A VARIANCE-DECOMPOSITION APPROACH TO INVESTIGATING MULTISCALE HABITAT ASSOCIATIONS

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Abstract. The recognition of the importance of spatial scale in ecology has led many researchers to take multiscale approaches to studying habitat associations. However, few of the studies that investigate habitat associations at multiple spatial scales have considered the potential effects of cross-scale correlations in measured habitat variables. When cross-scale correlations in such studies are strong, conclusions drawn about the relative strength of habitat associations at different spatial scales may be inaccurate. Here we adapt and demonstrate an analytical technique based on variance decomposition for quantifying the influence of cross-scale correlations on multiscale habitat associations. We used the technique to quantify the variation in nest-site locations of Red-naped Sapsuckers (*Sphyrapicus nuchalis*) and Northern Flickers (*Colaptes auratus*) associated with habitat descriptors at three spatial scales. We demonstrate how the method can be used to identify components of variation that are associated only with factors at a single spatial scale as well as shared components of variation that represent cross-scale correlations. Despite the fact that no explanatory variables in our models were highly correlated ($r < 0.60$), we found that shared components of variation reflecting cross-scale correlations accounted for roughly half of the deviance explained by the models. These results highlight the importance of both conducting habitat analyses at multiple spatial scales and of quantifying the effects of cross-scale correlations in such analyses. Given the limits of conventional analytical techniques, we recommend alternative methods, such as the variance-decomposition technique demonstrated here, for analyzing habitat associations at multiple spatial scales.

Key words: habitat selection, logistic regression, multicollinearity, nest site, scale, statistical analysis, variance decomposition.

Un Método de Descomposición de la Varianza para Investigar las Asociaciones de Hábitat a Escalas Espaciales Múltiples

Resumen. El reconocimiento de la importancia de la escala espacial en la ecología ha llevado a muchos investigadores a tomar enfoques de escalas múltiples para estudiar las asociaciones de hábitat. Sin embargo, pocos de los estudios que han investigado las asociaciones de hábitat a varias escalas espaciales han considerado los efectos potenciales de las correlaciones a través de escalas en las variables de hábitat medidas. Cuando las correlaciones a través de escalas en dichos estudios son fuertes, las conclusiones acerca de la importancia relativa de las asociaciones de hábitat a distintas escalas espaciales podrían ser inexactas. En este estudio adaptamos y demostramos el uso de una técnica analítica basada en la descomposición de la varianza para cuantificar la influencia de las correlaciones sobre las asociaciones de hábitat a través de escalas múltiples. Empleamos esta técnica para cuantificar la variación en la ubicación de sitios de nidificación de *Sphyrapicus nuchalis* y *Colaptes auratus* en asociación con descripciones del hábitat a tres escalas espaciales. Demostramos cómo puede utilizarse el método para identificar los componentes de la variación que están asociados sólo con factores a una escala espacial, además de los componentes compartidos que representan correlaciones entre escalas. A pesar de que las variables de predicción incluidas en nuestros modelos no estuvieron estrechamente correlacionadas ($r < 0.60$), encontramos que los componentes de variación compartidos que reflejan correlaciones entre escalas fueron responsables de cerca de la mitad de la desviación explicada por los modelos. Estos resultados resaltan la importancia de realizar estudios sobre el hábitat a escalas espaciales múltiples y de cuantificar los efectos de las correlaciones a través de escalas en dichos análisis. Dadas las limitaciones de las técnicas analíticas convencionales, recomendamos el uso de métodos alternativos

(como la técnica de descomposición de varianza aquí demostrada) para analizar las asociaciones de hábitat a escalas espaciales múltiples.

INTRODUCTION

Although it has long been hypothesized that animals respond to their environments at multiple spatial scales (Hildén 1965, Hutto 1985), only relatively recently have studies attempted to address the issue of habitat selection as a multiscale process (Gutzwiller and Anderson 1987, Morris 1987, Jorgensen and Demarais 1999). The difficulties associated with manipulating large areas have meant that most studies of habitat selection have been limited to correlative analyses in which the presence or abundance of a species is associated with a set of environmental factors (Verner et al. 1986). These correlative analyses provide important results where manipulative experiments are logistically infeasible, but they have a number of well-known limitations. One of the most basic of these limitations arises from multicollinearity among explanatory variables and has profound implications for many recently conducted multiscale analyses of habitat associations.

