The Condor 108:59–70
© The Cooper Ornithological Society 2006

CROSS-SCALE CORRELATIONS AND THE DESIGN AND ANALYSIS OF AVIAN HABITAT SELECTION STUDIES

JAMES BATTIN[1,3] AND JOSHUA J. LAWLER[2]

[1]*National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, 2725 Montlake Boulevard E., Seattle, WA 98112*

[2]*Department of Zoology, Oregon State University, c/o U.S. Environmental Protection Agency, 200 SW 35th St., Corvallis, OR 97333*

Abstract. It has long been suggested that birds select habitat hierarchically, progressing from coarser to finer spatial scales. This hypothesis, in conjunction with the realization that many organisms likely respond to environmental patterns at multiple spatial scales, has led to a large number of avian habitat studies that have attempted to quantify habitat associations at multiple scales. Typically, multiscale habitat selection studies involve the assessment of habitat selection separately at two or more scales. Until recently, these studies have ignored the potential for cross-scale correlations: correlations among habitat variables across scales. If environmental patterns are correlated across the scales being analyzed, researchers using traditional analytical methods may reach erroneous conclusions about the presence or strength of habitat associations at a given scale. We discuss the ways in which cross-scale correlations manifest themselves in two types of habitat selection studies: (1) "constrained" designs that assume a hierarchical ordering of habitat selection decisions, and (2) "unconstrained" designs, which do not assume such a selection process. We demonstrate approaches for quantifying and modeling cross-scale correlations, including a simulation model, a variance decomposition technique, and a hierarchical modeling approach based on classification tree analysis. We conclude that cross-scale correlations have the potential to affect data interpretation in all types of habitat selection studies and that, even with careful attention to experimental design and the application of newly developed statistical techniques, it is likely their effects cannot be eliminated.

Key words: classification tree analysis, collinearity, correlation, habitat selection, hierarchy, nest-site selection, variance decomposition.

Correlaciones entre Diferentes Escalas y el Diseño y Análisis de Estudios de Selección de Hábitat por las Aves

Resumen. Se ha sugerido desde hace mucho tiempo que las aves seleccionan el hábitat de modo jerárquico, en sentido progresivo desde escalas espaciales más amplias a más detalladas. Esta hipótesis, en conjunción con el entendimiento de que muchos organismos probablemente responden a los patrones ambientales a múltiples escalas espaciales, ha generado un gran número de estudios del hábitat de las aves que han intentado cuantificar las asociaciones con el hábitat a múltiples escalas. Típicamente, los estudios de selección de hábitat realizados a múltiples escalas incluyen la evaluación de selección de hábitat a dos o más escalas pero de modo separado. Hasta hace poco, estos estudios han ignorado el potencial de las correlaciones entre las diferentes escalas: correlaciones entre variables ambientales a través de las diferentes escalas. Si los patrones ambientales están correlacionados entre las escalas analizadas, los investigadores que usan métodos tradicionales de análisis pueden llegar a conclusiones erróneas sobre la existencia o fuerza de asociaciones con el ambiente a una escala dada. Las correlaciones entre las diferentes escalas se manifiestan en dos tipos de estudios de selección de hábitat: (1) diseños "restringidos" que asumen un orden jerárquico de decisiones de selección de hábitat, y (2) diseños "no restringidos" que no asumen un proceso de selección de este tipo. Demostramos diferentes modos de cuantificar y modelar las correlaciones entre las diferentes escalas, incluyendo un modelo de simulación, una técnica de descomposición de la varianza y un modelo jerárquico basado en análisis de clasificación de árboles. Concluimos que las correlaciones entre diferentes escalas tienen el potencial de afectar la interpretación de los datos en todos los tipos de estudios de selección de hábitat y que, incluso prestando mucho cuidado al diseño experimental y a la aplicación de nuevas técnicas estadísticas, es probable que sus efectos no puedan ser eliminados.

Manuscript received 28 February 2005; accepted 4 November 2005.

[3] E-mail: james.battin@noaa.gov

INTRODUCTION

How birds select breeding habitat remains one of the central questions of avian ecology. Avian habitat selection is generally thought to be a hierarchical process (Hildén 1965, Johnson 1980, Hutto 1985, Jones 2001), with different processes often operating at different scales (Wiens 1989). Scales at which habitat selection may occur range from the entire geographic range of a species to microsites selected for nesting or foraging, and in recent years it has become common to design avian habitat selection studies to look for evidence of habitat selection at multiple scales (Orians and Wittenberger 1991, Sedgwick and Knopf 1992, Huhta et al. 1998, Kershner et al. 2001).

In general, researchers conducting multiscale habitat selection studies analyze associations at each scale separately. While this approach may provide useful insights into habitat selection at different scales, it ignores relationships among scales. In particular, it disregards the potential for what we will refer to as cross-scale correlation: correlations between predictor variables at different scales. Cross-scale correlations have the potential to confound the interpretation of results at all scales (Cushman and McGarigal 2002, Lichstein et al. 2002, Lawler and Edwards 2006) and may lead to spurious conclusions about habitat selection at any scale. Cross-scale correlations are a problem for the same reason that correlations among predictor variables in any correlative analysis are a problem: when two or more predictors are correlated, it is difficult to determine which, if any, is causally linked to the observed pattern.

Here, we address cross-scale correlation in avian habitat selection studies. We discuss the ways in which habitat selection studies are designed and the mechanisms by which cross-scale correlations may affect the interpretation of results. We then examine some statistical approaches to addressing cross-scale correlation. While we focus on studies of nesting habitat selection, the same issues apply to other multiscale habitat studies.

