha square polygons. This layer was then overlaid on the digitized orthophoto image, and each grid cell occurring in potential Florida scrub-jay habitat (Breininger et al. 1991) was then assigned attributes for each of eight landscape variables (Table 1), based on photo-interpretation. Three additional attributes were derived from a combination of six of these variables using a modification of a Florida scrub-jay Habitat Suitability Index (Breininger 1992, Breininger et al. 1998, Burgman et al. 2001, Duncan et al.1995). HSI Scale 1 was calculated by modifying the habitat suitability index formula to fit the habitat variables determined by photo-interpretation within each cell (Figure 1). The remaining two variables were determined by taking the mean value of HSI Scale 1 for the focal cell and the surrounding cells at two scales. HSI Scale 2 was the mean of HSI Scale 1 for the focal cell and all cells within one cell of the focal cell. HSI Scale 3 was the mean of HSI Scale 1 for the focal cell and all cells within two cells of the focal cell.

2.3 Model selection

We used the information-theoretic approach described by Burnham and Anderson (2002) to model relationships between Florida scrub-jay habitat occupancy and habitat characteristics measured from GIS mapping procedures. This method is based on selecting among a set of candidate alternative hypothesis (models) using a model selection technique based on how well-supported each hypothesized model is by the data (see Johnson and Omland 2004 for a succinct summary). Prior to data analysis we devised a set of 20 alternative hypotheses (models) postulating relationships between habitat variables and Florida scrub-jay occupancy. These models were based on our knowledge of Florida scrub-jay biology and published studies describing such relationships (e.g. Breininger 1992, Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. 1995, 1998, Woolfenden and Fitzpatrick 1984). Logistic regression models with Florida scrub-jay occupancy as the response variable were then fit for each hypothesis using SPSS 12.0. Before model selection, the global model (i.e. a model that included all parameters considered in any model) was estimated and the fit assessed (Agresti 2002). Models were then ranked based on relative differences in the second order Akaike's information criterion (AIC_c). AIC_c is recommended by Burnham and Anderson (2002) when the sample size divided by the number of parameters in the most parameterized model is less than 40. For each model we rescaled AIC_c relative to the model with the lowest value to compute Δi (i.e. the model with the lowest AIC_c had $\Delta i = 0$) and also computed the Akaike weight, w_i (useful in evaluating the relative likelihood of one model compared with another). For all models with $\Delta i < 4$ we evaluated the model fit (based on a X^2 goodness-of-fit test, or the Hosmer-Lemshow test for models with continuous variables) and present model parameter estimates.

2.4 Model performance

Because our emphasis was on inference rather than prediction we wanted to maximize the information for available for model selection. Therefore, we chose not to partition the survey points into training and evaluation data sets. However, we did conduct a cross-validation (jackknife) procedure (Verbyla and Litvaitis 1989) to evaluate the predictive performance of the selected models. Each model was tested *n* times by removing one case at a time and model performance was evaluated using the receiver operator characteristic (Rushton et al. 2004, Fielding and Bell 1997). Future use of these models for predictive purposes will require collection of an independent validation data set (Fielding and Bell

1997). To demonstrate the utility of the method for predicting habitat occupancy, we used model averaging (see Burnham and Anderson 2002) to predict Florida scrub-jay occupancy for a region of the study site which had an independent data set of Florida scrub-jay habitat occupancy. This area was part of a demographic study of Florida scrub-jays; all of individuals were banded within this area and territory boundaries were mapped every year since 1988 (Breininger and Carter 2003). We included models in the set such that the sum of their w_i values exceeded 0.9 (analogous to a 90 % confidence set of models, Burnham and Anderson, 2002). We provide a visual presentation of these results.

3. Results

3.1 Field work

Of 4297 grid cells comprising the study site, 57% (*n*=2455) were potential Florida scrub-jay habitat. Within potential habitat we surveyed 74 randomly located field locations for Florida scrub-jays. Of these, 54% (*n*= 40) were occupied by Florida scrub-jays. On average 3 scrub-jays responded to playback in occupied sites; range = 1-7.

