

MULTI-SCALE BREEDING BIRD AND LAND-COVER ASSOCIATIONS

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ABSTRACT—The association patterns between breeding bird diversity and amount of different land cover types at five spatial scales were analyzed. Breeding bird surveys were conducted at 2,021 randomly selected roadside locations in a 500,000 ha area of north-central Tennessee. The land cover of the area was classified from satellite imagery. Both bird and land cover data were separated into relevant groups: birds into migration guilds, and land cover into natural and artificial types. The study area was subdivided into geographic blocks ranging from 36 to 62,000 ha. Study-area richness-distribution maps for each migration guild were created. The multiscale association patterns between bird species richness and proportion of land cover types were statistically analyzed using canonical and bivariate procedures. Residents displayed relatively even distributions. However, Neotropical migrant species displayed a large distribution gap in the southeast corner of the study area. Furthermore, residents did not display land cover associations, but Neotropical and short-distance migrants were significantly correlated with amount of land cover type over the breadth of the study scales. These findings suggest that migrants may be more sensitive to habitat changes than resident bird species. In addition, the multiscale results indicate the contextual and interrelated characteristics of the small- and large-scale patterns and processes. This suggests that local as well as regional scale areas need to be assessed in order to more effectively design management and conservation strategies.

Much ecological research has been undertaken without the consideration of scale. Phenomena observed and measured in small plots often have been extrapolated to broad, regional scales or vice versa. However, ecological processes and their resultant patterns act and are expressed at different scales (Wiens, 1989; Levin, 1992). This scale-dependence restricts the validity of conclusions to, at best, a narrow range of scales (Wiens, 1989). Thus, the scale at which a system is observed affects both the detection and interpretation of patterns (Wiens, 1987).

Exclusion of scale issues in research designs could produce opposing conclusions drawn on similar ecological phenomena when studied at different scales (Wiens, 1981; 1987). This type of problem is commonly encountered when extrapolating conclusions relevant at one scale to other scales (Levin, 1992). Thus, efforts to resolve effects of scale are considered vital within ecological investigations, and more multiple-scale studies are needed (Meetenmeyer and Box, 1987; Levin, 1992).

Birds are good study subjects because of their relative conspicuousness and ubiquity that in turn could be used as indicators of other taxa. However, relatively few studies (Hamel et al., 1986; Gutzwiller and Anderson, 1987; Wiens et al., 1987; Virk-kala, 1991; Rahbek and Graves, 2001) have assessed multiscale patterns between habitats and birds. Multiscale avian distribution studies can be instructive and important because: (1) they can be related to land use, (2) species conservation assessments can be identified through habitat and distribution associations, (3) relative site conservation value can be evaluated, and (4) baseline information can be generated from which future variations can be measured (Bibby et al., 1992).

I conducted a distribution study of breeding bird species. The large north-central Tennessee study area was subdivided into different spatial scales. Tennessee is an important eastern state for avian research as it straddles both the Mississippi and Atlantic

migration routes, is rich in breeding birds (Nicholson, 1991), and is physiographically varied.

The hypothesis that analytical results would vary depending on the spatial scale of the analysis was tested by analyzing the same avian and land cover parameters at each scale and by incorporating a relatively large number of spatial scales that differed significantly in size. The goal of this study was to infer the spatial scale(s) at which avian richness and land cover were most associated, further clarifying the role of scale in ecological research.

METHODS

Study Area—Most of the 500,000 ha study area lies within the Western Highland Rim and Pennyroyal physiographic region of Tennessee (Smalley, 1980), a topography that consists of low plateaus (≈ 300 m, above sea level), dissected hills, and within the study area, portions of the Cumberland and Harpeth Rivers (Fig. 1). The eastern edge of the study area encompasses the relatively level terrain of the Tennessee Central Basin (Smalley, 1980). However, similar landscapes are found across these two physiographic regions. Landscapes are large-scale geographic formations that display repetitive environmental and physiognomic features (Forman, 1995). When viewed as a whole, there are three main landscapes within the study area (Fig. 1). The first is a farmland mosaic, which covers relatively large portions of the study area's northern and western sections. At this scale, it appears as a patchy mixture of forests, grasslands, and other land cover categories. The second is the large swath of relatively continuous forest cover found along the central part of the study area. And, third is the urban/suburban area of the study area's southeastern corner (Fig. 1).

