Landscape patterns as habitat predictors: building and testing models for cavity-nesting birds in the Uinta Mountains of Utah, USA

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Abstract

The ability to predict species occurrences quickly is often crucial for managers and conservation biologists with limited time and funds. We used measured associations with landscape patterns to build accurate predictive habitat models that were quickly and easily applied (i.e., required no additional data collection in the field to make predictions). We used classification trees (a nonparametric alternative to discriminant function analysis, logistic regression, and other generalized linear models) to model nesting habitat of red-naped sapsuckers (*Sphyrapicus nuchalis*), northern flickers (*Colaptes auratus*), tree swallows (*Tachycineta bicolor*), and mountain chickadees (*Parus gambeli*) in the Uinta Mountains of northeastern Utah, USA. We then tested the predictive capability of the models with independent data collected in the field the following year. The models built for the northern flicker, red-naped sapsucker, and tree swallow were relatively accurate (84%, 80%, and 75% nests correctly classified, respectively) compared to the models for the mountain chickadee (50% nests correctly classified). All four models were more selective than a null model that predicted habitat based solely on a gross association with aspen forests. We conclude that associations with landscape patterns can be used to build relatively accurate, easy to use, predictive models for some species. Our results stress, however, that both selecting the proper scale at which to assess landscape associations and empirically testing the models derived from those associations are crucial for building useful predictive models.

Introduction

Traditionally, habitat models have been based on associations between the occurrence of a species and the composition and structure of vegetation at relatively fine spatial scales (i.e., fine grain and small extent) (Verner et al. 1986). More recently it has been recognized that animals, particularly birds, also respond to landscape patterns at coarser spatial scales (Freemark and Merriam 1986). Incorporating habitat associations based on landscape patterns into predictive models has the potential to improve the accuracy and/or ease of use of habitat models. To be useful as

conservation and management tools, predictive models of any spatial scale should be accurate, general, and easily applied (Van Horne and Wiens 1991). Because it is often difficult to simultaneously maximize all three of these characteristics, one or two are usually favored at the expense of the other(s).

Describing a model as easy to use implies that manipulating and running the model is not a difficult task, and that a minimal amount of effort is required to collect the data needed to make predictions. Both wildlife habitat relationships (WHRs) (Salwasser 1982) and the gap analysis project (GAP) terrestrial vertebrate models (Scott et al. 1993) are examples of

predictive tools that are easy to use and exhibit a high degree of generality. WHR models use pertinent literature and expert opinion to build a database consisting of range maps, species notes, a list of special habitat requirements, and a matrix of suitability levels for each species given different habitat factors (Verner and Boss 1980). The GAP approach combines vegetation associations, range maps, and ancillary data (e.g., locations of water bodies, elevation) to produce state-wide prediction maps of vertebrate distributions (Scott et al. 1993). Both types of models may be relatively accurate for addressing questions of species richness when managing for biodiversity at an ecosystem- or region-wide level (Raphael and Marcot 1986; Edwards et al. 1996), but are less accurate for addressing questions involving individual species occurrences at fine spatial scales. This is not a failure of these models, but rather a recognized limitation of their applicability.

Models that are built with more detailed data are likely to be more accurate at fine spatial scales than are region-wide WHR models. One example of a finer scale model is the habitat suitability index (HSI). HSIs use a collection of data gleaned primarily from previously published studies to build suitability curves defining the relationships between species abundance and a set of habitat variables (US Fish and Wildlife Service 1981). The accuracy of an HSI depends in part on its generality. For example, HSI models built with data collected across a number of habitat types may be too general to be accurate in any one habitat type (Stauffer and Best 1986). Nonetheless, HSIs are designed to make predictions about habitat suitability at scales that are relevant to local managers, such as that of a reserve or national park. At these scales they are likely to be more accurate than coarser scale WHR-type models.

Long-recognized associations of birds with the structure and composition of vegetation form the foundations for most avian habitat models. These patterns of vegetation may provide birds with the proximate cues for the ultimate factors that influence fitness (e.g., predation, environmental stressors, and competition) (Hildén 1965). Likewise, landscape patterns may also provide birds with proximate cues for selecting habitat (Freemark et al. 1995). Birds have been shown to be associated with basic landscape patterns such as patch size (Freemark and Merriam 1986), patch edges (Hawrot and Niemi 1996), fragmentation (Robinson 1992), and the spatial arrange-

ment of patches of vegetation (Hansen and diCastri 1992).

We modeled habitat associations, based on landscape patterns, for four species of cavity-nesting birds nesting in aspen forests in the Uinta Mountains in northeastern Utah, USA. Cavity-nesting birds are known to make up a large portion of birds nesting in aspen forests in the western United States (Winternitz 1980; Dobkin et al. 1995). We chose to work with red-naped sapsuckers (*Sphyrapicus nuchalis*), northern flickers (*Colaptes auratus*), tree swallows (*Tachycineta bicolor*), and mountain chickadees (*Parus gambeli*) because they occurred in numbers large enough for analysis. All four of these species are likely to be associated with landscape patterns. Both northern flickers and tree swallows are known to be associated with forest edges that border open areas (Conner and Adkisson 1977; Rendell and Robertson 1990). Because mountain chickadees are arboreal (feeding on insects, primarily by foraging on leaves and branches), and do not tend to spend time in open areas, we predicted that they would be associated with forested areas and might avoid edges to reduce the risk of predation (Wilcove 1985). Finally, red-naped sapsuckers exploit a number of different food resources, including willow bark, tree sap, and insects (Ehrlich and Daily 1988) and thus may select nest sites in landscapes that provide access to these diverse resources.