3.2 Model selection

For each of the twenty hypothesized models, Table 2 gives the maximized log-likelihood function and degrees of freedom of the fitted logistic regression equation (-2LL), the number of estimated parameters (k), the ration of k to the sample size (n=74), the AIC_c value, the difference between each model and the model with the lowest AIC_c (Δi), and the Akaike weight (w_i). The global model (the model that included all the terms included in any other separate model) was found to have an adequate fit (Hosmer and Lemeshow goodness of fit test X2 = 9.7, df = 8, $p = 0.287$). Four models were found to have Δi values less than 2

(Table 2); parameters of the fitted logistic regression equation for these models are given in Table 3.

The model with the lowest Δi included the habitat suitability index scale 2 (*HSI2*) as the only predictor variable. The inverse logistic transformation of the fitted logistic regression equation for this model was: probability of Florida scrub-jay occurrence = 0.2 + 167 * (*HSI2*). Since habitat suitability scale 2 was by definition between 0 and 1, for every 0.01 increase in a cell's measured *HSI2*, the predicted probability of Florida scrub-jay occurrence increased 1.6 times. Another way to explore the output of a logistic regression model is to examine the predicted probability of success for various combinations of the predictor variables (Agresti 1990). Table 4 shows the predicted probability of Florida scrub-jay occurrence for different levels of the predictor variables in each of the four models with Δi values less than 2. The model with the next lowest Δi (1.02) included scrub height (*H*) and ridge (*A*) as predictor variables. Scrub height (*H*) level 2 (optimal height) has the greatest positive effect on the predicted probability of Florida scrub-jay occurrence (Table 4). Also, by comparing between entries in Table 4 with the same values for the height variables but different values for *A*, it can be seen that when $A = 1$ (cell is not within one cell of a scrub ridge), the predicted probability of Florida scrub-jay occurrence is greatly reduced. The model with the next lowest Δi (1.44) included % suitable habitat (*Z*) and ridge (*A*) as predictor variables. As % suitable habitat (*Z*) increased, the predicted probability of Florida scrub-jay occurrence also increased (Table 4). Also, by comparing between entries in Table 4 with the same values for % suitable habitat but different values for *A*, it can be seen that when $A = 1$ (cell is not within one cell of a scrub ridge), the predicted probability of Florida scrub-jay occurrence is greatly reduced. This model however did not have an adequate fit

(Table 3). The model with the next lowest Δi (1.58) included the habitat suitability index scale 1 (*HSI1*)as the only predictor variable. The inverse logistic transformation of the fitted logistic regression equation for this model was: probability of Florida scrub-jay occurrence = 0.4 + 22.9 * (*HSI1*). Since habitat suitability scale 1 was by definition between 0 and 1, for every 0.0 1 increase in a cell's measured *HSI1*, the predicted probability of Florida scrub-jay occurrence increased 0.23 times.

3.3 Model performance

According to ROC plots of the jackknife samples, *HSI2* was best followed by *HA*, *ZA*, and *HSI1* respectively. The area under the ROC function (AUC) was 0.74 for *HSI2*, 0.70 for both *ZA*, and *HSI1*, and 0.66 for *HA* (ROC figure). Model average results for cells occurring in a long-term demographic study site are illustrated in Figure 1.

4. Discussion

4.1 Efficient habitat mapping

It might appear, based on the number of published studies that utilize GIS data to obtain predictor variables for models of species-habitat relationships, that this is a relatively direct and efficient process. However, many commonly used GIS data sources (e.g., land-cover maps and satellite imagery) must be further processed (e.g., vegetation mapping etc.) to allow predictive models with mechanisms that have biological significance. Unfortunately, this step in the model development process can be arduous (Beard et al. 1999). Furthermore, there are numerous other cases where pre-existing GIS data is not available or is unsuitable. For both cases, we believe that using grid cell-based classification of habitat characteristics is a more efficient alternative. Although some previous studies have used grid cell-based classification of GIS data (e.g. see, Collingham et al. 2000, Schadt et al. 2002, Gavashelishvili 2004) the classifications were typically based on topographic maps, land-cover maps or satellite images. Our classification scheme is based on interpretation of vegetation and landscape characteristics using high resolution digital orthophotographs. We believe this technique is superior to classification schemes based on other sources (e.g., topographic maps, land-cover maps or satellite images) for two reasons. First, while no GIS data sources allow direct measurement of habitat features that determine habitat suitability (Rushton et al. 2004), classification of high resolution digital orthophotographs can be quickly accomplished by the wildlife investigator with knowledge of the focal species. This knowledge is essential because the variables that characterize pre-existing GIS data may not correlate well with predictive species-habitat variables (Van Horne 2002). For example, land-cover maps represent classification schemes developed for other uses not specifically intended to predict species occurrence and consequently might lack sufficient detail to allow classification of potentially important variables (Seoane et al. 2003, Rushton et al. 2004). Second, high resolution digital orthophotographs allow features to be discerned that are not possible to map with satellite imagery.