The basic method for analyzing habitat associations generally involves measuring the presence or abundance of a species and a suite of environmental characteristics at a set of sample points. A statistical model is then built to identify the relationship between the environmental variables and the presence or abundance of the species in question (James and Shugart 1970). When building such models, the researcher often faces the problem of addressing correlated explanatory variables. Even relatively weak collinearity among explanatory variables has been shown to have profound effects on model parameterization and statistical power, making it difficult to assess the relative contribution of a given explanatory variable (Graham 2003). The most common approach to dealing with such variables is to remove all but one of a group of highly correlated variables from the model (Legendre and Legendre 1998). The selection of the single variable is generally based on its suspected biological significance. This choice, however, is not always entirely clear and may result in meaningful explanatory variables being removed from the model (Graham 2003).

Although the issue of collinearity is no less important for multiscale analyses of habitat associations, it has almost always been ignored in multiscale studies (Cushman and McGarigal 2002, Lichstein et al. 2002). Many of these studies build separate statistical models for each set of environmental variables measured at a different spatial extent (Bergin 1992, Saab 1999). Because ecological systems are inherently hierarchically organized, environmental variables often exhibit cross-scale correlations (Kristan 2006). When these correlations exist within a multiscale habitat study, the habitat relationships identified at different scales are not likely to be independent (Fig. 1). Therefore, the conclusions drawn about the relative strengths of those relationships may be misleading.

Variance decomposition, a statistical approach developed for investigating the effects of multicollinearity, can be applied to the problem of cross-scale correlations. Whittaker (1984) described the analytical technique with which he separated the variation in a single
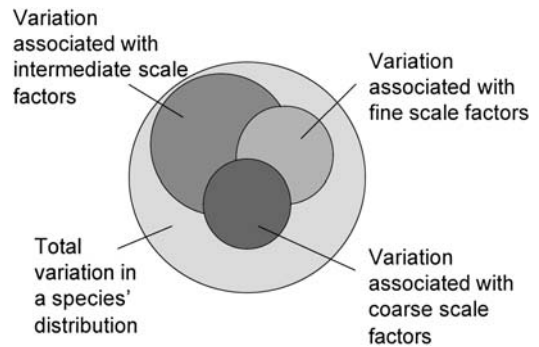

FIGURE 1. Conceptual relationship of three components of variation associated with a species' distribution. The largest (outer) circle represents the total variation in the species distribution. The inner circles represent the variation in the species distribution associated with sets of factors measured at each of three spatial scales. The fact that the three inner circles overlap indicates that some of the variation in the distribution of the species is simultaneously associated with factors at different scales. The area of the outer circle not included in any of the inner circles represents the variation that is not associated with any of the factors measured at the three spatial scales.

response variable into component parts that were explained purely by individual explanatory variables and parts that were explained jointly by groups of explanatory variables. Whittaker (1984) used the term "shared" to describe the variation that was explained jointly by two or more variables. Shared variation can arise in any of four potential situations. The shared effect of explanatory variables A and B, for example, could be 1) the joint effect of both A and B; 2) the effect of A, and B is merely correlated; 3) the effect of B, and A is merely correlated; and 4) some combination of any of these. The relative sizes of the different pure and shared components of variation determine whether conclusions about the relative strengths of different variables can be drawn. Only if the pure components of variation are large relative to the shared components can the influence of the variables be ranked. This method has been adapted to address spatial variation in ecological data (Borcard et al. 1992) and for addressing spatial scale in a community-level analysis (Cushman and McGarigal 2002, 2004).

Here we adapt and demonstrate a variance-decomposition technique for analyzing species-habitat relationships at multiple spatial scales. We used the technique to assess the relative strength of habitat associations for Red-naped Sapsuckers (*Sphyrapicus nuchalis*) and Northern Flickers (*Colaptes auratus*). Both species are common cavity-excavating birds in aspen forests in the western United States and Canada. Nest-site locations of both species have been found to be associated with factors measured at several different spatial scales (Conner and Adkisson 1977, Gutzwiller and Anderson 1987, Sedgwick and Knopf 1990, Dobkin et al. 1995, Lawler and Edwards 2002). We isolated the variation in nest-site locations of these two species associated purely with measured landscape patterns within a home range, purely with measured aspects of the structure and composition of vegetation in the "local" vicinity of the nest, and purely with measured nest-tree characteristics. In addition, we identified the proportion of variation that could not be isolated but that was shared by 1) a combination of measured home range and local factors, 2) a combination of measured home range and tree factors, 3) a combination of measured local and tree factors, and 4)

a combination of factors measured at all three scales.