DESIGN OF MULTISCALE HABITAT SELECTION STUDIES

The primary goal of most multiscale habitat selection studies is to assess what aspects of the environment (some combination of vegetation, topography, food resources, or other factors) birds select at different spatial scales. Such studies aim to address the effects of habitat characteristics on bird distributions (O'Connor et al. 1999), the relationship between habitat selection and habitat quality (Esely and Bollinger 2001, Tarvin and Garvin 2002), and avian responses to habitat change (Luck 2002), among other issues. Because it is almost always prohibitively difficult to manipulate the environment at scales necessary to address habitat selection experimentally, most habitat studies rely on observational and correlative approaches. With few exceptions, only at very fine spatial scales have experimental studies addressed habitat selection in birds (Klopfer 1963, Partridge 1974). In correlative studies, habitat preferences are often inferred by demonstrating the disproportionate use of particular habitat features (Block and Brennan 1993, Jones 2001, Manly et al. 2002). To show evidence of habitat selection, researchers compare measurements of habitat variables taken at "use" sites (e.g., a nest tree) with randomly or systematically selected "nonuse" (or "available") sites (e.g., a tree not used for nesting). Comparisons may be carried out across a wide range of spatial scales, from a 1-m diameter circle around an individual nest (Kershner et al. 2001) to selection among different habitat types in a heterogeneous landscape (Luck 2002). The results of such studies vary greatly among species and systems.

The scales of interest in a given study vary with the question being asked, but multiscale studies of nest-site selection by individual species generally fall into one of two categories based on the way in which nonuse sites are selected. We will refer to these as "constrained" and "unconstrained" study designs. Studies with constrained designs assume a hierarchical pattern of habitat selection, with selection at coarser scales constraining that at finer scales. Thus, the locations of nonuse sites at finer spatial scales are constrained by the locations of use sites at coarser spatial scales (Jones 2001). Consider, for example, a study with two scales of analysis: nest site (fine scale) and territory (coarse scale). With a constrained design, comparisons of nest and non-nest sites would

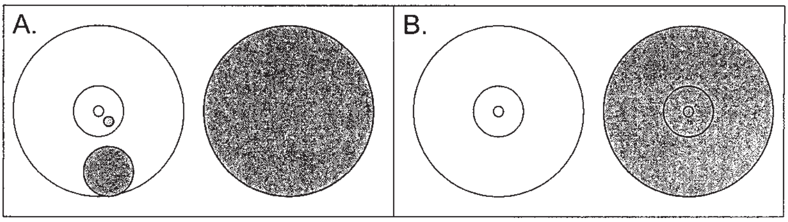

FIGURE 1. Two approaches to the design of multiscale habitat selection studies illustrating habitat survey plots at three scales: nest tree (smallest circle), nest patch (larger circle), and territory (largest circle). White circles represent "use" sample plots, gray circles "nonuse" plots. "Constrained" study designs (A) assume that birds select habitat factors at coarser spatial scales prior to selecting habitat factors at finer scales. In the constrained design, the placement of nonuse sample plots is constrained by the location of coarser-scale use plots. As illustrated in (A), nonuse nest patch plots are randomly placed within use plots at the territory scale, and nonuse nest tree plots are randomly placed within used nest patch plots. "Unconstrained" study designs (B) assume no hierarchical ordering of habitat selection decisions. Use plots are generally concentric and centered on a bird nest, and nonuse plots are concentric and centered on randomly selected points at some minimum distance from use plots.

only be made within the boundaries of each territory, the assumption being that the territory was selected first and thus its boundary constrains the area available for nest-site selection. It is assumed the bird will not search for a nest site outside the chosen territory. In this way, hierarchically structured constraints are explicitly incorporated into the study design (Fig. 1A). In contrast, studies employing what we have labeled an "unconstrained" design assume no constraints on selection at finer scales imposed by factors at coarser scales. In the unconstrained design, nonuse points are generally randomly located on the landscape, and plots for each different scale are centered on that point (Lawler and Edwards 2006). This approach produces a set of nested nonuse plots independent of the nested use plots (Fig. 1B). While we focus here on "use vs. nonuse" designs, the same issues apply to "use vs. available" designs in which use sites are compared to all available habitat. The key difference between "use vs. nonuse" and "use vs. available" designs is that "available" plots are placed randomly or systematically on the landscape and may overlap with use plots, while "nonuse" plots are generally paired with use plots and do not overlap with them.

In habitat selection studies, a cross-scale correlation results any time there is an association between habitat variables at two or more scales. One possible cause of cross-scale correlations is the modifiable areal unit problem (Openshaw 1984, Jelinski and Wu 1996). In cases where a scale of analysis does not represent a discrete biological unit, the results of the analysis may be an artificial byproduct of the size of the sample unit (Jelinski and Wu 1996). Although cross-scale correlations may result from the modifiable areal unit problem, it is not the only cause of cross-scale correlations. Because cross-scale correlations have not been explicitly investigated in most multiscale habitat selection studies, it is unclear how common or strong they tend to be. What little evidence exists, however, suggests that cross-scale correlations are common and, in some cases, quite strong. Every study of avian habitat associations that we are aware of that has looked for evidence of cross-scale correlations in predictor variables, whether based on count data (Cushman and McGarigal 2002, Lichstein et al. 2002) or nest locations (Battin 2003, Lawler and Edwards 2006), has found evidence of strong cross-scale correlations.