Our objective was to use associations with landscape patterns to build predictive habitat models that were accurate, general, and easy to apply. Our approach included a model-building phase followed by field testing at different, independent locations. To build the models we located nests of all four species at 11 field sites. We then measured several aspects of landscape pattern in plots centered on nest trees and on randomly selected non-nest points. We used classification trees (Breiman et al. 1984) to build predictive models that discriminated between nest and non-nest plots using a series of landscape metrics. To test the accuracy and the generality of the models, we used them to make maps of predicted nesting habitat for five unsampled field sites before searching these sites for nests. Finally, we compared the predictions of our landscape models to those of a simple WHR model based on gross habitat associations.
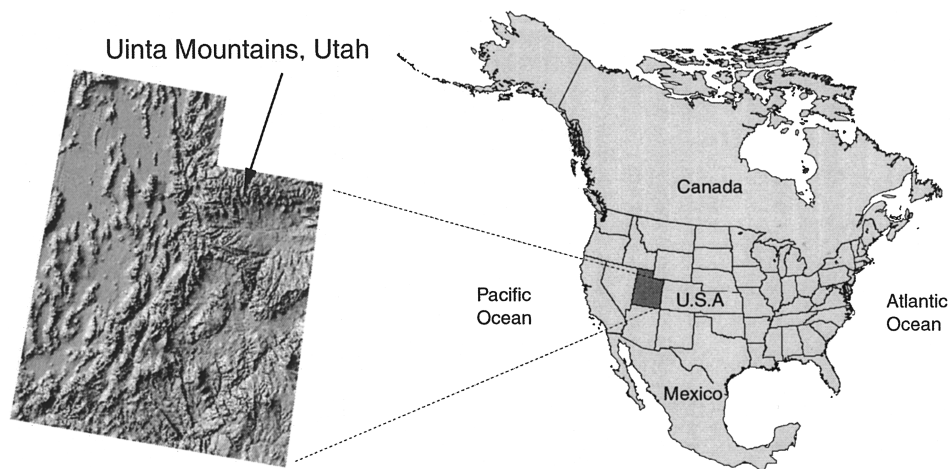
Figure 1. Location of the Uinta Mountains in northeastern Utah, USA

Methods

Study area

The study was conducted along the northern slope of the Uinta Mountains in northeastern Utah in the western United States (Figure 1). All study sites were between 40.7° and 41.1° N latitude and 110.0° and 111.0° W longitude. The north slope of the Uintas is dominated by lodgepole pine (*Pinus contorta*) and aspen forests (*Populus tremuloides*) at lower elevations, and mixed Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests at higher elevations. We selected 16 field sites; 11 were used for model building and 5 were reserved for field testing. We identified the sites in a geographic information system (GIS), selecting stream drainages that contained each of four general vegetation types (aspen forest, conifer forest, sage-grass meadows, and willow riparian) that characterize the Uintas. The size of each field site (between 25 and 400 ha) was determined by the extent of aspen forest and the size of the drainage. All sites were within 2 km of a road and were between 2750 m and 3050 m in elevation.

Nest searches and data collection

We first made hand-drawn maps of the aspen forest at each of the sites using a combination of ground surveys and aerial photos (1:16000 scale, color, taken in the summer of 1992). We then systematically searched all of the aspen at each site for nests from early June to early August. Nests were primarily found by following adults to cavities. We then ob-

served the adults at the cavity to determine if they were tending an active nest. We recorded the location of active nests using a global positioning system (GPS). In addition, nest locations were marked on the hand-drawn maps to allow for verification of nest locations in a GIS.

To measure attributes of landscapes in which birds did not nest, we selected a number of non-nest points such that sample-plots centered on these points could be compared to those centered on the nest locations. The non-nest points were randomly selected in proportion to the amount of unused aspen at each site. We defined unused aspen as the area where a sample plot could be placed and the center of the plot would not fall within any sample plot of a nest (see below). The number of non-nest points varied by species depending on how many nests were found at each site and how they were spatially distributed. This approach allowed us to make species-specific comparisons of habitat used and not used by nesting birds.

We calculated landscape metrics from a 30-m resolution digital vegetation map of the north slope of the Uinta Mountains. We used Imagine (version 8.2, Erdas Inc.) to perform a supervised classification of 1991 Landsat Thematic Mapper (TM) imagery using both field survey data and aerial photos (see above) to create five general land-cover types, including conifer, aspen, meadow, willow, and cut forest. We assessed the accuracy of the map using a stratified random sample of 50 ground survey points per vegetation class. Total accuracy across all classes was estimated at 70%, but accuracy of the map at the individual sites was likely to be higher because corrections were made using additional field data.

Table 1. Landscape metrics measured at nest and randomly selected non-nest points for four species of cavity-nesting birds.