METHODS

STUDY SITE

The study was conducted on the north slope of the Uinta Mountains in northeastern Utah. We located riparian aspen (*Populus tremuloides*) stands within a 100-km by 30-km area at approximately 110°W, 41°N. The stands were selected with a geographic information system (GIS) to meet two additional criteria. First, they were required to be associated with each of three other vegetation types: meadow dominated by sagebrush (*Artemisia* spp.); riparian areas dominated by willow (*Salix* spp.); and conifer forest (dominated by subalpine fir [*Abies lasiocarpa*], lodgepole pine [*Pinus contorta*], and Engelmann spruce [*Picea engelmannii*]). Second, the stands were selected to be between 2750 m and 3050 m in elevation. The sixteen resulting riparian sites had similar vegetation, topography, and climate.

SPATIAL SCALES

We measured environmental factors at three spatial scales considered to be biologically meaningful to both Red-naped Sapsuckers and Northern Flickers (Gutzwiller and Anderson 1987, Daily 1993, Dobkin et al. 1995, Lawler and Edwards 2002). We labeled these the "tree", "local", and "home-range" scales to correspond to the areas and factors sampled at each scale. The home-range scale was based on the estimated home range sizes of the species (8–15 ha; JJL, pers. obs.) and thus likely contained the range of vegetation types and resources used by birds during the breeding season. At this scale, we measured components of landscape composition and configuration in a GIS using 11-ha sample plots centered on each nest (Table 1). Nesting and foraging habitat of both Red-naped Sapsuckers and Northern Flickers is known to be associated with several home-range scale factors including forest edges, proximity to riparian vegetation, and the area of open meadows or fields (Conner and Adkisson 1977, Gutzwiller and Anderson 1987, Lawler and Edwards 2002).

The local scale sample plots encompassed a 0.04-ha area surrounding a nest tree. This area has been suggested as the appropriate

TABLE 1.   Variables measured at three spatial scales to assess habitat associations of Red-naped Sapsuckers and Northern Flickers in the Uinta Mountains, Utah, 1996–1998.

Variable name	Description
Home-range scale variables[a]	
ASPEN	Area of aspen (ha)
WILLOW	Area of willow (ha)
MEADOW	Area of open meadow (ha)
CUT	Area of logged forest (ha)
EDGE	Meters of aspen-meadow edge per ha of aspen
EDGEDIST	Distance to aspen-meadow edge (m)
RICHNESS	Number of different types of habitat patches
Local-scale variables[b]	
CANCOV	Canopy cover (%)
CANHGT	Canopy height (m)
TREES	Number of trees
TREES>15	Number of trees >15 cm dbh
SNAGS	Number of standing dead trees
DSNAGS	Number of fallen dead trees
CONIF	Number of conifers
Tree-scale variables[c]	
DBH	Diameter at breast height
HEIGHT	Height
LIVE	Condition (live or dead)
CONKS	Presence of fungal conks
ROT	Percentage of heart rot (at breast height)
TREES<2	Number of trees within 2 m
BRANCHES	Number of branches <2 m high

[a] The home-range scale was defined as an area approximating the home range of each species.
[b] The local scale was defined using a 0.04-ha sampling plot.
[c] The tree scale encompassed a nest tree or randomly selected non-nest tree.

extent for measuring aspects of the structure and composition of vegetation that provide perching sites near the nest, most directly affect nest microclimates, and affect the ability of a nesting bird to detect and avoid predators (James and Shugart 1970, Li and Martin 1991). We used circular plots centered on each nest to make field measurements of several aspects of the structure and composition of vegetation around the nest (Table 1). Nest sites of cavity-nesting birds in general have been found to be associated with open understories (Flack 1976, Brawn 1988), and nest sites of Northern Flickers in particular have been found to be associated with lower tree densities (Gutzwiller and Anderson 1987, Sedgwick and Knopf 1990).

The tree scale encompassed only the nest tree itself. At this scale, we measured aspects of tree structure, condition, and size. Red-naped Sapsuckers are known to place nests in trees with fungal conks and heart rot (Daily 1993) and both Northern Flickers and Red-naped Sapsuckers are known to nest in trees with relatively large diameters (Dobkin et al. 1995). In addition, Red-naped Sapsuckers nesting in aspen trees tend to build nests in live trees (Walters et al. 2002) whereas flickers will often nest in dead trees (Moore 1995).

Our analyses at the three spatial scales were based on aspects of the structure, composition, and condition of vegetation. We considered including topographic variables in the study, but preliminary analyses showed no associations between nest locations and either slope or aspect.