CAUSES AND CONSEQUENCES OF CROSS-SCALE CORRELATION

Cross-scale correlation in predictor variables generally results from spatial autocorrelation of predictors. For instance, if large trees tend to occur in older stands, and older stands occur patchily on the landscape, the distribution of large trees will be spatially autocorrelated, and there will be a cross-scale correlation between the fine-scale variable "large trees" and the coarse-scale variable "stand age." Likewise, if a tree species grows in monotypic stands, the fine-scale variable "tree species" will be associated with the coarse-scale variable "stand composition." In nature, complex patterns of spatial autocorrelation and the association of multiple habitat variables at different scales can create complicated patterns of cross-scale correlation in predictors.

The behavioral response of birds to a patchy landscape adds another layer of complexity to any analysis of nest-site selection. The ways in which birds use information from different scales when selecting habitats is poorly understood, but in the types of multiscale habitat selection studies described above, the scale of the unit being selected and the habitat variable(s) driving that selection decision are usually assumed to be the same. For example, it is assumed that species select territory locations based on large-scale variables such as overall vegetation composition at the scale of the territory. A territory selection decision (selection at the "territory scale"), however, could just as easily be driven by a fine-scale variable such as a high-quality nest site. A bird might search a wide area for a tree with the best nesting cavity and then defend a territory around that tree regardless of the coarser-scale characteristics of the territory, a scenario that is plausible when quality nest sites are rare. The problem faced by an investigator wishing to understand what habitat features are important to birds in selecting nesting habitat is thus threefold. (1) Birds select habitat at multiple scales (e.g., territory vs. nest site). (2) Habitat variables at a variety of scales may affect selection at any given scale. (3) Habitat variables are often correlated within and among scales in complex ways. Our aim in this paper is to address the third item: cross-scale correlations. We illustrate the identification and analysis of cross-scale correlations using two traditionally designed studies, one with a constrained and one with an unconstrained design.

Cross-scale correlations affect studies with constrained and unconstrained designs differently. In constrained designs, because each pair of use and nonuse plots is contained within the use plot of a coarser spatial scale, fine-scale habitat selection may, as a result of cross-scale correlations, produce patterns at coarser scales that would be interpreted as evidence of habitat selection at those scales, but selection at coarser scales cannot cause the appearance of selection at finer scales. To understand this phenomenon, consider a bird inhabiting a simplified landscape in which its preferred nest tree is patchily distributed across the landscape. The bird's only criterion for choosing a nest tree is that it be of the preferred species, so it selects its nest site based solely on the species of tree. Because the tree is patchily distributed, however, investigators looking for evidence of selection at the nest patch scale—the area immediately surrounding the nest tree—would likely find that nest patches contained a disproportionate amount of the preferred tree and any other variables correlated with the presence of that tree species. Taking the traditional analytical approach of analyzing each scale separately would lead to a spurious conclusion that the bird was selecting habitat at the nest patch scale based on the species of trees within close proximity of the nest. Attempts to generalize these findings to other landscapes where patterns of tree species aggregation differed would likely fail. The converse, however, would not occur. If the bird chose to place its nest in an area with a high density of the preferred tree species without regard to the species of tree in which the nest was placed (i.e., selection for patch characteristics but no selection for nest tree species), a constrained study design would accurately reflect evidence of selection at the patch scale but not at the tree scale because tree-scale selection is measured within the nest patch. In contrast, in an unconstrained design, cross-scale correlations can cause coarse-scale habitat selection to be confused with fine-scale habitat selection and vice versa.

IDENTIFYING CROSS-SCALE CORRELATIONS: CORRELATIONS AND SIMULATIONS

To illustrate the identification and analysis of cross-correlations using correlation analyses and simulations, we use an example from Battin (2003), who studied habitat selection by the Plumbeous Vireo (*Vireo plumbeus*) in ponderosa pine (*Pinus ponderosa*) forests in northern Arizona. Four spatial scales were examined. (1) At the treatment scale, the propensity of birds to nest in areas that had undergone a forest restoration treatment versus those areas that had not was investigated. (2) At the territory scale, habitat variables measured at vegetation survey points falling within a 4-ha circular plot (the approximate size of a Plumbeous Vireo territory at the study site) centered on the nest

TABLE 1. Cross-scale correlation coefficients for all pairs of habitat variables measured at use sites at the territory and nest patch scales for Plumbeous Vireo nests at the Mount Trumbull Resource Conservation Area, Arizona in 2000. A positive correlation indicates that nest patches with, for example, high oak basal area, tended to be found in territories with high levels of oak basal area. Likewise, a negative correlation indicates that, for example, nest patches with low shrub cover tended to be found in territories with high ponderosa pine basal area.

	Territory scale				
	Ponderosa pine basal area	Gambel oak basal area	Total basal area (all trees)	% canopy cover	% shrub cover
Nest patch scale					
Ponderosa pine basal area	0.51	−0.08	−0.04	0.02	0.11
Gambel oak basal area	−0.16	0.56	0.54	−0.01	0.14
Total basal area	−0.06	0.51	0.60	−0.02	0.22
% canopy cover	−0.41	0.54	0.42	−0.11	0.54
% shrub cover	−0.39	−0.05	−0.12	−0.51	−0.09

tree were compared to variables measured at survey plots outside territory boundaries. (3) At the scale of the nest patch, defined as a 0.04-ha circular plot centered on the nest tree, habitat variables at each nest patch were compared to those in a similar-sized plot centered on a tree 35 m away in a random direction—still within the boundaries of the territory but far enough away that the plots would not overlap. (4) At the nest tree scale, the nest tree (species and size) was compared to the other trees within the nest patch. Using a constrained design and analyzing each scale independently, evidence of selection for Gambel oak (*Quercus gambeli*) was found at the three finest scales, and evidence of selection for restored forest areas was found at the treatment scale. To assess the potential for cross-scale correlations, a set of simple correlation matrices for the sets of variables measured at each pair of spatial scales in the study was created (Table 1). Correlations between pairs of habitat variables at different scales were found across all four scales of investigation (Battin 2003), suggesting that conclusions about selection at coarser spatial scales must be viewed with caution.