The major historical natural ecosystem is the Western Me-

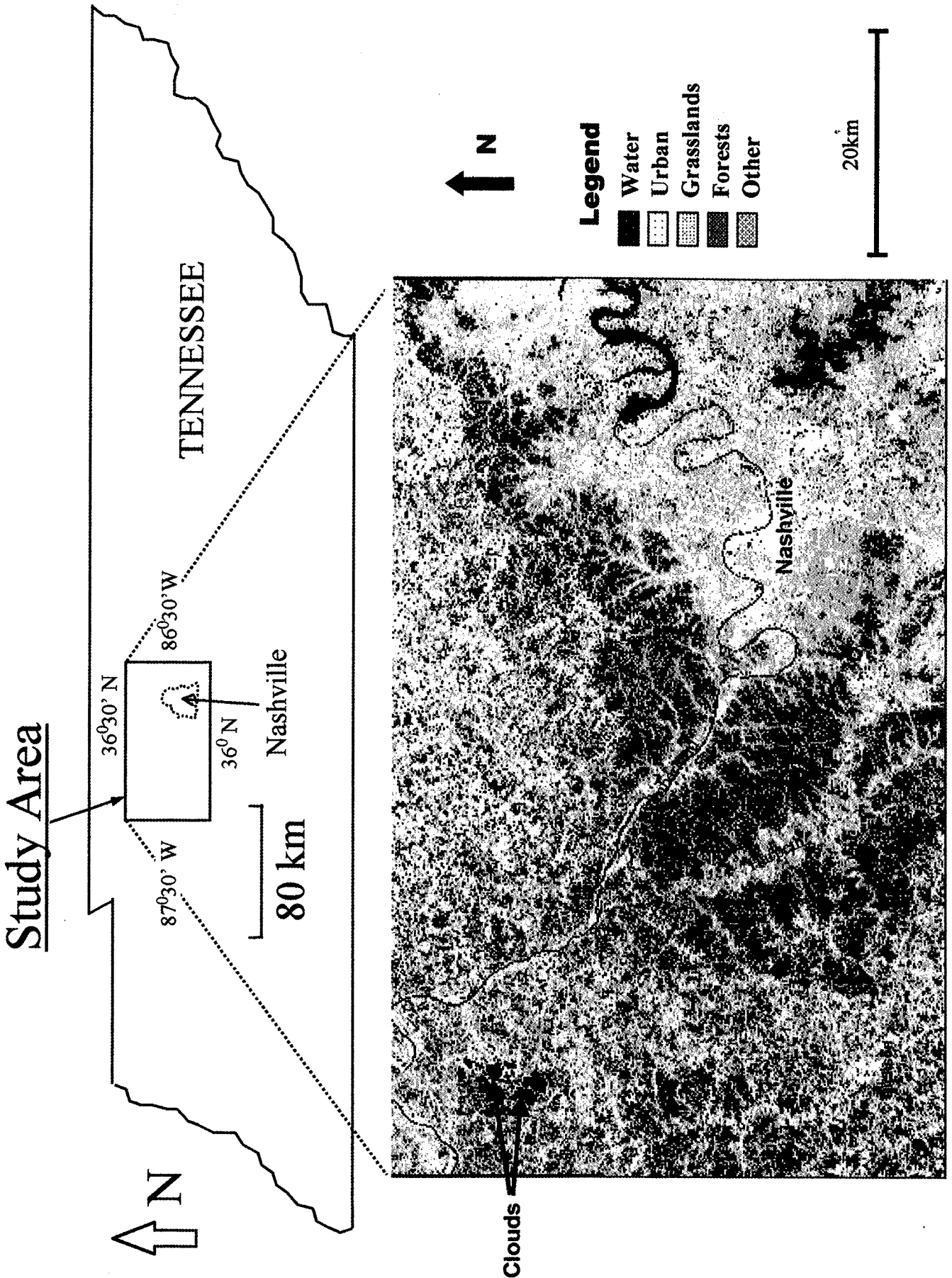


FIG. 1. Study area location and digitally classified land-cover classes.

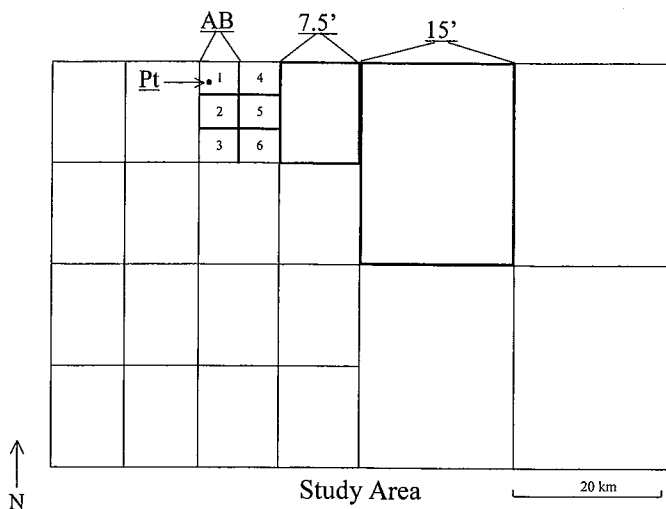


FIG. 2. Spatial-scale subdivisions used in the multi-scale analysis range in number and average area from points (Pts.; 2021, 36 ha), atlas blocks (ABs; 190, 2,580 ha), United States Geological Survey 1:24,000 scale, 7.5 degree-minute topographic quadrangles (7.5' quads; 32, 15,480 ha), 15 degree-minute scales (15'; 8, 61,920 ha), and the study area (500,000 ha). Each Pt, AB, 7.5', and 15' scale element was uniquely identified. The Atlas Block subdivisions follow methods used in the Tennessee Breeding Bird Atlas (Nicholson and Hamel, 1986).

sophytic Forest region (Braun, 1950), which is characterized by a mix of oak (*Quercus*) and hickory (*Carya*) tree species. Much of the study area's historical land cover has been replaced or altered. As in most of eastern North America, the present landscape was primarily formed by a post-European settlement history of deforestation to agriculture followed by farmland abandonment and urban sprawl (Braun, 1950; Clawson, 1979; Smalley, 1980).