NEST SEARCHES AND DATA COLLECTION

We searched five of the 16 sites for nests in 1996, six in 1997, and five in 1998. In addition, we searched one of the larger sites all three years. The data collected in 1997 and 1998 at this large site were only used to assess interannual variation in abundance and nest-site occupancy. Because Red-naped Sapsuckers and Northern Flickers primarily nest in aspen trees

in the Uinta Mountains, we restricted nest searches to aspen woodlands. The aspen woodlands at each site were mapped using aerial photographs and systematically searched for all nests of both species from early June to mid-July. Nests were most often found by following birds to cavities and then determining whether the cavity contained an active nest as evidenced by incubating or feeding behavior. Due to the conspicuous behavior of the two species, it is unlikely that many nests went undiscovered. The locations of all nests were recorded with a geographic positioning system (GPS).

We randomly selected non-nest points in proportion to the area of unused aspen woodland at each site. We defined unused aspen as the area in which a home-range scale sample plot could be placed and not overlap the home-range scale sample plot of a nest. Non-nest points were selected to be at least 30 m apart to prevent overlap in the sample plots used for the tree- and local-scale measurements. Given the size of the home-range scale sample plots, it was impossible to prevent overlap among nest plots and among non-nest plots at this scale. The differences in the number and location of nests found for each species resulted in the selection of 105 non-nest points for building the Red-naped Sapsucker models and 219 non-nest points for building the Northern Flicker models. At each non-nest point location, we randomly selected a focal tree to be used for the tree-scale measurements as well as to serve as the center of the local and home-range scale plots. We recorded the locations of all focal trees with a GPS.

The composition and structure of vegetation at the home-range scale were assessed using a digital vegetation map in a GIS. The vegetation map was created by classifying Landsat Thematic Mapper satellite imagery of the north slope of the Uinta Mountains (Lawler and Edwards 2002). The map had a resolution of 30 m and had six land-cover classes, including aspen, conifer, willow, meadow, cut forest, and water. Map accuracy was assessed using a stratified random sample of 50 ground survey points for each vegetation class. Map accuracy across all classes was estimated at 70%.

At the end of the breeding season, we visited each nest and non-nest point to measure aspects of the surrounding vegetation at the local scale. We categorized the trees in local-scale plots as being greater or less than 15 cm in diameter at breast height (dbh)—a classification based on our observation that most cavities were in trees >15 cm dbh. Likewise, our counts of standing dead trees and fallen dead trees included only those >15 cm dbh. Canopy cover was assessed by averaging four readings taken with a densiometer in the four cardinal directions at 1 m from the focal tree. The fact that canopies were not all the same height likely reduced the accuracy of our canopy-cover estimates, as slightly larger areas were sampled when canopies were taller. We estimated canopy height by measuring the height of an average tree in the plot using a clinometer. We also used a clinometer to measure the height of the focal tree for the tree-scale assessment. At the tree scale, we estimated the degree to which trees were rotten using an increment borer at breast height by determining the percentage of the core length that exhibited signs of rot, and we also recorded the presence of fungal conks (*Phellinus* spp.). Although *Phellinus* fungi often cause rot in much of the heartwood of an aspen tree, many trees with heart rot do not exhibit fungal conks and many trees with conks show little sign of heart rot. Thus, we used both the measure of heart rot and the presence of conks to evaluate tree condition.

ANALYSES

We used the variance-decomposition technique described by Whittaker (1984) to quantify the variation in nest locations associated with factors at the three spatial scales. The technique involved fitting seven statistical models (a full model and six subset models) to produce estimates of the variation explained by different sets of variables (Borcard et al. 1992). We fit the seven logistic regression models for each species using presence or absence as a binary response. We began by fitting three models for each of the species, one for each spatial scale. Models were selected from all possible combinations of the seven candidate variables we measured at each scale using Akaike's information criterion (AIC; Burnham and Anderson 1998). We then used all of the variables included in the three models to build a full model for each species. The full model explained the differences between nest and non-nest points associated with all seven components of variation—the three pure components and the four shared compo-

nents (equation 1). The three original models we built for each species explained a subset of this variation, which included one pure and three shared components (equations 5–7). From the original models, we also built an additional three models for each species that used 1) the home-range and local-scale variables, 2) the home-range and tree-scale variables, and 3) the local- and tree-scale variables. Each of these models explained subsets of the seven components of variation including two pure and four shared components (equations 2–4).