Although correlations among individual variables provide a basis for assessing the degree to which measured factors are correlated across scales, they do not necessarily provide an adequate assessment of whether apparent habitat associations observed at a given scale are the result of cross-scale correlations or of actual selection at that scale (Lawler and Edwards 2006). Birds are likely to respond to combinations of physical factors at a given spatial scale. These multivariate associations can be correlated to a degree not reflected in the strength of the component bivariate correlations. In cases such as the vireo example described above, where a particular spatially aggregated variable (e.g., Gambel oak) seems to be important at all scales, a simulation modeling approach may be applied to assess whether habitat selection at finer scales could explain apparent patterns of habitat selection at coarser scales. Of particular interest in the Plumbeous Vireo study was the question of whether apparent selection at the treatment scale for restored forest patches might be explained by finer-scale habitat variables not affected by the restoration treatment.

Field data showed that Plumbeous Vireo density was significantly higher in treated than in untreated patches (the coarsest scale of analysis), suggesting birds responded positively to the treatment. However, the areas that had been treated contained higher densities of Gambel oak than those that had not both prior to and following the treatment, i.e., their higher oak densities were not a result of the treatment. Plumbeous Vireos showed evidence of selection for Gambel oak at the nest tree, nest patch, and territory scales, presenting the possibility that the pattern of bird distribution between treated and untreated areas was simply the result of birds selecting habitat at the nest patch or territory scale. Battin (2003) developed a simulation model of a landscape containing patches of treated and untreated habitat in which oaks were distributed between treated and untreated patches in the same proportion as in the study area. He then simulated birds moving through the landscape, searching for a nest patch, settling in nest patches that met patch selection criteria, and establishing territories around the selected nest patches. He simulated two different scenarios: one in which birds preferentially nested in treated areas and one in which birds selected nest patches that contained more than a specified threshold quantity of Gambel oak trees. The simulations based on selection for oak fit the data on the between-habitat distribution of nesting pairs much better than did the simulations based on selection for treated forest, suggesting the apparent selection for the treated area resulted from a cross-scale correlation between the density of oak and the restoration treatment. A similar approach could be taken to assess the effects of cross-scale correlations in spatially aggregated resources at other scales. For instance, if the pattern of spatial aggregation of oaks at finer scales were known, one could simulate selection for oak at the nest-patch scale and assess whether this could explain apparent selection at the territory scale.

A simulation-based approach can elucidate specific cross-scale correlations that are of particular interest to a study, but it can do little to address complex patterns of cross-scale correlations. Other analytical techniques, such as those described below, may provide more information. These techniques can be applied to both unconstrained and constrained designs as long as the number of sample plots (both use and nonuse) is equal for all scales; we illustrate these methods using as an example a study with an unconstrained design.

MEASURING THE STRENGTH OF CROSS-SCALE CORRELATIONS

We use a study of habitat selection in Red-naped Sapsuckers (*Sphyrapicus nuchalis*) to demonstrate several approaches to identifying and modeling cross-scale correlations in multiscale habitat studies with unconstrained designs. This study was part of a project investigating multiscale habitat associations of a community of cavity-nesting birds (Lawler 1999, Lawler and Edwards 2002). The study took place on the north slope of the Uinta Mountains in northeastern Utah. We searched for Red-naped Sapsucker nests in aspen (*Populus tremuloides*) forests in 16 drainages across an area of roughly 3000 km^2. At each nest, we measured habitat variables at three spatial scales. At the coarsest scale (the home range scale), we measured aspects of landscape composition and pattern using a digital vegetation map in a geographic information system. The 11-ha digital sample plots used to measure home-range scale factors were centered on each nest tree. At the intermediate scale (the local scale), we used 0.04-ha plots centered on each nest tree to measure aspects of the structure and composition of vegetation surrounding the nest. The finest spatial scale (the tree scale) consisted of the nest tree itself. At this scale we measured aspects of tree size, structure, and condition. In addition, we measured all variables at the three scales at 105 randomly selected nonuse points. Points were selected so that nonuse plots did not overlap any use plots at any scale. Each home range and local scale nonuse plot was centered on a randomly selected focal tree that was the object of the tree scale assessment. See Lawler and Edwards (2006) for a complete description.

As in studies using a constrained design, simple correlation matrices can be used as a first step in identifying cross-scale correlations. We calculated matrices for the three combinations of the three scales investigated in the Red-naped Sapsucker study. Variables were either transformed to meet the assumption of normality for Pearson correlations, or Spearman rank correlation coefficients were calculated. We used point biserial tests for identifying associations between binary variables and continuous variables.