Label	Landscape Metric
Aspen	Area of aspen (ha)
Willow	Area of willow (ha)
Open	Area of meadow and willow (ha)
Cut	Area of logged forest (ha)
Edge density	Meters of aspen meadow edge per hectare of aspen
Aspen interior	Area of aspen > 30 m from a meadow edge
Patch richness	Number of different types of patches
Contagion	A measure of how clumped patches of vegetation are (0–100%)
Patches aspen	Number of patches of aspen
Patches willow	Number of patches of willow
Patches open	Number of patches of meadow and willow
Largest patch aspen	Largest patch of aspen (ha)
Largest patch willow	Largest patch of willow (ha)
Largest patch open	Largest patch of meadow and willow (ha)

We placed all of the 1996 and 1997 nest locations, as well as the randomly selected non-nest points on the digital vegetation map in a GIS. Sixteen plots, each of different size, were centered on each nest and non-nest location. Plots ranged in size from 0.8 ha to 98.0 ha. By using a range of sample plot sizes, we hoped to capture the various extents over which the different species respond to landscape patterns. With the exception of tree swallows, these plot sizes covered the range of home range sizes among the four species (Laudenslayer and Balda (1976); Evans and Conner (1979), J. Lawler pers. obs.). Tree swallows have been noted to travel up to 100 km to reach foraging sites (Robertson et al. 1992); however, we believe that our largest plot of approximately 1 km^2 adequately covered the area used by the tree swallows in the Uinta Mountains.

We used FRAGSTATS (McGarigal et al. 1993) to calculate a set of landscape metrics for each sample plot (Table 1). We chose a set of landscape metrics that estimated both the composition and the structure of the landscape-level vegetation patterns, including the area of each vegetation type, the number of patches of each of the types, and the size of the largest patch of each type. We also computed the area of interior aspen (defined as aspen that was at least 30 m from a meadow edge), the density of aspen-meadow edge (meters of aspen-meadow edge per hectare aspen), and a simple measure of patch richness (the number of different vegetation types in the plot).

Models

We used classification trees (Breiman et al. 1984; Venables and Ripley 1997; S-PLUS 4.3 1998) to build predictive models for each of the four species. Classification and regression trees offer a flexible and simple alternative for modeling complex ecological relationships (De'ath and Fabricius 2000). Trees explain the variation in a single response variable with respect to one or more explanatory variables. They work by recursive partitioning of the data into smaller and more homogenous groups with respect to the response variable. Each split is made by the explanatory variable and the point along the distribution of that variable that best divides the data. Tree models have several advantages over linear and generalized linear models when analyzing ecological data. First, decision trees are invariant to monotonic transformations of the explanatory variables. Second, tree-based models are more adept at capturing nonadditive behavior and complex interactions. Third, decision tree models have a unique method of dealing with missing values, particularly when used as predictive models. Fourth, tree models are capable of modeling a large number and mixture of categorical and continuous explanatory variables. Finally, because their structure is easy to conceptualize and graphically represent, they are often easy to interpret and explain. This latter point in particular is a critical aspect of building useful habitat models.

Several of the landscape metrics used to build the models in this study were correlated (e.g., largest patch of aspen and total aspen area). The treatment of

such collinearity in classification tree analysis is different than in other parametric models such as logistic regression. In the latter, multiple correlated variables that are associated with the response variable can potentially be included in the model and often produce misleading coefficients. Classification tree analysis, on the other hand, only allows one of any set of correlated variables to enter the model at any given split. Only the variable that best classifies the data is selected. As the data are split into smaller groups in the modeling process, the relationships among explanatory variables may change. Thus variables that are highly correlated over the whole data set may not be as strongly associated in subsets of the data. For these reasons we chose to include variables that we felt were biologically meaningful in the modeling process, despite several being cross-correlated.

We built 16 models for each of the four species (except for red-naped sapsuckers for which we built 8 models), each using a different size sample square. Because red-naped sapsuckers were prevalent and spread throughout the study sites, non-nest point sample sizes were restricted when larger plots were used. We thus limited the range of plot sizes for red-naped sapsucker to from 0.8 ha to 26.0 ha. We used cross-validated deviances (after Breiman et al. (1984)) to prune the 56 tree models.

The process of selecting one model for each of the four species involved two steps. First, because classification trees produce proportions (which can be interpreted as probabilities) a threshold level must be chosen for determining when observations will be predicted in each response class (as presences or absences in our case). A similar choice must be made when using logistic regression or any other statistical technique that produces predicted probabilities. With classification trees, each terminal node of the model (see Figure 2) contains a set of observations. In our models these observations are either nest or non-nest points. The simplest and most common approach to setting a threshold is to use a majority rule such that the node is classified in accordance with the majority of the observations in that node. Thus if a node contained 30 nest and 20 non-nest points, any observation in that node would be predicted to be a presence (i.e., nesting habitat). However, this approach neglects any knowledge of the distribution of the response variable and fails to take into account the objectives of the model. Several alternative techniques have been suggested (Fielding and Bell 1997).