We believe grid cell classification improves on vegetation mapping because only variables of interest are classified, thus providing necessary detail with out having to map potentially time consuming detail. Another benefit is that the resolution at which the model operates is determined by the size of the cell. Furthermore, grid cells allow predictor variables to be determined at various resolutions by averaging cell values in a windowing process. This is useful because a full understanding of the issue of scale as it applies to a particular situation is often not available (Rushton et al. 2004). In our example we used this process to calculate the HSI variable, as described earlier, at three scales. Subsequently, the *HSI2* model (Table 2) was selected as the best fitting model. These results demonstrate the advantages of grid cells in determining appropriate scale and potentially revealing other important mechanisms that influence habitat occupancy. In this case the intermediate scale of the *HSI2* model is probably related to behavioral traits exhibited by Florida scrub-jays other than habitat selection, such as philopatry, conspecific attraction (see Woolfenden and Fitzpatrick 1984) and their sentinel system (see McGowan and Woolfenden 1989) used for predator avoidance.

4.2 Variable selection and model development

Selection of the variables to be used to classify grid cells should be based on a careful review of existing knowledge of the system being modeled. This fits well with the information-theoretic model selection approach, because the validity of these procedures depends heavily on *a priori* hypothesis specification based on existing knowledge (Burnham and Anderson 2002). The hypothesis formulation stage of the model selection procedure should serve to determine the classification scheme as well as the candidate set of models. Integrating these steps also helps ensure a robust study design because sample points can be screened to ensure adequate coverage amongst all of the variables of interest.

We relied on a combination of expert opinion and a HSI (Breininger 1992, Breininger et al. 1998, Burgman et al. 2001, Duncan et al.1995) to generate hypotheses (models) that relate habitat and landscape variables to scrub-jay habitat occupancy. The use of a HSI in the model development stage is not necessary but given the significance of HSI in management decisions (Brooks 1997) and their utility in generating hypotheses (Van Horne 2002) we believe that more emphasis should be placed on using existing HSIs to investigate the mechanisms of species-habitat relationships. Our results show that HSI (particularly well developed ones) can be used to develop models that predict well (ROC figure).

4.3 Model interpretation

If the goal of a modeling effort is to interpret the meaning of the selected models and make inference to the process being modeled then care should be taken to develop models that can be easily interpreted. In our case, using the actual HSI (geometric-mean algorithm) as a candidate model led to a model that performed well for prediction but was difficult to interpret ecologically. If inference is the primary goal, HSI will be more useful when used to develop simpler models based on the components of the index. For example, in the (*H A*) and (*ZA*) models it is easy to see how the probability of occupancy is related to the predictor variables (Table 4). Ridge (*A*) is clearly an important variable because the probability of occupancy is greatly reduced when a scrub ridge (*A*) is not present within or adjacent to a cell, *A*=1 (Table 4). This makes sense ecologically because scrub oaks Q*uercus spp*. are an important component of scrub-jay habitat (Woolfenden and Fitzpatrick 1984, Breininger and Oddy 2004) and are dominant on ridges with well drained soil (Schmalzer and Hinkle 1992). Probability of occupancy is also influenced by the % of suitable scrub habitat (*Z*) in the cell. This agrees with the results of Breininger and Oddy (2004) who showed that poorly drained ridges with little oak cover were occasionally unoccupied whereas well drained ridges in which oaks dominate were always occupied. We also found that level two of Height (*H*) had a large positive effect on probability of occupancy (Table 4). Scrub height is important factor in determining habitat quality and our level two represents optimal conditions (Breininger and Carter 2003). In population centers Scrub-jays prefer and compete for breeding opportunities in optimal habitat (Woolfenden and Fitzpatrick 1984, Breininger et al. 1995).