$$\begin{aligned} \text{FULL} = \; &p(HR) + p(LO) + p(TR) + s(HR \\ &+ LO) + s(HR + TR) + s(LO \\ &+ TR) + s(HR + LO + TR) \quad (1) \end{aligned}$$

$$\begin{aligned} HR + LO = \; &p(HR) + p(LO) + s(HR + LO) \\ &+ s(HR + TR) + s(LO + TR) \\ &+ s(HR + LO + TR) \quad (2) \end{aligned}$$

$$\begin{aligned} HR + TR = \; &p(HR) + p(TR) + s(HR + LO) \\ &+ s(HR + TR) + s(LO + TR) \\ &+ s(HR + LO + TR) \quad (3) \end{aligned}$$

$$\begin{aligned} LO + TR = \; &p(LO) + p(TR) + s(HR + LO) \\ &+ s(HR + TR) + s(LO + TR) \\ &+ s(HR + LO + TR) \quad (4) \end{aligned}$$

$$\begin{aligned} HR = \; &p(HR) + s(HR + LO) + s(HR \\ &+ TR) + s(HR + LO + TR) \quad (5) \end{aligned}$$

$$\begin{aligned} LO = \; &p(LO) + s(HR + LO) + s(LO \\ &+ TR) + s(HR + LO + TR) \quad (6) \end{aligned}$$

$$\begin{aligned} TR = \; &p(TR) + s(HR + TR) + s(LO \\ &+ TR) + s(HR + LO + TR). \quad (7) \end{aligned}$$

The models, named for the types of variables they contained (HR = home range, LO = local, and TR = tree), are given on the left-hand side of equations 1–7. The p and s terms denote pure and shared components of variation, respec-

tively, associated with the spatial scales represented in parentheses.

By subtracting different components of variation from the deviance explained by the full model, we were able to isolate each of the seven components of variation as follows:

$$p(HR) = d(FULL) - d(LO + TR) \quad (8)$$

$$p(LO) = d(FULL) - d(HR + TR) \quad (9)$$

$$p(TR) = d(FULL) - d(HR + LO) \quad (10)$$

$$\begin{aligned} s(HR + LO) = \; &d(FULL) - d(TR) \\ &- p(HR) - p(LO) \quad (11) \end{aligned}$$

$$\begin{aligned} s(HR + TR) = \; &d(FULL) - d(LO) \\ &- p(HR) - p(TR) \quad (12) \end{aligned}$$

$$\begin{aligned} s(LO + TR) = \; &d(FULL) - d(HR) \\ &- p(LO) - p(TR) \quad (13) \end{aligned}$$

$$\begin{aligned} s(HR + LO + TR) = \; &d(FULL) - p(HR) \\ &- p(LO) - p(TR) \\ &- s(HR + LO) \\ &- s(HR + TR) \\ &- s(LO + TR), \quad (14) \end{aligned}$$

where d denotes the deviance explained by the model in parentheses. Equations 8–14 were derived from simple algebraic manipulations of equations 1–7. For example, by subtracting the deviance explained by the model containing both local- and tree-scale variables from the deviance explained by the full model (equation 8), we essentially subtracted the right-hand side of equation 4 from the right-hand side of equation 1, which left only the pure component of variation explained by home-range scale factors. The three pure components of variation identified with equations 8–10 were then used to compute the four shared components (equations 11–14).

RESULTS

We found 93 Red-naped Sapsucker nests and 37 Northern Flicker nests. There was little

TABLE 2. The composition and fit of seven logistic regression models for each of two woodpecker species. The models were used to partition the variance in nest presence associated with habitat factors at three spatial scales (home range, local, and tree). Variable names are explained in Table 1.

Model	Variables	% deviance explained
Red-naped Sapsucker		
Full	ASPEN + WILLOW + EDGEDIST + EDGE + DSNAG + CANCOV + CONIF + TREES>15 + DBH + ROT + CONKS	92
Home range + Local	ASPEN + WILLOW + EDGEDIST + EDGE + DSNAG + CANCOV + CONIF + TREES>15	62
Home range + Tree	ASPEN + WILLOW + EDGEDIST + EDGE + DBH + ROT + CONKS	84
Local + Tree	DSNAG + CANCOV + CONIF + TREES>15 + DBH + ROT + CONKS	81
Home range	ASPEN + WILLOW + EDGEDIST + EDGE	40
Local	DSNAG + CANCOV + CONIF + TREES>15	38
Tree	DBH + ROT + CONKS	69
Northern Flicker		
Full	MEADOW + EDGEDIST + CANCOV + CONIF + DSNAG + DBH + HEIGHT + ROT + TREES<2 + BRANCHES	65
Home range + Local	MEADOW + EDGEDIST + CANCOV + CONIF + DSNAG	48
Home range + Tree	MEADOW + EDGEDIST + DBH + HEIGHT + ROT + TREES<2 + BRANCHES	61
Local + Tree	CANCOV + CONIF + DSNAG + DBH + HEIGHT + ROT + TREES<2 + BRANCHES	59
Home range	MEADOW + EDGEDIST	32
Local	CANCOV + CONIF + DSNAG	34
Tree	DBH + HEIGHT + ROT + TREES<2 + BRANCHES	54