For the first step in the model selection process, we used receiver-operation characteristic (ROC) plots to determine the threshold with which to classify the observations in each of the terminal nodes of the tree model. ROC plots, developed in the field of signal processing, are created by plotting sensitivity values (the proportion of all positive observations correctly classified) against their corresponding proportion of negative observations incorrectly classified (1-specificity) for each possible classification threshold (Fielding and Bell 1997). Using this curve, a threshold can be selected by determining the point at which a line with slope m (Equation 1), moved from the left of the ROC plot to the right, first intersects the curve (Zweig and Campbell 1993).

$$m = (FPC/FNC) \times ((1 - p)/p) \qquad (1)$$

The slope m is calculated using both the proportion of positive cases (p) and the ratio of the expected cost of false positives (FPC) (incorrectly predicted absences) to the expected cost of false negatives (FNC) (incorrectly predicted presences). We took the approach that our models would be used for selecting areas, which when conserved, would protect the species in question. With this purpose in mind, we assigned the cost of false negatives to be five times the cost of false positives. Alternatively, if the purpose of the models was to select areas for the reintroduction of an endangered species, the cost of false negatives might have been determined to be a fraction of the cost of false positives. Although the magnitude of our estimated cost ratio was arbitrarily selected and did not take into account the complex economic and ecological costs involved in making conservation decisions, we felt that it was adequate for the purpose of selecting models for this study.

The second step in the process of selecting one model for each species involved calculating the correct classification rate for both nests and non-nest points (for all 56 models) and selecting the model for each species that had the largest proportion of correctly classified nests. In the event of ties, we then selected the model with the highest proportion of non-nest points correctly classified. Again, this step biased us towards selecting models that would correctly classify nests at the expense of incorrectly classifying non-nest points.
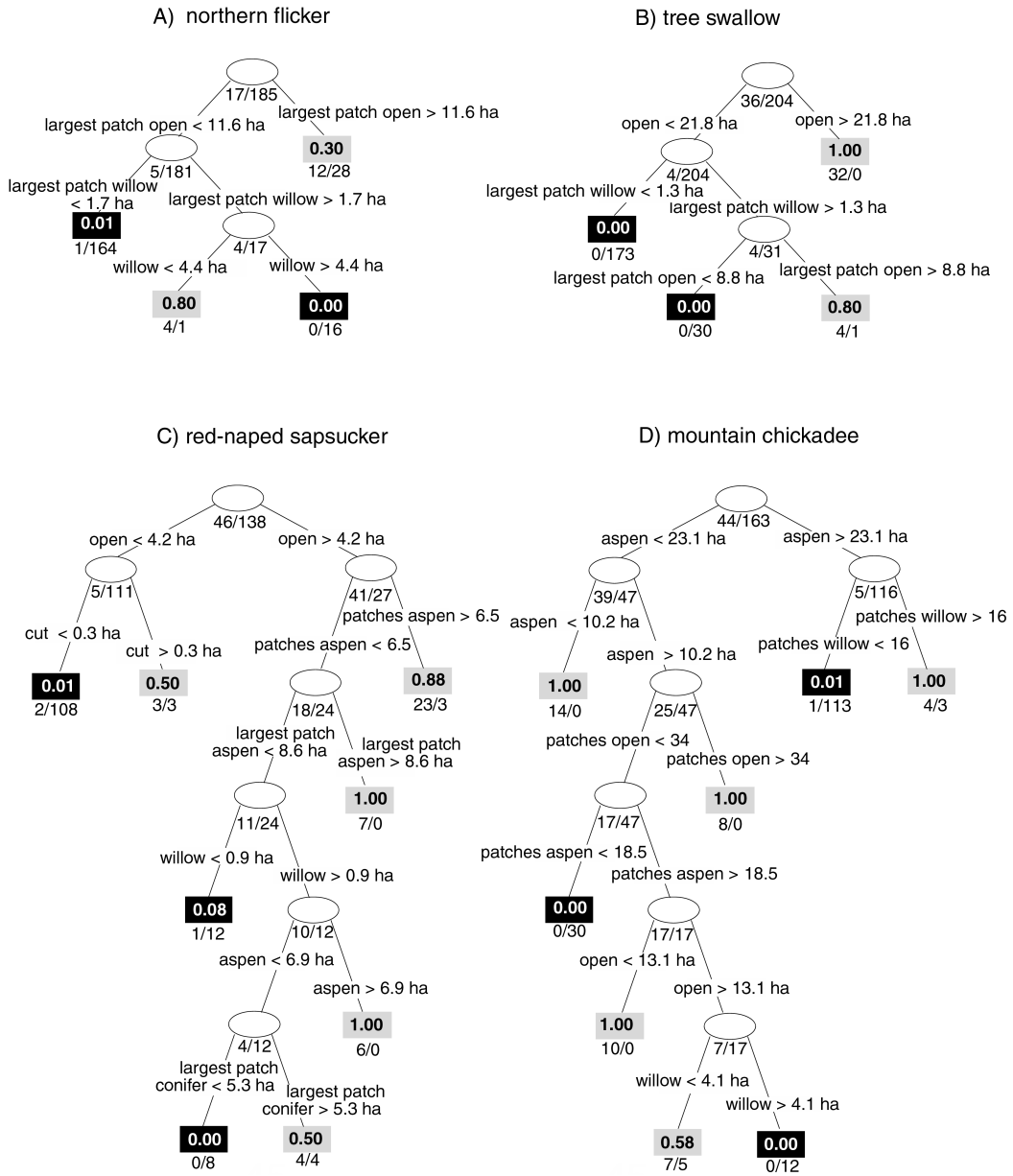
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Figure 2. Classification trees modeling the presence of (a) northern flicker nest sites, (b) tree swallow nest sites, (c) red-naped sapsucker nest sites, and (d) mountain chickadee nest sites. Each diagram depicts the binary recursive partitioning of data performed by the tree algorithm. The explanatory variables and the point along their distribution with which a split was made are written as labels on the branches of the trees. Each node in the tree represents a subset of data; the highest node containing all observations. The numbers below the nodes represent the number of nests and non-nest points at each node (nests/non-nest points). Rectangles represent terminal nodes of the tree; the final subsets into which the data were split. The numbers in the rectangles are the probabilities of nest presence calculated using the proportion of nests at each node. Finally, the shading of the terminal nodes (gray or black) indicates predicted presence and absence, respectively.