Interpretation of our results confirmed existing knowledge of Florida scrub-jay habitat preferences but clearly we did not consider some important processes that influence habitat occupancy because the pattern of occupancy observed did not always agree with known habitat preferences. Future work should consider patch history and scrub-jay behavioral traits not directly related to habitat preference. scrub-jay habitat quality varies temporally primarily as a function of the time elapsed since the last fire (Duncan et al. 1995) and although species can be abundant in marginal habitats, populations in these areas cannot persist without immigration (Van Horne 1983). Given the short dispersal distances of Florida scrub-jays (Woolfenden and Fitzpatrick 1984, Stith 1999) it is obvious that, despite current conditions, scrub-jay habitat may be unoccupied (and there may be a considerable lag time before an area is re-colonized) if historical conditions were marginal and a source of immigrants is not within the typical dispersal distance.

4.4 Relating modeling results to conservation and management

A primary objective in developing species-habitat models is to provide managers and conservation biologists with decision support. For example, predictive models can aid in determining habitat suitability or occupancy which in turn can aid in reserve design (Cabeza et al. 2004). The grid cell technique is well suited to developing maps of habitat suitability (e.g., Rubec et al. 2001) or occupancy (Figure 1) and thus could be used in this manner. A grid cell map could be also used to prioritize management or restoration efforts by distinguishing habitat suitability across a landscape (e.g., Lauver et al. 2002). Grid cell classification will be especially useful for situations where vegetation data require frequent updates due to continually changing vegetation conditions from management activities or natural processes. Furthermore, successive classification of grid cells through time will allow transition probabilities to be calculated for pertinent predictor variables and these may be used via Markov chain modeling for planning or to develop management strategies based on pre-determined scenarios (see Breininger and Carter 2004). The grid cell classification approach to habitat mapping demonstrated here can greatly benefit conservation efforts by providing an efficient method to obtain appropriate data for predictor variables from readily available digital ortho-photographs while circumventing some of the common limitations of other types of GIS data.

Predicting patterns and producing maps is important for management activities but understanding the mechanism that produces the pattern is equally important. Combining knowledge of an animal's ecology with objective model selection is an effective method to elucidate the mechanism underlying the process being modeled which may lead to more robust models, direct future investigation, and potentially have significant bearing on species management (Van Horne 2002).

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Table 1. Eleven landscape variables were mapped into each 10 ha grid cell based on photointerpretation of 2000 orhtophotos.

Variable	Type	Description
Scrub Height (H)	Categorical	Height of scrub oaks: 1 = all scrub oaks < 1.2 m, 2 = scrub oaks 1.2 - 1.7 m, 3 = some scrub oaks 1.2 - 1.7 m, and some > 1.7 m, 4 = all scrub oaks > 1.7 m.
Scrub Type (S)	Categorical	Florida Scrub-Jay Habitat potential (see Breininger et el. XXXX): 0 = unsuitable, 1 = optimal, 2 = secondary, 3 = tertiary
Tree Cover (T)	Categorical	Density of pine tree (overstory) cover: 1 = savanna, 2 = woodland, 3 = forest
Open (O)	Categorical	Amount of sandy openings: 0 = none, 1 = abundant, 2 = ruderal near scrub oaks
Forest (F)	Categorical	Forest present in cell or adjacent cell: 0 = no, 1 = yes
Road (R)	Categorical	Road present in cell or adjacent cell: 0 = no, 1 = yes
Percent Scrub (Z)	Continuous	Percent of suitable Florida Scrub-Jay habitat within cell
Ridge (A)	Categorical	Scrub ridge present in cell or adjacent cell: 0 = no, 1 = yes
HSI Scale 1 (HSI1)	Continuous	modified Habitat Suitability Index (Figure 1) for cell
HSI Scale 2 (HSI2)	Continuous	mean modified Habitat Suitability Index (Figure 1) of all cells within one grid-cell (9 cells)
HSI Scale 3 (HSI3)	Continuous	mean modified Habitat Suitability Index (Figure 1) of all cells within two grid-cell (25 cells)

Table 2. Of the 20 *a priori* models hypothesized to relate landscape variables to Florida Scrub-Jay habitat occupancy, the model selection proceedure identified four model as clearly superior to the others (bold type). All of these models were well-supported, and should be considered if prediction of occupancy is a desired goal (see text for details). Models are designated in shorthand by referencing the explanatory variables included. For identification of variables see table 1. When an interaction term was included all main effect terms were also included. For example, model S*H had the response variable Logit(Florida Scrub-Jay Occupancy) and included the explanatory variables Scub, Height and the interaction of Scrub and Height.