Land Cover Classifications—A Landsat 5 (30 August 1993; path 21, row 35) Thematic Mapper (TM) satellite image was classified by using a supervised method. Supervised classification methods incorporate field collected land cover information to classify raw "pixel" ("picture-element" of the digital satellite image) reflectance values into land cover classes (Jensen, 1986). The identity and location of different land cover types within the study area was determined during the bird distribution study. These known land covers and locations were used as 'training' areas on the digital image. These training areas utilize the pixel reflectance values of the known land covers to locate like pixels across the digital image (Jensen, 1986).

Both parallelepiped and maximum likelihood algorithms were utilized to classify the pixel reflectance signatures from the training sites into land cover categories. The parallelepiped algorithm is based on Boolean logic that assesses the brightness values for each pixel in the training sites to produce an n-dimensional mean vector image. A one-standard deviation upper and lower threshold is created for each class. Following these initial calculations, the maximum likelihood algorithm assigns each pixel to a class if it meets the statistical criteria that were initiated by the mean vector calculations in the parallelepiped computation (Jensen, 1986).

The different land cover classes are: (1) water, (2) urban, (3) grasslands, (4) forests, and (5) other (Fig. 1). Water represents ponds, lakes, rivers, and streams. Urban was classified from un-

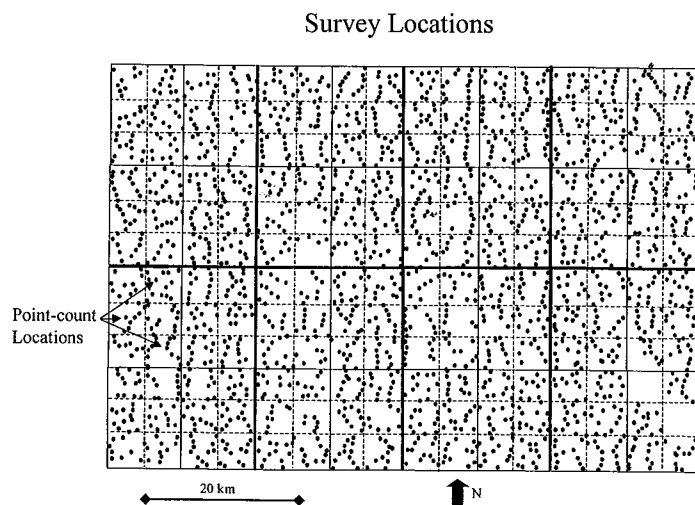


FIG. 3. Distribution of the 2,021 roadside survey locations.

vegetated areas such as roadways, parking lots, industrial sites, railway yards, rooftops, and airport runways. Grasslands are field and pasture type areas that were either being grazed, in fallow, or in early successional stages. They were composed mostly of grasses, herbs, and forbes with very little woody plant cover. Forests were classified from field sites with a closed canopy of trees, including deciduous as well as smaller patches of mixed deciduous and coniferous forest. Finally, other consisted of relatively small areas of agricultural, transitional, edge, or brushy and shrubby areas. In addition, other also included suburban areas around Nashville where pixel reflectances tended to be mixed. This occurred where house rooftops mixed with shade-tree crowns, streets, lawns, and small parks and playgrounds.

Spatial Scales—A total of five spatial scales were evaluated (Fig. 2). The spatial scales range in number and average area from (1) points (Pts.; 2021, 36 ha), (2) atlas blocks (ABs; 190, 2,580 ha), (3) United States Geological Survey (USGS) 1:24,000 scale, 7.5 degree-minute topographic quadrangles (7.5' quads; 32, 15,480 ha), (4) 15 degree-minute scales (15'; 8, 61,920 ha), and (5) the study area (500,000 ha). The ABs were designed after the Tennessee Breeding Bird Atlas project (Nicholson and Hamel, 1986).

Breeding Bird Groups, Sampling, and Distribution Mapping—North American breeding birds can be separated into three migration guilds: residents (RSs) breed and over-winter in the same area; short-distance migrants (SDs) generally winter farther south than their breeding ranges, but not often to Central or South America; and Neotropical migrants (NTs) breed in North America and winter in the Neotropics (Hamel, 1992; DeGraaf and Rappole, 1995). Species among these migration guilds were analyzed because NTs have been experiencing population declines (Wilcove, 1985; Terborgh, 1989; Askins et al., 1990; Bohning-Gaise et al., 1993; Askins, 1995; Flather and Sauer, 1996), and their multiscale patterns of land cover associations were analyzed for possible differential associations between the bird groups and/or land cover across the different spatial scales.

The 2,021 breeding bird surveys (Fig. 3) were performed in good weather, were each three minutes in duration, and were sampled from 1993–1996, 15 May–17 July each year and from 0500–1000. Three minutes per roadside location follows methods used in the American Breeding Bird Survey (BBS methods and information can be found on their website at <http://monitoring2>.

er.usgs.gov/bbs). A trade-off exists when trying to assess bird communities from field samples: fewer field sites for longer periods or more field sites for shorter durations. Smith et al. (1993) indicate that more accurate inferences of avian diversity can result by increasing the number of field sites rather than conducting fewer while spending more time per site. Therefore, I adopted the Smith et al. (1993) approach to avian diversity sampling.