The absolute values of the correlation coefficients ranged from 0.00 to 0.56. The strongest correlations were found between variables at the home range and the tree scales (Table 2) and between the local and tree scales. On average, however, the strengths of the correlations across the three pairs of scales were similar (0.15, 0.15, 0.16 for tree-local, local-home range, and home range-tree comparisons, respectively). Not surprisingly, the strongest bivariate cross-scale correlation was between focal tree height and canopy height. Other relatively strong correlations included those between the presence of fungal conks on the focal tree and (1) the number of fallen snags in the local plot (0.43), (2) the area of meadow in the home-range scale plot (0.47), and (3) the area of willow in the home-range scale plot (0.41), as well as between the degree of rot in the focal tree and both the area of aspen

TABLE 2. Correlation coefficients for all pairs of variables at two spatial scales at a set of randomly sampled (i.e., nonuse) points. At the home range scale, all variables were measured in a GIS using an 11-ha sample plot. Richness refers to the number of land-cover types in the plot. Aspen, meadow, willow, and cut refer to the area in the home range of aspen woodland, sagebrush meadow, willows, and clearcuts, respectively. Edge is the amount of aspen-meadow edge in the plot and distance to edge is the distance from the center of the plot to the nearest aspen-meadow edge. All variables measured at the tree scale pertain to a single focal tree at the center of the 11-ha sample plot. The variables at this scale included the number of branches less than two meters from the ground, tree height, tree diameter at breast height (dbh), whether the tree was a snag, number of trees within 2 m of the focal tree, a measure of heart rot, and whether or not the tree had fungal conks.

	Tree scale						
	Branches	Tree height	Tree dbh	Snag	Trees within 2 m	Rot	Conks
Home range scale							
Richness	0.08	−0.07	0.28	0.00	−0.17	0.21	0.23
Aspen	−0.04	0.20	−0.17	−0.09	0.08	−0.41	−0.32
Edge	0.02	−0.13	0.26	0.06	−0.16	0.21	0.30
Meadow	0.05	−0.16	0.37	0.04	−0.16	0.41	0.47
Willow	−0.05	−0.18	0.30	0.02	−0.08	0.28	0.41
Cut	−0.13	0.13	−0.08	−0.08	−0.21	−0.14	−0.13
Distance to edge	−0.17	−0.19	−0.35	−0.07	0.06	−0.36	−0.33

(−0.41) and the area of meadow (0.41) in the home range plot. Because we are primarily concerned with cross-scale correlations, we did not investigate correlations among variables measured at the same scale, but a number of these (e.g., focal tree height and focal tree diameter at breast height [dbh]) are likely to be quite strong.

As discussed above, correlations among individual variables do not necessarily provide an adequate assessment of whether habitat associations are correlated across scales. To investigate these associations it is necessary to model habitat relationships at the different spatial scales. It is then possible, using a statistical technique known as variance decomposition (Whittaker 1984), to quantify the degree to which habitat associations are correlated across spatial scales.

Lawler and Edwards (2006) applied a variance decomposition analysis to the Red-naped Sapsucker data set. They used a set of seven logistic regression models that incorporated the presence or absence of sapsucker nests as the dependent variable and different combinations of habitat variables measured at the three spatial scales as the independent variables. In contrast to the relatively weak bivariate correlations in this data set, the shared components of variation that could not be attributed to any one spatial scale were relatively large (Fig. 2). Taken together, the shared components accounted for 43% of the total variance or 47% of the explained variance. Thus, almost half of the explained variance could not be attributed to factors at any one spatial scale.

The relative sizes of the pure and shared components of variation indicate the degree to which models built at individual spatial scales or the coefficients of a model built with variables at all spatial scales accurately represent the relationship with presence or abundance. When the shared components comprise a small proportion of the total variance explained, cross-scale correlations in habitat associations are weak and habitat relationships at separate scales can be interpreted with confidence. In contrast, when shared components represent a large proportion of explained variation, it is difficult to model multiscale habitat relationships accurately without prior knowledge of the relative importance of factors at different spatial scales. In the following section we present some statistical approaches that can be applied when cross-scale correlations are strong.

MODELING CROSS-SCALE CORRELATIONS

In addition to variance decomposition, several techniques originally developed to address multicollinearity at a single spatial scale can be adapted to the analysis of cross-scale correlations (Legendre and Legendre 1998,

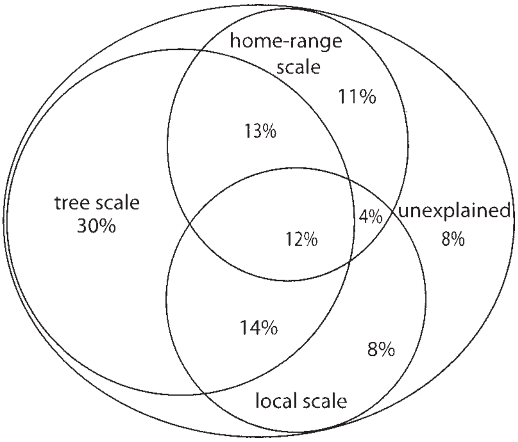

FIGURE 2. The percentages of variation in Red-naped Sapsucker nest locations associated with variables at three spatial scales. The largest (outer) oval represents all of the variation in nest-site locations. The three smaller ovals represent the variation associated with each of the three scales. Variation that is associated purely with factors at one spatial scale is represented by the portions of the smaller ovals that do not overlap. The overlapping portions of these ovals represent variation in nest-site locations that is simultaneously explained ("shared") by factors at more than one scale. Seven variables were measured at each spatial scale. Tree scale variables included tree height, tree dbh, and degree of heart rot; local-scale variables included number of trees, number of snags, and canopy height within 11 m of the focal tree; and home-range scale variables included area of aspen woodland, area of sagebrush meadow, and distance to the aspen-meadow edge.