difference in the abundance of either species at the one site we monitored over all three years of the study. At this site we found 15, 16, and 13 sapsucker nests and 7, 5, and 6 flicker nests in 1996, 1997, and 1998, respectively. Because both species demonstrated a high degree of nest-site reuse, it is not surprising that we found only minor differences in the 21 habitat-related variables measured at the nests at this site across the three years.

The full model for sapsuckers explained 92% of the variation in the locations of these nests (Table 2). At the home-range scale, sapsucker nests were located close to aspen-meadow edges and were associated with smaller areas of aspen woodlands, more willows, and areas with more aspen-meadow edge. At the local scale, sapsucker nests were found in areas with more fallen dead trees, less dense canopies, fewer conifers, and lower densities of trees. At the tree scale, they were found in trees with larger diameters, more rot, and more fungal conks.

The locations of the Northern Flicker nests were explained with a slightly different set of factors than those used in the models for the Red-naped Sapsuckers. The full model explained 65% of the variation in flicker nest-site locations (Table 2). At the home-range scale, flicker nests were closer to aspen-meadow edge and were associated with larger areas of open meadow. At the local scale, flicker nests were associated with more open canopies, fewer conifers, and more fallen dead trees. Flickers tended to nest in shorter trees with larger diameters, more heart rot, fewer low branches, and few close neighboring trees.

To examine the relative importance of the factors at each of the three spatial scales, it is necessary to turn to the results of the variance-decomposition analyses (Table 3). The most striking result of this analysis was that only approximately half of the explained variation (less than a third of the total variation) in nest-site locations of either species could be attributed purely to the measured factors at single spatial scales. A slightly higher percentage of the explained deviance in the Red-naped Sapsucker data ($49\% \div 92\% = 53\%$) was associated purely with factors at single spatial scales than in the Northern Flicker data ($27\% \div 65\% = 42\%$). The largest pure component of variation for both species was explained by tree-

TABLE 3.   Variation in nest-site locations of two woodpecker species explained by habitat factors at three spatial scales. Pure components of variation are those that can be attributed solely to factors at one scale. Shared components are those that cannot be attributed to factors at any one scale, due in part to cross-scale correlations. The deviance explained by each of these components was derived through an algebraic manipulation of the deviance explained by seven logistic regression models.

	% of total deviance explained	
Isolated component of variation	Red-naped Sapsucker	Northern Flicker
Pure (Tree)	30	17
Pure (Home range)	11	6
Pure (Local)	8	4
Shared (Local + Tree)	14	12
Shared (Home range + Tree)	13	8
Shared (Home range + Local)	4	1
Shared (Home range + Local + Tree)	12	17

scale factors, i.e., tree size and condition (Table 3). Shared associations across scales explained a larger percentage of the deviance in the local and home-range scale models (inserting numbers from Table 3 in equations 5 and 6, 79% and 73% for sapsuckers and 88% and 81% for flickers) than in the tree-scale models (inserting numbers from Table 3 in equation 7, 57% for sapsuckers and 69% for flickers). Three of the four shared components of variation were of similar magnitude in the analysis of both species (Table 3). In contrast, the deviance in both the flicker and sapsucker data that was explained by some shared aspect of local and home-range scale factors stood out as being much smaller than the deviance explained by the other shared components.

DISCUSSION

A surprising number of ecological studies tend to ignore the issue of multicollinearity in explanatory models (Graham 2003). The closely related issue of cross-scale correlations in multiscale studies has received even less attention (Cushman and McGarigal 2002, Lichstein et al. 2002). Our results indicate that these correlations can be relatively large, obscuring the ability to rank the relative effects of factors at different spatial scales. We found that about half of the explained deviance in models of Red-naped Sapsucker and Northern Flicker habitat associations could not be attributed to factors at any one spatial scale, but were instead "shared" by explanatory factors from each of four cross-scale combinations. This proportion is even higher than that attributed to the shared variation identified in the only comparable

multiscale analysis of which we are aware. Cushman and McGarigal (2004) found that the variation in avian community structure that could be attributed to variance shared across each of three spatial scales accounted for between 37% and 47% of the explained variance.