Survey locations were visited once from roadside positions, each of which had been randomly selected in both space and time, were no closer than 0.8 km to each other, and were within 20 m from the edge of the road surface. Furthermore, the random sampling design prevented geographic clustering of survey locations in any one year. Surveying birds from roadsides: (1) allows for the collection of a large number of samples in a relatively short amount of time, (2) is comparatively economical, (3) has sample sites that are easily located and revisited, and (4) roads are in the public domain (Bibby et al., 1992). A possible disadvantage could be that roads disturb birds within the habitats through which they pass (road-effect). Forman and Deblinger (2000) observed "road-effect" for a busy four-lane highway in the northeastern United States, whereas Rottenberry and Knick (1995) did not observe this effect for smaller road types. The predominant habitat type through which roads pass as well as road size could be factors that contribute to road-effect. Assuming that the importance of road-effect would decrease as a function of road size, 98% of the roadside surveys analyzed in this study were conducted along secondary or tertiary roads (two-lane, light-duty, minor, and dirt roads).

The bird species that were recorded were seen or heard within a circular area estimated to be 600 m in diameter centered on the observer. Because of the breeding bird objective to this study, non-breeding migrants were excluded. All of the survey locations were incorporated into a geographic information system (GIS) and linked to both the bird and land cover information.

Each of the migration guild survey-location distributions were mapped (IDRISI, 1995) at three species richness levels. These levels were functions of overall species richness distribution profiles. First are the survey locations with at least one species. Second are survey locations with at least the study-area wide average number of species. And third are survey locations with at least the study-area wide 75th percentile number of species.

Statistical Analyses—The association between breeding bird richness and amount of land cover at the Pt., AB, 7.5', and 15' scales was analyzed by canonical and bivariate correlation statistical techniques (Parker, 1991). Canonical correlation analysis (CCA) is a multivariate statistical procedure that identifies the maximum correlation between linear functions of two sets of measurements (Cooley and Lohnes, 1971; Manly, 1991). In this study, the two sets are the migration guilds and land cover. In addition, CCA produces as many canonical axes as the number of variables. The axes are listed in descending order of their canonical correlation magnitudes and they are orthogonal (uncorrelated) to one another (Cooley and Lohnes, 1971). In the bivariate analyses, Pearson's product moment correlation, r , was used. This statistical method facilitated the interpretation of the multivariate canonical results.

The metrics used in the statistical analyses were breeding bird richness and amount or proportion of each land-cover type. Breeding bird richness was defined as the number of species observed in three minutes in each migrant category. Bird richness at the point scale was the number of species recorded at each

survey location. For the larger scales, richness was the average number of species observed per three minutes of effort. This value was calculated for each of the 'blocks' at each scale. A block is simply a given AB, 7.5' quad, or 15' scale subdivision. Amount of land cover, at all scales, was calculated by dividing the number of pixels in each land cover category by the total number of pixels found in each of the scale's blocks.

Because of the geographic nature of the data, it was assumed that elements at small spatial scales (Pts) would have a relatively higher probability of being autocorrelated than the larger scale elements. Autocorrelation is a condition where a resultant correlation value may artificially be raised because each point is relatively close to another: a correlation of proximity or time. By randomly selecting half of the points, the average distance between survey locations doubles and in turn reduces the possible effects of autocorrelation. Therefore, 1000 Pts were randomly selected and used in the statistical analyses. Correlation values could be increased as a result of averaging species richness on a per survey location basis that was used at the AB, 7.5' quad, and 15' scales. Thus, correlation results were evaluated by their statistical significance, which was assessed at a correspondingly smaller alpha level and by their relative magnitudes in context to the overall set of bivariate tests.

RESULTS

Bird Richness and Relative Abundance—There were 91 species observed and 20,035 individual species observations. In descending order of number of species, NTs tallied 44 and 5,697 observations, followed by SDs with 28 and 5,500, and lastly RSs with 19 and 8,838 (Appendix 1). Three bird species: Northern Cardinal (*Cardinalis cardinalis*) (RS), Indigo Bunting (*Passerina cyanea*) (NT), and American Robin (*Turdus migratorius*) (SD), were the most relatively abundant, comprising $\approx 15\%$ of the total number of observations. Twenty-nine species accounted for 68% of the observations, and 59 species were the least relatively observed at 16% of the total observations. Twenty-eight species were not songbirds (Appendix 1).

The average number of species increased with increasing scale or size of the scale blocks (Fig. 4). Two trends emerged. First, when average number of species was plotted as a function of area in ha, the trend line was less steep at the largest scales (Fig. 4). The second occurred when the log of average species was plotted against the log of the area. This function resulted in a near linear relationship between number of species and area (Fig. 4).