Graham 2003, Lawler and Edwards 2006), including hierarchical or sequential models. Applying hierarchical models to multiscale analyses requires *a priori* knowledge of the relative importance of factors at different spatial scales. In essence, the approach assigns the various shared components of variation to a given spatial scale based on the predetermined order of parsimony. There are at least two methods of applying a hierarchical modeling approach, both of which begin with the building of one statistical model using only the explanatory variables from the spatial scale thought to be the most influential. The two techniques differ in the way the variables from additional scales are subsequently modeled. Using the first technique, each variable measured at the spatial scale deemed to be the second-most influential is regressed on the suite of explanatory variables already in the model. The residuals from these regressions then become the next set of explanatory variables to be added to the model in a stepwise manner (Graham 1997). This partial-regression procedure is repeated at all remaining spatial scales, adding additional explanatory power from variables at each scale. The second approach is similar, but differs in the way in which residuals are modeled. Instead of adding to the original model, this technique involves building multiple models, one for each additional spatial scale. The residuals from the original model are used as the response variable for a second model, and the variables from the scale thought to be second most important are then used as the independent variables in this new model. Subsequent models are produced in a similar way using the residuals from the previous model as the response variables.

We use the Red-naped Sapsucker dataset to demonstrate a variation of the second of these two hierarchical modeling approaches. Because the response variable in the dataset was the presence or absence of a bird nest, we employed a technique that allowed us to model a binary response. A more flexible technique than logistic regression was needed for the sequential, hierarchical approach. Using logistic regression for the initial model would require us to use linear regression models on all the resulting sets of residuals. Because we were unable to transform the residuals to meet the assumption of normality for a linear regression, we used classification tree analysis for the hierarchical modeling process. Classification trees and regression trees—their counterpart for modeling continuous response variables—are flexible and powerful analytical techniques for exploring complex ecological relationships (De'ath and Fabricius 2000). Classification tree analysis is a nonparametric analytical technique in which a categorical response variable is modeled with any number and combination of continuous and categorical explanatory variables. Classification trees work through a recursive binary partitioning of the dataset into progressively smaller subsets that are increasingly homogeneous with respect to the response variable (Breiman et al. 1984). The resulting model is an inverted tree-like structure with one node at the top and a proliferation of branches and nodes below it (Fig. 3). Each binary split of the data is made using the point along

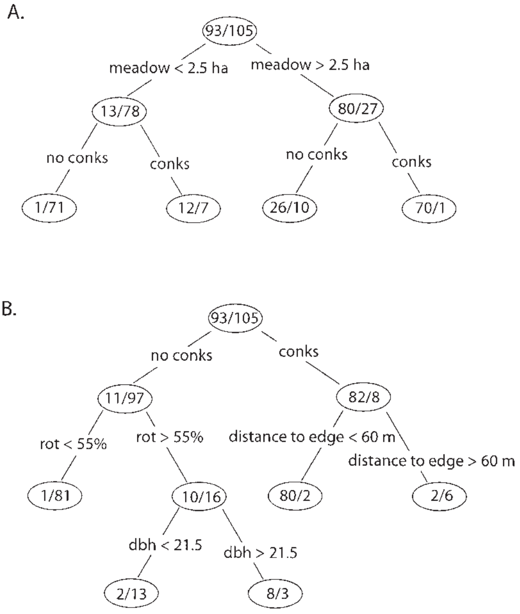

FIGURE 3. Regression tree models explaining habitat associations of Red-naped Sapsuckers. The ovals are nodes of the tree representing groups of data. The numbers inside the ovals (nodes) represent the number of nest points (first number) and nonnest points (second number) in the node. The variables and thresholds used to split the internal nodes are given along the branches descending from the nodes. The models were built with two different assumptions: (A) that birds select habitat hierarchically progressing from coarser spatial scales to finer spatial scales and (B) that birds are constrained by finer-scale habitat factors. The variables included in the models were: area of meadow within a home range ("meadow"), the presence of fungal conks on the focal tree ("conks"), the diameter at breast height (dbh) and percentage of heart rot ("rot") in the focal tree, and the distance from the tree to the aspen-meadow edge.

a particular variable's distribution that best divides the data. Splitting stops when predetermined criteria are met. This process often results in an overfitted model. There are several methods for reducing or "pruning" trees to better fit the data. We used a "one standard error" cross-validation approach to prune our tree models (De'ath and Fabricius 2000), taking the mode of the tree sizes suggested by 100 such cross-validations. Although classification tree analyses address the issue of cross-scale correlations using a hierarchical sequential modeling approach, they address correlations between variables measured at the same spatial scale in a different way. Because tree models only allow one variable to enter a model at a given split, there are no variables in the model that account for the same variation in nest presence. However, it is possible that an alternative variable could perform a given split almost as well as the chosen variable. Thus, alternative, correlated variables have in essence been ignored in the modeling process at individual splits.

Instead of calculating residuals in the usual sense of the word (i.e., the difference between predicted and observed values), we used the terminal nodes of the initial tree model as new datasets with which to model relationships at the subsequent spatial scale. The terminal nodes are the smallest subsets of data the model creates. Because these new data sets have had the variance measured at the initial spatial scale removed, the variation in the response variable within these data sets (but not among them) is residual variance. One advantage to using classification tree analysis in this way is that the final models can be represented as a single tree with the models built at subsequent spatial scales emerging from the terminal nodes of models built at the previous scale.

To perform the hierarchical analysis, it was necessary to prioritize the three spatial scales with respect to their suspected influence on nest-site selection. We prioritized the scales to explore two alternative hypotheses. First, we prioritized the scales from the coarsest to the finest to explore the hypothesis that birds respond to habitat characteristics in this order. Thus, we used the home-range scale variables to build the initial model and then built models for each of the terminal nodes of the initial model using the local-scale variables. Finally, we used the terminal nodes created by the local-scale models to build models using the tree-scale variables. In this analysis, we assumed that any shared component of variation that included home-range scale factors could actually be attributed to home-range scale factors and that any shared component of variation that involved both local- and tree-scale factors could be attributed to local-scale factors. For our second prioritization, we ordered the scales from the finest to the coarsest to explore the hypothesis that the selection process was driven largely by tree-scale constraints. Cavity-nesters are often highly specialized with respect to nesting substrate (e.g., species, size, and condition of nest tree; Gutzwiller and Anderson 1987, Li and Martin 1991, Dobkin et al. 1995). Red-naped Sapsuckers in particular are known to nest preferentially in trees with fungal infections and some degree of heart rot (Daily 1993), presumably because healthy trees are too difficult or time-consuming to excavate. The modeling process prioritizing fine-scale variables directly reversed the steps of the process prioritizing coarse-scale variables and assumed that shared components of variation are attributable to the finer of each pair of scales.