Our results have significant implications for our current understanding of avian habitat selection. First, our findings stress the importance of taking a multiscale approach to investigating habitat selection. The relatively large shared components of variation identified in our analyses highlight the fact that studies conducted at any one spatial scale may be influenced by variables acting at spatial scales not investigated in the study. Although we have recognized the importance of scale in structuring ecological systems for some time (Wiens 1989), we have been slow to explicitly incorporate multiscale relationships into management-based assessments. Our results indicate that accurately predicting habitat availability or habitat quality for Red-naped Sapsuckers and Northern Flickers will require a multiscale approach.

Second, our results suggest that ignoring cross-scale correlations can lead to erroneous estimates of the relative strength of habitat associations at different spatial scales. Although we can draw some tentative conclusions about the relative strength of the habitat associations at the three spatial scales in our study based on the pure components of variation in our analyses, the relative sizes of each of the shared and pure components of variation determine whether strong scale-spe-

cific conclusions can be drawn. When shared components are large relative to pure components, it may be impossible to rank the relative strength of factors at different scales. In the present study, the relatively large shared components of variation preclude a simple interpretation of the relative effects of the measured variables at each spatial scale. For example, the ranking of the pure components of variation in Northern Flicker nest-site locations implies that tree-scale factors (17% of the deviation explained) were more influential than local factors (4%) and home range factors (6%). However, if each of the shared components of variation that involved local scale factors (12% + 1% + 17% = 30%) were in actuality due solely to effects at the local scale, the deviance explained by local factors (4% + 30% = 34%) would be greater than the greatest potential contributions of the tree scale (17% + 8% = 25%) or the home-range scale (6% + 8% = 14%). Because we assumed in this example that all shared components of variation involving local-scale factors were in actuality due to factors at the local scale, variation shared between the home range and tree scales (8%) is the only shared variation that can potentially be assigned to the tree and home-range scales.

Variance decomposition should be seen as a diagnostic tool. It is not a method for removing multicollinearity or cross-scale correlations, but instead a method for determining the degree to which those correlations should influence model interpretation. In contrast to the case presented by our results, when the pure components of variation are large relative to the shared components, the interpretation of the relative strengths of associations is possible. In this case, no matter how one theoretically assigns the shared components of variation, the ranking of the factors at the different spatial scales remains the same as that of the ranking of the pure components. In many cases, the relative sizes of the pure and shared components may allow for simple model interpretations. It is important to note, however, that even relatively weakly correlated variables can produce large shared components of variation; none of the explanatory variables in any of our models were highly correlated ($r < 0.60$).

There are several other methods for addressing multicollinearity that could potentially be used to address cross-scale correlation in multiscale habitat studies (Graham 2003). Residual and sequential regression (Graham 1997), principal components regression (Legendre and Legendre 1998), and structural equation modeling (Shipley 1999) each offer different approaches for addressing the pure and shared components of variation in models containing correlated variables. Residual and sequential regression require the researcher to assign priorities to the correlated variables. Thus, an understanding of which variables are more and less functionally meaningful is required. Similarly, structural equation modeling requires some knowledge of how the correlated variables functionally interact with both each other and with the response variable. In contrast, principal components regression does not require assumptions about the relative functional importance of the correlated variables. This technique involves conducting a principal components analysis on the explanatory variables and then regressing the response variable on the scores of the resulting orthogonal principal components. Depending on the variable loadings on each of the principal components, however, it can be difficult to interpret the results with respect to the relative influence of individual spatial scales.

Because residual and sequential regression and structural equation modeling all require *a priori* knowledge of the relative functional importance of, or the functional relationships among, the factors in the analysis, they are of little use if this information is unavailable. In the case of the two woodpecker species studied here, our knowledge of the natural histories of the species provided us with some clues as to the relative importance of some of the factors but did not allow us to clearly prioritize the factors at the three spatial scales. For example, the selection of specific trees for nesting is constrained by the birds' habit of excavating cavities in trees. As one might expect, several studies have demonstrated strong relationships between nest presence and tree size and condition (Conner and Adkisson 1977, Raphael and White 1984, Daily 1993, Dobkin et al. 1995). At the home-range scale, both species have been shown to nest near forest edges in areas central to a diverse set of resources (willow cambium, tree sap, and insects for sapsuckers; ant hills and other insects for

flickers), thereby potentially reducing overall foraging time (Dobkin et al. 1995). Additional evidence indicates that home-range factors may be more important than local factors for sapsuckers (Crockett and Hadow 1975). Furthermore, few strong local-scale associations have been identified for these species in other studies. Thus, it might be reasonable to attribute much of the variation shared among local- and tree-scale factors to tree-scale associations and much of the variation shared among local and home-range scale factors to associations with home-range factors. However, because we know less about the relative importance of home-range and tree-scale factors, it is more difficult to theoretically assign the two shared components of variation that include tree and home-range scale factors to associations at either of these scales.