Nicholson (1991) found that relative to this study area the number of species per AB would likely range between 60 and 70. Survey methods for the Tennessee Breeding Bird Atlas utilized road-counts as well as off road censuses and multiple observers in the field, all of which could have contributed to the greater number of species observed per AB. However, at the 7.5' quad scale, I observed a similar number of species as Nicholson (1991) assessed at a similar scale.

Bird-richness Distributions—All of the distributions that contained at least one species were similar; a regular pattern throughout the study area (Fig. 5). The gaps are generally a function of the survey location distribution (Fig. 3). Distributions containing survey locations with at least the average number of species are similar to the previous ones, except for NTs. Their distribution displays a large gap in the southeastern corner of the study area (Fig. 5). Furthermore, distribution gaps also exist on

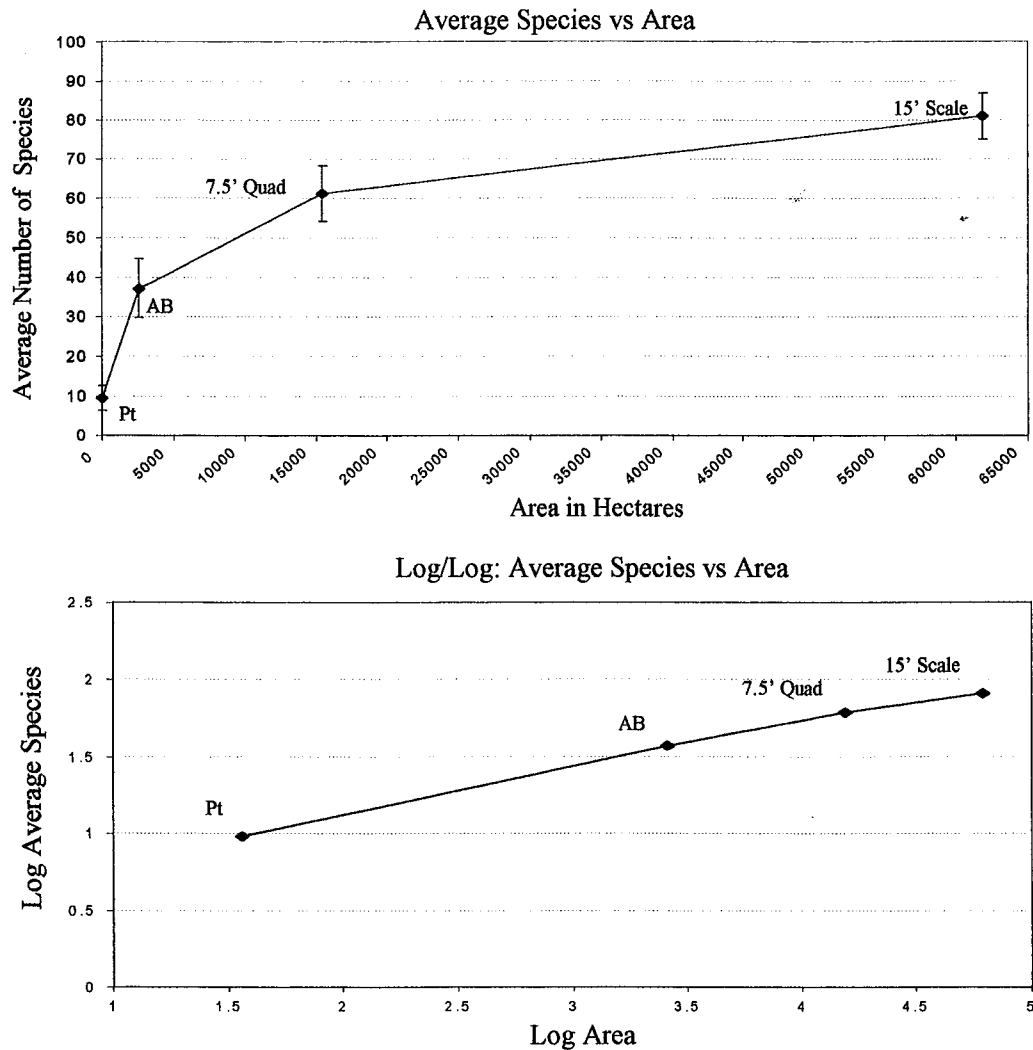


FIG. 4. Mean (\pm SD) average number of species versus area, where Pt = points, AB = atlas blocks, 7.5' Quads = 7.5 degree-minute topographic quadrangles, and 15' Scale = 15 degree-minute scales.

the maps with the highest relative species richness. Here the total species map contains a gap in the southeast corner: SD-species rich points were not found in the southeastern corner and south-central portions of the study area, and the gap in the southeastern corner for NTs is even greater than in its previous distribution (Fig. 5). In contrast, RS-species locations were evenly distributed at the three different richness levels (Fig. 5). Results of these distribution patterns indicate that there are fewer total species, SDs, and NTs in urban areas. Additionally, relatively species rich SD locations were also absent from the most heavily forested regions and RS appear to be insensitive to land cover.