Prediction maps

We created four maps (using the single best model for each species) of predicted nesting habitat for each of the five test sites selected to be searched in 1998. We generated landscape pattern data for each new 1998 field site by moving a square sample window across the sites on the digital vegetation map. The size of the moving window corresponded to the different sizes of the sample plots used to build the final four models.

We calculated the landscape metrics for each sample window using FRAGSTATS (McGarigal et al. 1993). By applying the classification tree models to the data for the new sites, we produced a prediction value for every pixel of aspen at each site. We mapped the predictions to produce images that included the original five classes of vegetation; aspen, however, was represented by two classes depicting where nesting habitat was predicted to be present or absent.

Testing predictions

In 1998 we searched the five new field sites, recorded the position of all nests with a GPS and then plotted the nests on the prediction maps. Because spatial error in the underlying vegetation map and slight errors in the GPS recorded positions occasionally placed nests in conifer forests or meadows, we assessed the accuracy of the prediction maps and the accuracy of the models separately. Positions taken with the GPS (with a few exceptions) were accurate to within ±10 m. In addition to this spatial error, the process of classifying the TM imagery to create the vegetation map introduced a similar amount of error, estimated at ±30 m. Although these errors are relatively small, they did cause some nests that were on the edges of meadows or conifer stands to be mapped incorrectly on the prediction maps.

We assessed the accuracy of the maps by classifying the nests as correctly or incorrectly predicted based on their placement on the prediction maps. Those nests in aspen that had been predicted to have nests were classified as being correct; all others were classified as incorrect. For our separate assessment of the accuracy of the models, nests that appeared to be in meadows or conifers on the prediction maps were assigned a predicted absence or presence from the model regardless the vegetation type on the map.

Finally, to determine whether the four models were improvements over coarse scale WHR-type models, we compared the area of aspen that the models predicted as nesting habitat to the total area of aspen at each site (the area that would have been classified as suitable habitat by a model based solely on the species' associations with aspen forests). For a model to be an improvement over such a null model, it would have to accurately predict a large portion of the nests and predict them in an area of aspen substantially less than that predicted by the null model.

Table 2. Sample sizes and correct classification rates of four classification tree models built for four species of cavity-nesting birds.

Species	Nests	Non-nest Points	% Nests Correct	% Non-nest Points Correct
Red-naped sapsucker	46	138	93	93
Tree swallow	36	163	100	100
Mountain chickadee	44	204	98	95
Northern flicker	17	185	94	86

Results

The models

We found a total of 143 nests at the 11 field sites in 1996 and 1997. Sample sizes for each of the species ranged from 17 for northern flickers, to 46 for red-naped sapsuckers (Table 2). Given the distribution of nests, the number of non-nest points varied for each of the four species. For example, the model for the red-naped sapsucker was built using 138 non-nest points because the nests of this species were numerous and spread relatively evenly throughout the 11 field sites, limiting the area of aspen that could be sampled as non-nesting area. The model for the tree swallow, on the other hand, was built using 204 non-nest points because nests of these birds were less evenly dispersed allowing more non-nest points to be collected.

Models built using the 16 different size sample plots varied in their ability to fit the data. The four models selected (one for each species) corresponded to those built with a 20.3-ha plot for the red-naped sapsucker, 56.3-ha plot for the northern flicker, 65.6-ha plot for the tree swallow, and a 75.7-ha plot for the mountain chickadee. The percent of nests correctly classified by each of the four models ranged from 93% (43/46) for the red-naped sapsucker to 100% (36/36) for the tree swallow (Table 2). The percentage of non-nest points correctly classified ranged from 86% (180/210) for the northern flicker, to approximately 100% (203/204) for the tree swallow.