Selecting ecologically meaningful spatial scales is a critical step in the design of a multiscale habitat study. The extent over which to measure tree-scale factors in our study was easily defined. Each measurement made at the tree scale pertained to the focal tree. However, determining the appropriate extent over which to measure factors that likely influence predator detection and avoidance at the local scale and resource accessibility at the home-range scale was not as straightforward. At the local scale, we used a 0.04-ha plot, the plot size traditionally used to assess avian habitat (James and Shugart 1970). These plots generally fit within the territories of most birds. However, 0.04 ha is an arbitrary size and obviously not scaled to the habitat use of either of the two birds in our study. Calculating a local-scale plot size from some measure of resource use within a home range would likely provide a much more meaningful scale at which to measure aspects of the structure and composition of vegetation associated with foraging and predator detection (Johnson 1980). Although our home-range scale plots were based on the home range sizes of the two species, it is possible that factors acting over even larger spatial scales were associated with nest locations. Thus, measuring patterns at an additional scale much larger than a home range may have allowed us to identify other aspects of the landscape that influenced the selection of the home range. The fact that the tree scale was easily defined and clearly ecologically meaningful may have contributed

to the relatively large contribution of factors at that scale.

In addition to ensuring that each spatial scale in a study is ecologically meaningful, it is important to maintain consistency in the precision of the measurements made at each scale. Multiscale habitat studies often involve measurements made from digital maps as well as measurements made at the study site (Saab 1999). The types and amounts of error associated with these measurements are often quite different. For example, in our analyses, the error inherent in the digital vegetation map used to measure home-range scale variables may have biased us toward finding weaker habitat associations at that scale.

Because our goal was to demonstrate an approach for investigating cross-scale correlations, we did not address two important and related issues. Thoroughly addressing the issues of multicollinearity within spatial scales and spatial autocorrelation would have improved the applicability of the models, but at the expense of complicating the analyses. First, in addition to manifesting itself in the cross-scale correlations that we investigated, multicollinearity was likely to have been a factor within spatial scales. Although we did not apply it to this end, variance decomposition can be used to determine the relative shared and pure components of variation associated with each explanatory variable in the study (Whittaker 1984, Cushman and McGarigal 2004). Such an analysis would allow the researcher to determine how much emphasis should be placed on associations with individual variables. Any multicollinearity within spatial scales in our study did not influence the general conclusions we drew from our analyses. Second, as with any study in which samples are taken over a heterogeneous area, spatial autocorrelation could potentially have influenced the results of our models (Borcard et al. 1992). Spatial autocorrelation is only an issue if it accounts for variation in the response that is not correctly attributed to environmental gradients. Due to the size of the home-range scale sample plots, the effects of spatial autocorrelation were likely to be strongest at this scale. Because pure home-range scale factors ranked relatively low in our analyses, any overestimates of the relative strength of these factors due to spatial autocorrelation is unlikely to have drastically

affected our results. Accounting for spatial autocorrelation in the modeling process, however, may reduce the shared components of variation generated by cross-scale correlations and thus aid in identifying the relative strengths of multiscale factors.

Because ecological systems operate at multiple spatial scales, understanding ecological processes often requires a multiscale approach (Allen and Starr 1982, O'Neill 1989, Wiens 1989, Peterson and Parker 1998). Such approaches will often necessitate alternative study designs and analytical techniques (Battin and Lawler 2006, Kristan 2006). Our results emphasize the importance of conducting multiscale analyses, demonstrate the necessity of quantifying cross-scale correlations in multiscale studies that rely on correlative approaches, and demonstrate a diagnostic tool for examining cross-scale correlations. As we expand the scope of ecological analyses, it is important that the appropriate tools are adapted or developed to meet the new challenges that emerge. Our analyses demonstrate one such tool for analyzing habitat associations in multiscale ecological studies.

ACKNOWLEDGMENTS

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