Statistical Analyses—Whereas bivariate correlation assesses the linear correspondence between paired measurements and calculates a coefficient (r) to quantify this relationship, CCA calculates the linear correspondence between two groups of variables. CCA produces a coefficient, but this coefficient also includes the effects of interactions within the groups (Manly, 1991). The results of the CCA produced six canonical axes, or variates. Each variate has a resultant correlation coefficient, canonical r . Two of the six variates accounted for most of the observed variation, were statistically significant at $P \leq 0.05$ for all scales analyzed, and thus were interpreted (Table 1). Because

the sum of the three migration guilds equals the total number of species, this would produce artificially high correlations in the CCA and thus total species was not used. However, because each bivariate statistical test was performed independently, total species could be analyzed for land-cover associations.

Canonical variate 1 (CV1) at the Pt scale has a canonical r of 0.508 (Table 1). This r -value represents the correlation between the most associated variables in the bird and land cover groups. For CV1 at the Pt scale, both NTs and forests have the highest canonical coefficient (CC) and canonical loading (CL) values, respectively (Table 1). Thus, NTs and forests were most highly correlated with their canonical variable. Based on their respective loading magnitudes, forests and NTs are interpreted to be the two variables that are the most highly correlated and the canonical r is the measure of this association.

The Pt-scale association between NTs and forests also is exhibited by the bivariate correlation analyses (Fig. 6). The correlation between NT-richness and proportion of forest is 0.405, and is the highest Pt-scale pair-wise correlation between the bird and land cover variables (Fig. 6). Because CCA analysis also assesses within group interactions, it indicated an even greater association between NT-richness and amount of forest at the Pt-scale than

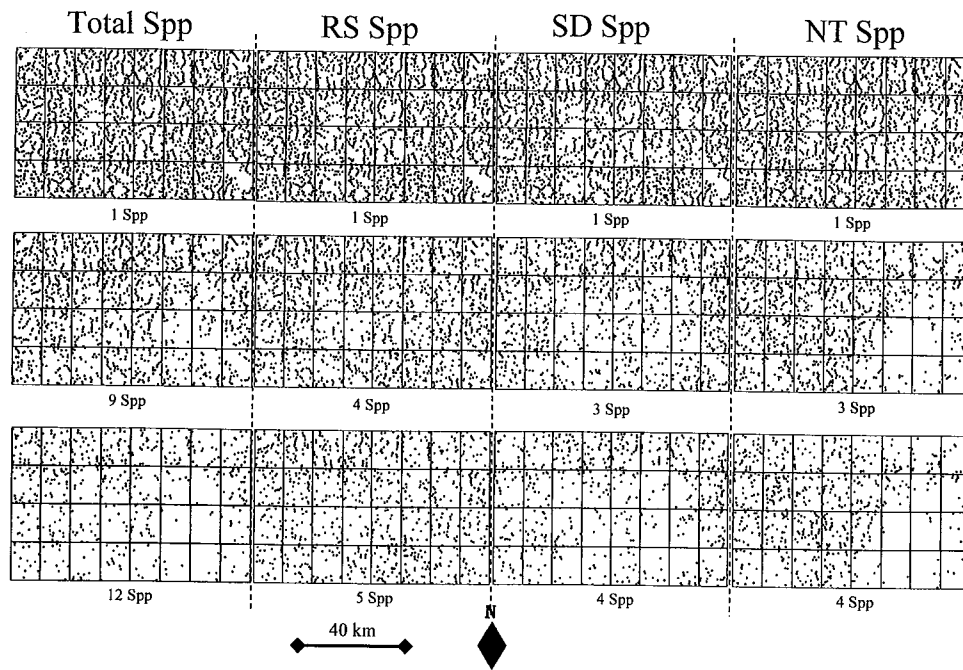


FIG. 5. Bird richness distribution maps. For each of the four breeding bird categories, the distributions where at least one species (top row) and the study area mean number of species (Total = 9; residents, RS = 4; short-distant migrants, SD = 3; and Neotropical migrants, NT = 3) were mapped. The bottom row is the point-count distributions where at least the study-area wide 75th percentile number of species (Total = 12, RS = 5, SD = 4, and NT = 4) is found.

did the bivariate analysis alone (Table 1; Fig. 6). What was instructive about the bivariate analyses was that they revealed the trends of the associations.

The CCA, canonical coefficient, and loading values for NTs, forest, and urban land cover at AB, 7.5', and 15' scales illustrate a condition whereby variables in two different groups can be correlated, although one variable has negative values and the other has positive ones (Table 1). The salient feature is the relative absolute magnitude of the CC and CL values as compared to the other variables.

The CCA further revealed that at both the AB and 15' scales, there are relatively important suppressor variables, grasslands and forests, respectively. Suppressor variables occur when the canonical coefficient and loading of a variable within a particular canonical variate have different signs (Cooley and Lohnes, 1971). Suppressor variables help to enhance the correlation between the highest loading variables within a particular canonical variate. In this case, grasslands enhance the correlation between NTs and forests at the AB scale and forests augment the correlation between NTs and urban land cover at the 15' scale.