Model Description	-2 LL	df	AICc	Δi	n/k	w_i
HSI Scale 2	86.21	1	90.37	0.00	37.00	0.36
H, A	80.54	4	91.40	1.02	14.80	0.22
Z, A	85.48	2	91.82	1.44	24.67	0.18
HSI Scale 1	87.78	1	91.95	1.58	37.00	0.16
Z	90.81	1	94.97	4.60	37.00	0.04
HSI Scale 3	92.14	1	96.31	5.93	37.00	0.02
S, H, O, Z	74.74	9	98.13	7.75	7.40	0.01
S, R	89.09	4	99.95	9.57	14.80	0.00
S	91.39	3	99.96	9.58	18.50	0.00
S, H, O, R	76.98	9	100.36	9.99	7.40	0.00
S, H, O	79.84	8	100.57	10.19	8.22	0.00
S, H, O, Z, T	72.35	11	101.30	10.93	6.17	0.00
S, H, O, R, T	73.10	11	102.05	11.68	6.17	0.00
S, H, O, T	76.25	10	102.38	12.00	6.73	0.00
S, H, O, R, T, Z, F	67.61	13	102.49	12.12	5.29	0.00
S, H, O, F	79.33	9	102.72	12.35	7.40	0.00
H	94.47	3	103.03	12.66	18.50	0.00
S*R	86.75	7	104.90	14.53	9.25	0.00
S*H	79.54	12	111.41	21.04	5.69	0.00
O, S*H	74.67	14	112.67	22.30	4.93	0.00
Global (variables used in any model included)	50.70	25	131.36		2.85	

Table 3

Parameters of the fitted logistic regression equation for selected models

Model	Variables	B	S.E.	df	Exp(B)	X^{2} [a]	df	p
HIS Scale 2	HIS Scale 2	5.11	1.45	1	166.10	7.93	8	0.44
	constant	-1.47	0.51	1	0.23			
H, A	H(1) [b]	0.82	1.02	1	2.27	1.01	4	0.91
	H(2) [b]	2.86	1.45	1	17.45			
	H(3) [b]	2.16	0.98	1	8.66			
	A	-2.06	0.61	1	0.13			
	constant	-0.58	0.87	1	0.56			
Z, A	A	-1.27	0.55	1	0.28	13.39	6	0.04
	Z	0.03	0.14	1	1.03			
	constant	-1.40	1.24	1	0.25			
HIS Scale 1	HIS Scale 1	3.13	0.92	1	22.87	4.54	5	0.48
	constant	-1.04	0.43	1	0.35			

a Resu;ts of Hosmer and Lemeshow Goodness of fit test.

b H is a categorical variable with four levels so three dummy variables are used to fit the model. For H=1:{H(1)= 1, H(2)=0, H(3)=0}, H=2:{H(1)=0, H(2)=1, H(3)=0}, H=3:{H(1)=0, H(2)=0, H(3)=1},H=4:{H(1)=0, H(2)=0, H(3)=0}.

Table 4

The predicted probability of Florida scrub-jay occurrence for different levels of the predictor variables in each of the four models with Δi values less than 2.

Model Z,A			Model H,A			Model HSI1		Model HSI2	
Z	*A*	p (occ.)	*HT*	*A*	p (occ.)	*HSI1*	p (occ.)	*HSI2*	p (occ.)
0	1	0.06483	1	1	0.13943	0	0.26076	0	0.18679
10	1	0.08402	2	1	0.55503	0.1	0.32541	0.1	0.27694
20	1	0.10823	3	1	0.38225	0.2	0.39747	0.2	0.38974
50	1	0.21943	4	1	0.06673	0.3	0.47427	0.3	0.51572
70	1	0.32982	1	0	0.56045	0.4	0.55231	0.4	0.63973
90	1	0.46282	2	0	0.90754	0.5	0.62785	0.5	0.74753
100	1	0.5327	3	0	0.82963	0.6	0.69762	0.6	0.83157
0	0	0.19766	4	0	0.36008	0.7	0.75933	0.7	0.89169
10	0	0.24583				0.8	0.81184	0.8	0.9321
20	0	0.30132				0.9	0.85508	0.9	0.95814
50	0	0.49975				1	0.88973	1	0.97447
70	0	0.63622							
90	0	0.7538							
100	0	0.80203							