The models produced by the two different prioritizations were quite different (Fig. 3). When we assumed that habitat decisions progressed from coarser to finer spatial scales, the hierarchically structured model accounted for 80% of the deviance in the data. Home-range scale factors (specifically the area of meadow in the home-range scale plot) accounted for 57% of the deviance, and tree-scale factors (specifically the presence of fungal conks) accounted for 23% of the deviance in the data. None of the local-scale variables entered the model. Almost all nests were in home-range scale plots with >2.5 ha of meadow and in trees with fungal conks.

When we prioritized the three spatial scales from fine to coarse scales—assuming that tree size and condition were strong constraints on the nest-site selection process—the resulting hierarchical model explained 89% of the deviance in the data. In contrast to the coarse-to-fine model, the fine-to-coarse model relied heavily on tree-scale variables. Tree-scale associations accounted for 85% of the deviance and were based on the presence of fungal conks, the degree of heart rot, and tree dbh. Again, local-scale factors were not incorporated into the model. Home-range scale factors (specifically distance to aspen-meadow edge) accounted for only 4% of the deviance in the data. In the fine-to-coarse scale model, most nests were in trees with fungal conks and were closer to aspen-meadow edges. Nests that were in trees without fungal conks tended to be in larger trees with more heart rot. The striking differences between the two hierarchically structured models highlights the importance of the initial prioritization of spatial scales.

Because of the differences in the modeling techniques we used to decompose the variance in the Red-naped Sapsucker dataset (logistic regression) and to hierarchically model nest-site habitat associations (classification trees), the pure and shared components of variation identified in the decomposition analysis and the proportion of the deviance explained by the various spatial scales in the classification tree analyses are not directly comparable. The difference, in part, highlights one of the drawbacks to using classification or regression tree models for this type of hierarchical analysis. Because the data are divided into progressively smaller subsets throughout the modeling process, the ability to model associations with variables from spatial scales given lower priority can be substantially diminished. For this reason, relatively large datasets are necessary when using tree-based models in general, and particularly for the type of hierarchical modeling demonstrated here.

CROSS-SCALE CORRELATIONS AND STUDY DESIGN

To understand the relative contribution of factors at different spatial scales to the habitat selection process, it is crucial that we understand to what degree cross-scale correlations influence multiscale habitat analyses, and that we use appropriate modeling techniques to identify the unique associations at different spatial scales. Investigators are generally careful to address within-scale correlations among predictor variables. Equal care should be taken to address correlations among predictor variables at different scales.

The scales and habitat features driving habitat selection are likely to vary considerably among species, and some species may select for a combination of variables at multiple scales (Kristan 2006). Different study designs may therefore be appropriate for different species, depending upon what is known or suspected about how they select habitats. It has been argued that constrained study designs are more appropriate because they more accurately mirror the process by which habitat selection occurs (Jones 2001), but it is almost certainly not always appropriate to assume that birds are making "top-down" hierarchically structured decisions (Kristan 2006). Indeed, rather than assuming we know at what scale a given habitat variable is selected, we may want to ask the question: at what scale (if any) is that variable selected?

The statistical methods we illustrated for assessing cross-scale correlations may provide a clearer picture of habitat selection. However, when a large proportion of variance is shared among scales, these methods can only serve to quantify the degree to which cross-scale correlations affect the results. When cross-scale correlations are strong, it is difficult, based on these analyses, to draw any reliable inferences about which scale is most important for nesting habitat selection, much less about the question we generally most want to answer with this type of study: which individual habitat features are most important to habitat selection at each scale?

Currently, there is no easy solution for the problem of cross-scale correlations, but it is clear that ignoring them can lead investigators to draw erroneous conclusions about habitat selection. To address cross-scale correlations in multiscale habitat selection studies, we suggest that investigators take the following steps. (1) Plan to quantify cross-scale correlations in all analyses, and design studies to facilitate the application of statistical methods such as variance partitioning for quantifying the strength of cross-scale correlations (Lawler and Edwards 2006). (2) Think carefully about the scale(s) at which each variable of interest might be selected and design studies to capture selection of that variable at the pertinent scales. It may be desirable to incorporate an assessment of the spatial extent over which selection occurs, perhaps by placing a series of nonuse plots at different distances from use plots. While careful *a priori* selection of variables and scales of analysis will not eliminate the problem of cross-scale correlations—indeed, in some cases it may lead to even more complex patterns of cross-scale correlation—it will likely make results more interpretable and robust. (3) Whenever possible, quantify the extent of spatial autocorrelation in response variables. Understanding the spatial pattern underlying observed cross-scale correlations will assist in developing models that capture the habitat-selection process. It may also be possible to apply statistical approaches designed to measure and control for spatial autocorrelation (Legendre et al. 2004).