In general, the CVI correlations at all scales are a function of NTs and either forest or urban land cover. Forest was the most correlated land cover variable at the Pt, AB, and 7.5' scales, and urban land cover was the most correlated at the 15' scale (Table 1). These results are repeated in the bivariate analyses (Fig. 6). From Pt to 7.5' scale, NTs and forests had the highest magnitude r -values between bird and land cover and all were significant at $P < 0.01$. (Because of the large number of bivariate correlation analyses and other factors, an alpha of 0.01 or less (Bonferroni correction) was considered statistically significant.) At the 15' scale, NTs and urban land cover were the most correlated ($r = -0.906$, $P < 0.005$). However, the association between NTs and forest was still relatively high at 0.826 ($P < 0.014$). Also at this

scale was the relatively high correlation (0.895, $P < 0.005$) between SDs and grasslands. Furthermore, SDs and grasslands were relatively highly correlated at the three smaller scales in the bivariate analyses (Fig. 6).

The bivariate results of SDs and grasslands being relatively highly correlated are partially observed in the CCA. SDs are consistently the highest loading bird variable in CV2, but grasslands is not among the land cover variables (Table 1). What is likely occurring is that interaction effects and associations between forests/urban, forests/grasslands, and grasslands/urban, as revealed in the bivariate analysis, tend to overwhelm grasslands' association with SDs in the CCA (Table 1). The statistical analyses reveal that although the amount of grassland affects SD richness, the overall composition of the landscape appears to be a better indicator.

Forests or urban had the highest CC and CL loadings. In the bivariate analyses, forests were consistently negatively associated with either grasslands or urban land cover (Fig. 7). In the first case, the correlation at the four scales in Figure 7 was virtually identical. In the second association case, forest's and urban's negative association increased with increasing scale size. Lastly, there were relatively low correlations between grasslands and urban land cover (Fig. 7).

The within bird group bivariate results have relatively low magnitudes (Fig. 7). Whereas, there are significant results for at least three scales in all other bivariate analyses, the within bird results contain statistically significant values at only the two smaller scales (Fig. 7).

Between the four scales, several different bird and land cover association trends exist. One trend is that for every scale the bivariate correlation between a bird and land cover variable is significant ($P \leq 0.01$) with this first trend being exhibited by SDs/grasslands and NT/urban (Fig. 6). A second trend is that

TABLE 1. The Canonical correlation results are summarized. There are two groups of variables, one bird and one land cover (separated by a horizontal line at each scale).

	Canonical Variate 1 Canonical <i>r</i>		Canonical Variate 2 Canonical <i>r</i>	
	Canonical coefficient	Canonical loading	Canonical coefficient	Canonical loading
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Pts (36 ha) <i>n</i> = 1000		<i>0.509</i>		<i>0.366</i>
RS	-0.14	-0.246	-0.181	-0.297
SD	-0.591	-0.608	-0.726	-0.763
NT	0.7821	0.777	-0.623	-0.63
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Forest	0.818	0.98	0.04	-0.076
Grassland	-0.258	-0.704	-0.33	-0.453
Urban	-0.059	-0.298	0.912	0.936
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AB (2580 ha) <i>n</i> = 100		<i>0.828</i>		<i>0.609</i>
RS	0.231	0.346	-0.152	-0.423
SD	0.199	0.26	-0.892	-0.945
NT	-0.927	-0.937	-0.304	-0.308
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Forest	0.988	0.98	0.33	0.195
Grassland	<i>0.144</i> ²	<i>-0.424</i>	-0.546	-0.69
Urban	-0.143	-0.65	0.854	0.654
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7.5' Quad (15,480 ha) <i>n</i> = 32		<i>0.877</i>		<i>0.816</i>
RS	0.269	0.43	-0.085	0.286
SD	0.295	0.477	0.953	0.877
NT	-0.844	-0.881	0.474	0.398
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Forest	1.075	0.999	0.433	-0.015
Grassland	0.057	-0.542	-0.393	-0.624
Urban	0.069	-0.629	1.027	0.741
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15' Scale (61,920 ha) <i>n</i> = 8		<i>0.994</i>		<i>0.963</i>
RS	0.157	0.041	0.267	0.623
SD	-0.841	-0.476	0.615	0.867
NT	-0.9	-0.658	-0.429	-0.701
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Forest	<i>0.716</i>	<i>-0.29</i>	0.722	0.937
Grassland	-0.045	-0.514	-0.412	-0.785
Urban	1.385	0.855	-0.003	-0.51

¹ For each scale and canonical variate, the highest loading variables (absolute value) in each group are indicated by bold type.

² The suppressor variables are italicized.

bird/land cover correlations are virtually the same magnitude at each scale (NT/grasslands) (Fig. 6). The third trend is, depending on scale, a bird/land cover correlation was either significant or not significant or negative at one scale and positive at another. RS/urban, RS/grasslands, and SD/urban each exhibit this type of trend (Fig. 6).

Overall, the statistical results indicate that NT-richness was more closely associated with land cover than was either RS_i or SD richness. However, SDs tended to be relatively strongly associated with grasslands. The results also indicate that NT/land cover correlations were relatively consistent across all scales. Moreover, even though NT- and SD-species richness were more strongly correlated with particular land covers than RSs, the overall landscape composition also was important to bird richness because the different land covers were relatively strongly associated with each other and the migrant groups were relatively less so (Table 1; Figs. 6 and 7).