Figure 1

V1A
If Scrub = 1, V1A = 1
If Scrub = 2, V1A = 0.8
If Scrub = 3, V1A = 0.5
If Scrub = 4, V1A = 0

V1B
If Ridge = 1, V1B = 1
If Ridge = 0, V1B = 0

V2A
If Open = 0, V2A = 0.1
If Open = 2, V1A = 1
If Open = 3, V1A = 0

V2B
If Scrub = 1 or 2 AND
Open =2, V1B = 1

otherwise V2B = 0

V3A
If Forest = 0, V3A = 1
If Forest = 1, V1A = 0.1
If Forest = 2, V1A = 0

V3B
If Tree = 1, V3B = 1
If Tree = 2, V3B = 0.59
If Tree = 3, V3B = 0

V4
If Height = 1, V4 = 0.33
If Height = 2, V4 = 1
If Height = 3, V4 = 0.67
If Height = 4, V4 = 0.33

$$HSI = \sqrt[4]{\{Max(V1A,V1B) + Max(V2A,V2B) + Min(V3A,V3B) + V4\}}$$

Figure 2

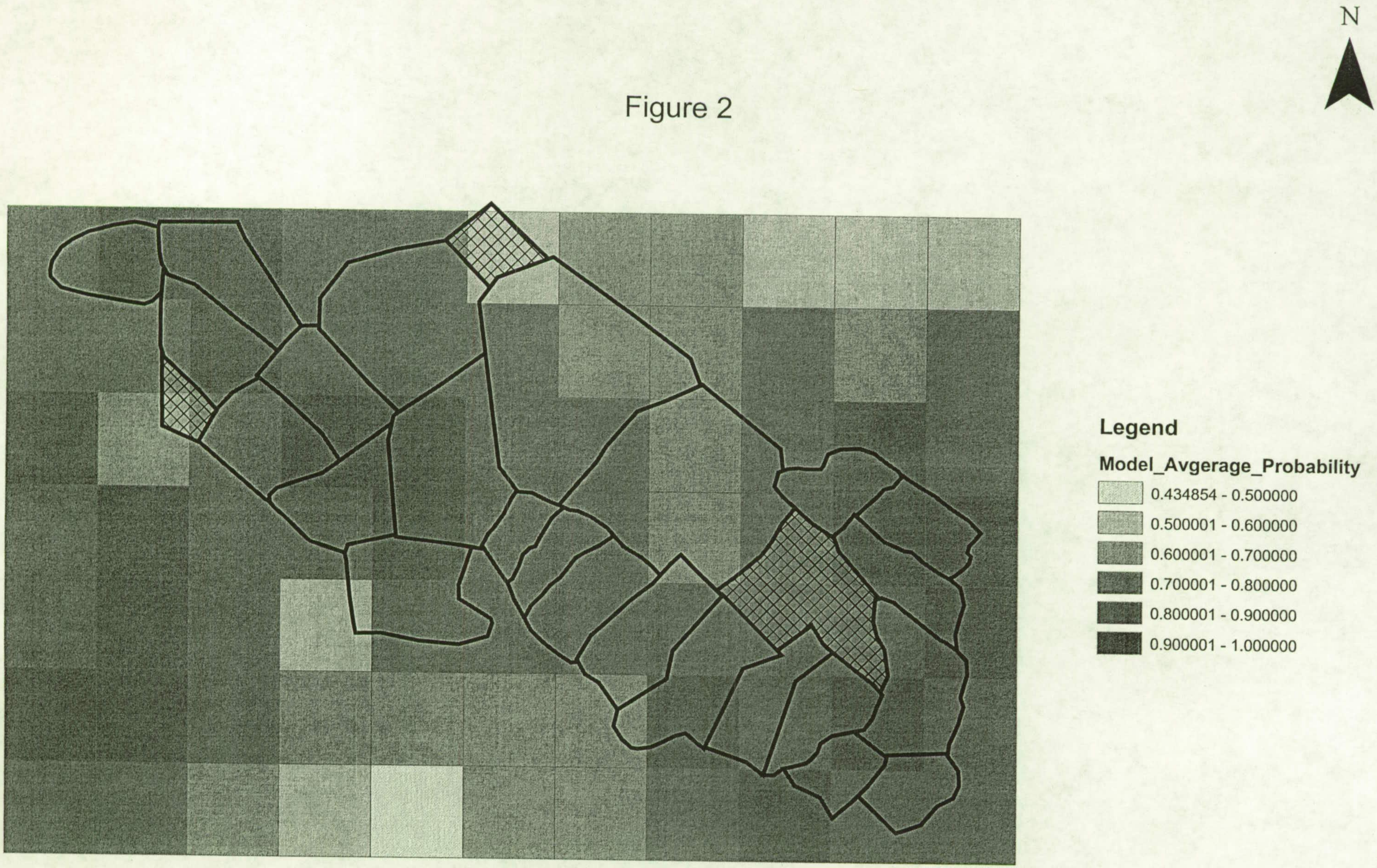
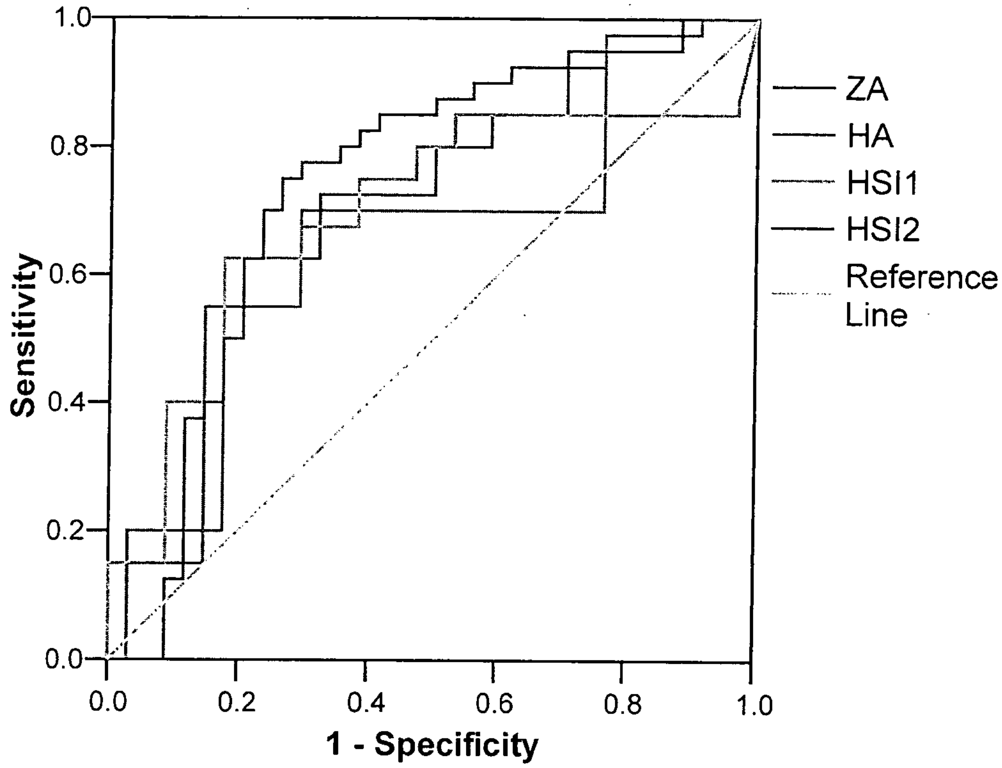

N
Legend
Model_Avgerage_Probability
0.434854 - 0.500000
0.500001 - 0.600000
0.600001 - 0.700000
0.700001 - 0.800000
0.800001 - 0.900000
0.900001 - 1.000000

Figure 3



1.0
0.8
0.6
0.4
0.2
0.0
Sensitivity
0.0
0.2
0.4
0.6
0.8
1.0
1 - Specificity
ZA
HA
HSI1
HSI2
Reference Line

Figure 1. Calculation of Habitat Suitability Index (HSI) values for 10 ha grid cells was based on a modification of methods described in Breininger et al. (1998, 2001). Variables refer to landscape features mapped onto grid cells (see Table 1).

Figure 2. An example of grid cell map (based on model predictions) was overlain by territory maps of a long-term demographic study site. Each polygon represents a territory and hatched polygons were unoccupied during the period that random points were sampled for scrub-jay occupancy. The probability of occupancy for each cell was calculated using model averaging.

Figure 3. The predictive performance of the selected models was evaluated by calculating the area under the receiver operator characteristic function.