ACKNOWLEDGMENTS

We would like to thank A. Guerry, S. Jackson, and J. Neyme for their invaluable assistance in the field. We are grateful for discussions and insights provided by P. Beier, J. Bissonette, R. Cutler, R. Dueser, T. Edwards Jr., M. Kearsley, D. Roberts, J. M. Scott, T. Sisk, C. van Riper, J. Van Sickle, D. White, and T. Whitham. W. Kristan, R. O'Connor and two anonymous reviewers provided extremely helpful comments on an earlier draft of this manuscript. Our research was funded by the Canon National Parks Science Scholars Program, the USDA Forest Service Rocky Mountain Research Station, Project CS-1100 of the Strategic Environmental Research and Development Program (SERDP), the U.S. Geological Survey Biological Research Division Cooperative Research Unit at Utah State University, the U.S. Geological Survey Biological Resources Gap Analysis Program, a grant from the U.S. Fish and Wildlife Service, The Ecology Center at Utah State University, and a grant from the Utah Wildlife Society. In addition, part of this work was performed while JJL was supported by The Nature Conservancy Fellows program and JB was supported by a National Research Council post-doctoral fellowship. Order of authorship was determined by a coin toss.

LITERATURE CITED

Battin, J. 2003. Habitats and the animals that love them: avian habitat selection in a post-restoration landscape. Ph.D. dissertation, Northern Arizona University, Flagstaff, AZ.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology. Current Ornithology 11:35–91.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth and Brooks/Cole, Monterey, CA.

Cushman, S. A., and K. McGarigal. 2002. Hierarchical, multiscale decomposition of species-environment relationships. Landscape Ecology 17:637–646.

Daily, G. C. 1993. Heartwood decay and the vertical distribution of Red-naped Sapsucker nest cavities. Wilson Bulletin 105:674–679.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

Dobkin, D. S., A. C. Rich, J. A. Pretare, and W. H. Pyle. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97:694–707.

Esely, J. D., Jr., and E. K. Bollinger. 2001. Habitat selection and reproductive success of Loggerhead Shrikes in northwest Missouri: a hierarchical approach. Wilson Bulletin 113: 290–296.

Graham, M. H. 1997. Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* (Agardh), along the Monterey Peninsula, central California, USA. Journal of Experimental Marine Biology and Ecology 218:127–149.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84: 2809–2815.

GUTZWILLER, K. J., AND S. H. ANDERSON. 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. Condor 89:534–548.

HILDÉN, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53–75.

HUHTA, E., J. JOKIMÄKI, AND P. RAHKO. 1998. Distribution and reproductive success of the Pied Flycatcher *Ficedula hypoleuca* in relation to forest patch size and vegetation characteristics: the effect of scale. Ibis 140:214–222.

HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory, land birds, p. 455–476. *In* M. L. Cody [ED.], Habitat selection in birds. Academic Press, San Diego, CA.

JELINSKI, D. E., AND J. WU. 1996. The modifiable areal unit problem and implications for landscape ecology. Landscape Ecology 11:129–140.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

JONES, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557–562.

KERSHNER, E. L., E. K. BOLLINGER, AND M. N. HELTON. 2001. Nest-site selection and renesting in the Blue-gray Gnatcatcher (*Polioptila caerulea*). American Midland Naturalist 146: 404–413.

KLOPFER, P. H. 1963. Behavioral aspects of habitat selection: the role of early experience. Wilson Bulletin 75:15–22.

KRISTAN, W. B. 2006. Sources and expectations for hierarchical structure in bird-habitat associations. Condor 108:5–12.

LAWLER, J. J. 1999. Modeling habitat attributes of cavity-nesting birds in the Uinta Mountains, Utah: a hierarchical approach. Ph.D. dissertation, Utah State University, Logan, UT.

LAWLER, J. J., AND T. C. EDWARDS JR. 2002. Landscape patterns as habitat predictors: building and testing models for cavity-nesting birds in the Uinta Mountains of Utah, U.S.A. Landscape Ecology 17:233–245.

LAWLER, J. J., AND T. C. EDWARDS JR. 2006. A variance-decomposition approach to investigating multiscale habitat associations. Condor 108:47–58.

LEGENDRE, P., M. R. T. DALE, M.-J. FORTIN, P. CASGRAIN, AND J. GUREVITCH. 2004. Effects of spatial structures on the results of field experiments. Ecology 85:3202–3214.

LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical Ecology. Elsevier, Amsterdam.

LI, P., AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108: 405–418.

LICHSTEIN, J. W., T. R. SIMONS, AND K. E. FRANZREB. 2002. Landscape effects on breeding songbird abundance in managed forests. Ecological Applications 12:836–857.

LUCK, G. W. 2002. The habitat requirements of the Rufous Treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. Biological Conservation 105: 383–394.

MANLY, B. F. J., L. L. MCDONALD, D. L. THOMAS, T. MCDONALD, AND W. P. ERICKSON. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer, Dordrecht, The Netherlands.

O'CONNOR, R. J., R. B. BOONE, M. T. JONES, AND T. B. LAUBER. 1999. Linking continental climate and land use patterns with grassland bird distribution in the conterminous United States. Studies in Avian Biology 19:45–59.

OPENSHAW, S. 1984. The modifiable areal unit problem. Geo Books, Norwich, UK.

ORIANS, G. H., AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29–S49.

PARTRIDGE, L. 1974. Habitat selection in titmice. Nature 247:573–574.

SEDGWICK, J. A., AND F. L. KNOPF. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. Condor 94: 720–733.

TARVIN, K. A., AND M. C. GARVIN. 2002. Habitat and nesting success of Blue Jays (*Cyanocitta cristata*): importance of scale. Auk 119:971–983.

WHITTAKER, J. 1984. Model interpretation from the additive elements of the likelihood function. Applied Statistics 33:52–64.

WIENS, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.