The four models included a number of variables pertaining to the amount and configuration of aspen, willow, and open area (Figure 2). Both the northern flicker and the tree swallow model were relatively simple. The northern flicker model used only three variables to predict nest presence (Figure 2a). This model predicted nests in plots in which the largest patch of open area (meadow area + willow area) was
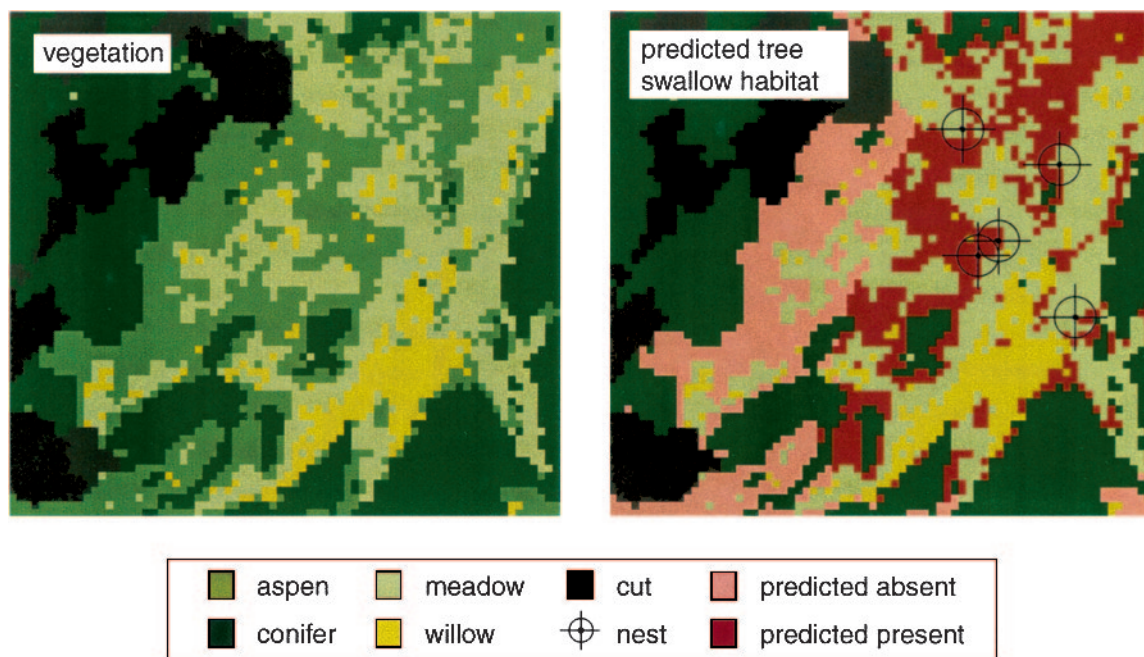
Figure 3. Representative maps of vegetation and the predictions of a nesting-habitat model for the tree swallow at one study site in the Uinta Mountains, Utah. Pink and red areas on the prediction map represent aspen forest predicted as non-nesting and nesting habitat, respectively. Tree swallow nests located at the site were plotted on the map to test the predictive capability of the model.

> 11.6 ha, and in plots in which the largest patch of open area was < 11.6 ha, the largest patch of willow was > 1.7 ha, and there was < 4.4 ha of willow. The tree swallow model also used only three variables (Figure 2b). It predicted nest presences in plots in which there was > 21.8 ha of open area, and in plots in which there was < 21.8 ha of open area with the largest patch of willow being > 1.3 ha and the largest patch of open > 8.8 ha.

Both the red-naped sapsucker model (Figure 2c) and the chickadee model (Figure 2d) were relatively complex. The red-naped sapsucker model generally predicted nests for plots with > 4.2 ha of open area. The model had three exceptions to this general association that can be found by following the branches of the tree diagram in Figure 1c to the black terminal nodes. For example, plots with > 4.2 ha of open area, < 7 patches of aspen, a largest patch of aspen that was < 8.6 ha, and < 0.9 ha of willow tended not to have nests. In the chickadee model, most nest plots were differentiated from non-nest plots by having smaller areas of aspen forest. In addition, nests were predicted in areas with more patchy distributions of aspen forest and open spaces.

Prediction maps

We produced 20 prediction maps (one for each of the four species at each of the five sites, e.g., Figure 3). The spatial configuration of aspen that was predicted as suitable habitat was different across the four species. The red-naped sapsucker maps indicated that nesting habitat was often spread throughout the sites, but tended to be closer to meadow edges and not deep in the interior of aspen stands or in aspen stands surrounded by conifers. The tree swallow and northern flicker maps were quite similar to each other. Both of these sets of maps depicted nesting habitat that was more closely associated with meadow edges and riparian areas than did the red-naped sapsucker maps. The mountain chickadee maps generally showed rather patchy distributions of predicted nesting habitat that was not necessarily associated with aspen-meadow edges.

Testing predictions

We found 103 nests of the four species at the five sites used to test the models (Table 3). Two of the sites had relatively few nests (8,9) and two of the sites had more nests (43,33). All four species were found at all

Table 3. Accuracy assessments from the field testing of four predictive landscape-pattern models for four species of cavity-nesting birds. The number of nests found at five test sites as well as the percentage of those nests correctly predicted, both on prediction maps and as direct output from predictive models are presented. The difference in the map accuracy and the model accuracy largely represents spatial error inherent in the underlying vegetation map.

Species	Nests	Prediction map % Correctly predicted	Model output % Correctly predicted
Red-naped sapsucker	46	70	80
Tree swallow	16	38	75
Mountain chickadee	34	35	50
Northern flicker	19	68	84

of the sites except for one site that was devoid of tree swallows.

The models varied in their ability to correctly predict nests at the new sites (Table 3). The northern flicker model was the most accurate (84% of nests correctly classified). The red-naped sapsucker and tree swallow models were also relatively accurate (80%, and 75% of the nests correctly classified, respectively). The mountain chickadee model was far less accurate, correctly predicting only 50% of the nests at the test sites. There was a large difference in the accuracy of the map predictions and the model prediction for the tree swallows (Table 3). This discrepancy resulted from the fact that most tree swallows nested on meadow-aspen edges and thus nest locations were highly susceptible to slight spatial errors in the vegetation map.

Comparisons to a null model

All four models predicted smaller areas of suitable habitat than would be predicted by a null model that classified all aspen as suitable habitat (Figure 4). The prediction maps for the red-naped sapsucker delineated the largest areas of aspen as nesting habitat. These maps predicted that between 39% and 78% of the aspen at each of the sites was suitable nesting habitat. Maps for the other three species predicted more modest amounts of suitable habitat. The tree swallow maps, for example, predicted between 23% and 54% of the aspen forest at the different sites to be suitable habitat.

Discussion

Although predictive habitat models have the potential to be useful tools for management and conservation, it is crucial that they are tested in the field before they are used. Although all four of our models fit the data on which they were built quite well, only three proved to be accurate when tested in the field. The model we built for the mountain chickadee correctly classified 98% of the nests used to build the model, but only 50% of the nests at the new sites used for field-testing. Whereas the models for the other three species generally reflected their known biology, the associations highlighted in the mountain chickadee model did not correspond with those we had predicted. Both the red-naped sapsucker and the tree swallow models were based on positive associations with open areas and, to a lesser degree, with willows. These relationships are consistent with the feeding behavior of both species. The northern flicker model also predicted an association with open areas, as might be expected for an edge-nesting species.

Although predictive models based on landscape patterns may prove to be a promising technique in light of their ease of use and relative accuracy, like all models they have distinct shortcomings. The ability to build such models depends on having access to remotely sensed data. Fortunately, remotely sensed data are not only becoming more diverse but they are also becoming more widely available. In addition, because the field of landscape ecology is relatively young, associations between given species and landscape patterns are not as prevalent in the literature (Karl et al. 1999) as are associations with the composition and structure of vegetation at relatively fine spatial scales (e.g., Cody (1985)). Thus many of the basic habitat associations related to landscape patterns will need to be determined in the field for the first time.

Selecting the scales at which to measure landscape patterns is difficult when modeling several different species. Different species are likely to respond to their environment at different spatial scales (Wiens 1989). Both species movements and use of habitat features
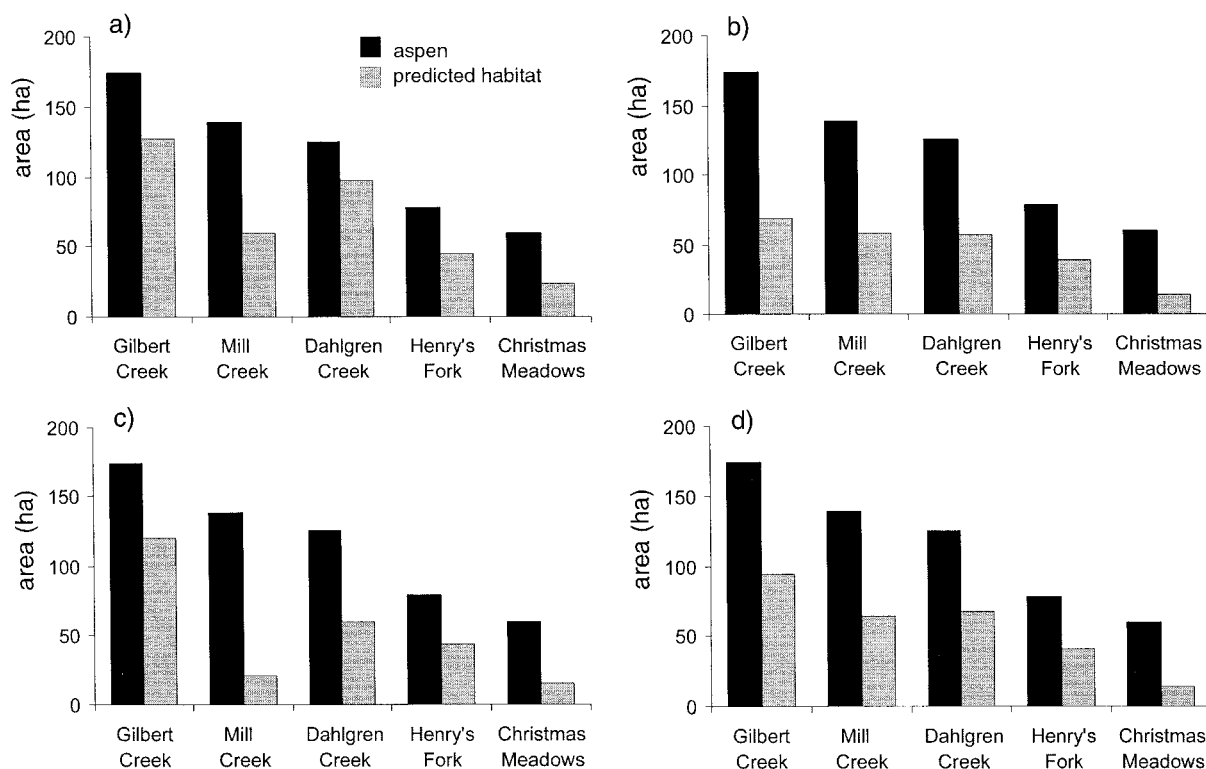
Figure 4. Area of aspen (the predictions of a null model) and area of aspen which has been predicted as nesting habitat by classification tree models for four species of cavity nesting birds at five field sites; a) red-naped sucker, b) northern flicker, c) mountain chickadee, d) tree swallow.

may be scale-dependent processes that are related in part to body size (With 1994). The body sizes of the four species for which we built models range from roughly 10 g for the mountain chickadee to 135 g for the flicker (Dunning 1993). Although we examined patterns at a range of spatial scales, it is possible that we did not capture the scales at which all four species respond to landscape patterns. Because they are relatively small birds, and have small home ranges (Laudenslayer and Balda 1976), mountain chickadees are less likely to select habitat at coarse spatial scales. Thus a landscape to a mountain chickadee might be even smaller than that captured by the smallest of the plot sizes (0.8 ha) used in the present study and may be finer grained than could be depicted on a map with 30-m resolution.

There is at least one other factor that potentially contributed to the poor predictive capability of the mountain chickadee model. Although the other three species nest predominantly in aspen trees in the Uinta Mountains, mountain chickadees also nest in conifers. By only sampling a subset of this species' nesting habitat, we may have incorrectly delineated non-

nesting habitat, thus confounding the non-nest point samples with some nesting habitat and making it more difficult for models to discern between nest and non-nest points. In addition, because mountain chickadees use conifers for foraging and nesting, one might suspect that the negative associations with aspen in the model may be spurious associations driven by a negative correlation of the area of aspen forest with that of conifer forest. However, although this negative correlation did exist (r = −0.68), an alternative model built without aspen related variables performed no better (44% of nests in the test set correctly classified) than our chickadee model.

Models built solely at coarse spatial scales, using landscape pattern associations, are likely to be less accurate when finer scale associations are strong. Gutzwiller and Anderson (1987) demonstrated that several species of cavity-nesting birds respond to patterns of vegetation at three spatial scales; all finer than those used in the present study. Snag density (Raphael and White 1984), tree density (Flack 1976), nest tree size and condition (Dobkin et al. 1995), and cavity availability (for secondary cavity nesters) (Brawn and

Balda 1988) may all influence nest-site selection decisions. Unless these fine scale attributes are correlated with landscape patterns, models built with only landscape-pattern associations are likely to over-predict bird presence.

Having large enough sample sizes for statistical modeling is often an issue for wildlife managers, particularly with rare or threatened species. Although we selected four species that were relatively common, their numbers ranged from 46 for the red-naped sapsucker to 17 for the northern flicker. The relative accuracy of our models does not appear to have been affected by the ratios of nest to non-nest points used to build the models. In a logistic modeling exercise for three bird species, Fielding and Haworth (1995) investigated the effects of the ratio of presence and absences in the data on the fit of the models to training sets (those data used to build the models) and the test sets (those data reserved for testing the models). They demonstrated that increasing the ratio of presences to absences from 1:1 to roughly 1:15 reduced the fit of the models to the training set presences from between 5% and 15%. The decrease in accuracy of the predictions made on the testing set of presences was less dramatic, ranging from 6% to 3%. Furthermore, they showed that the effect on the correct prediction of training set absences was negligible, but the increase in the correct classification of test set absences could be substantial, increasing from between 7% and 15%.

The ratio of nest to non-nest points in our four models ranged from 1:3 for the red-naped sapsucker to roughly 1:12 for the northern flicker. Based on the findings of Fielding and Haworth (1995) alone, we might have expected to find that the northern flicker model would be the poorest of the four models at predicting nests both at the sites used to build the models and at the test sites. We would also have expected the flicker model to be more accurate at predicting absences at the test sites (i.e., predict nest presences in a smaller area of aspen). Because neither of these expectations were borne out (largely due to our use of a model selection process that incorporated a method for choosing classification thresholds based in part on the distribution of the response variable) we conclude that differences in sample sizes contributed little to the differences in the accuracy of the four models.

Conserving biodiversity often requires decisions to be made in short time frames with limited knowledge and funding. One of the most basic pieces of information that managers often lack is the knowledge of what is where. Coarse scale models such as the habitat models of GAP (Scott et al. 1993) and genetic algorithms for rule-set prediction (GARP) models (e.g., Peterson and Cohoon (1999)) can help to provide estimates of species distributions at coarse spatial scales. Predictive habitat models based on associations with landscape patterns may provide an easily applied method of making more accurate predictions at local scales. The use of new, more flexible modeling techniques such as regression and classification trees (De'ath and Fabricius 2000) may further improve the predictive capability of models as well as the ease of model building and interpretation. Our results indicate that this approach may not work equally well for all species and that like all habitat models, models based on associations with landscape patterns should be empirically tested. We found, however, that when tested and refined, models of this type that rely on landscape patterns may provide a reliable alternative to traditional HSI-type models that require the collection of additional habitat data in the field to make predictions.

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