DISCUSSION

Migrant breeding-bird richness had stronger associations with amount of particular land covers than RSs and many of these association trends were scale independent. Scale independence occurs when a result or pattern observed at one scale is also observed at others. At all study scales, NT-richness was positively correlated with amount of forest, as were SDs and grassland, and negatively so with amount of urban land cover. These results differed from the hypothesis. It was expected that this wide range of spatial scales would reveal or frame spatial scales at which bird/land cover associations were greatest, which would then elucidate spatial scales at which management strategies could more effectively be applied. Even though a spatial scale was not explicitly inferred, a more interrelated and broader-scale range of bird/land cover associations emerged.

The multiscale positive NT/forest and negative NT/urban correlations may not simply be an expression of one land cover replacing the other. For example, only at the two larger scales did forest cover and urban land cover exhibit larger negative correlation values than did forest and grassland. Furthermore, the virtually opposite statistical trends displayed between NTs with forest and urban land covers suggest that relatively similar amounts of either land cover, per scale, were affecting NTs. However, from the smallest to largest scales, forest cover averaged 23–33% and urban land cover averaged only 6–7%. On average, the blocks within the different scales contained from three to four times as much forest as urban land cover. However, this amount of urban land cover evoked a virtually equal in magnitude but opposite correlation trend with NT-richness than did forest cover. The effect is that much less urban land cover than forest cover resulted in opposite association trends that were similar in magnitude.

The change from NT-richness being more associated with amount of forest cover at the smaller scales to NTs and urban land cover being the most correlated at the 15' scale may reflect individual versus population effects. Breeding bird habitat selection appears to occur at an individual, small scale, level (Wiens, 1989). Relatively stronger forest-cover associations with NT-richness at smaller spatial scales indicates the importance of there being sufficient habitat area for individuals to establish territories. Thus, amount of suitable habitat at small scales could be relatively more important to local avian richness than amount of unsuitable habitat. However, when associations between habitat and species richness are assessed at larger scales, species population and community processes are more likely being analyzed instead of individual effects. The number of species in relatively large areas may be more closely tied to number of habitats. Thus, even relatively small patches of unsuitable habitat in large areas could prevent or restrict the number and amount of suitable hab-

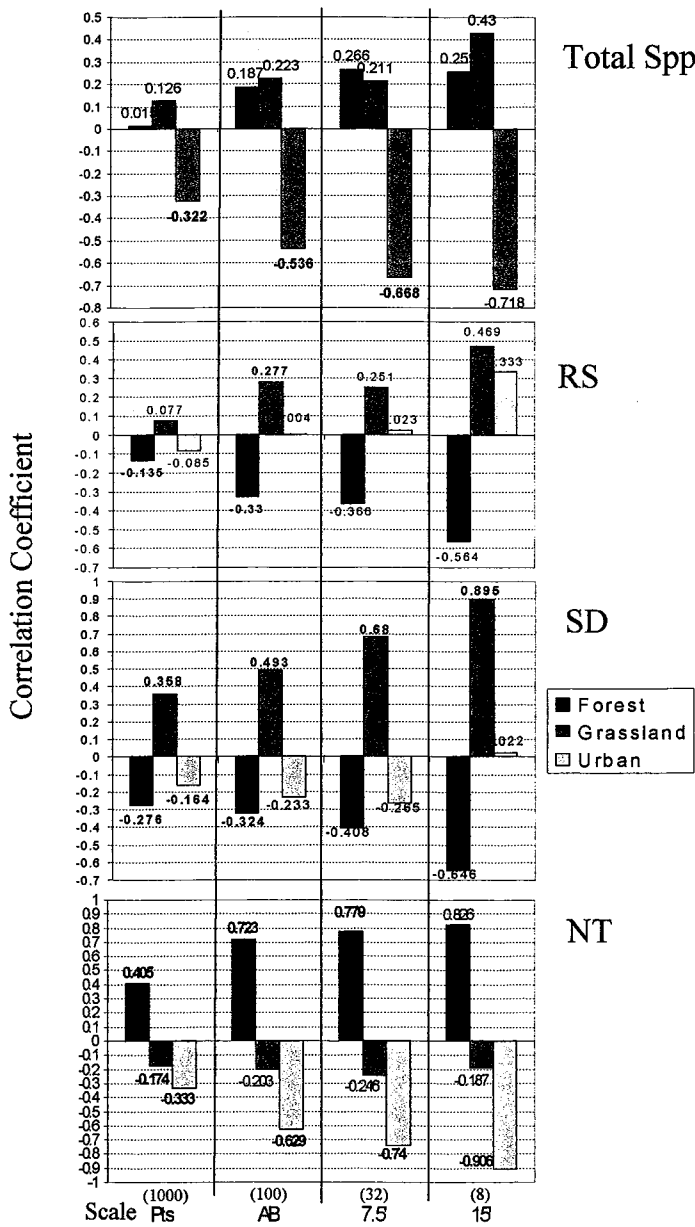


FIG. 6. Multiscale correlation coefficients, r , between species richness and proportion of land cover for total species (Spp), resident species (RS), short-distant migrants (SD), and Neotropical migrants (NT). Spatial-scales were Pt = points, AB = atlas blocks, 7.5' Quads = 7.5 degree-minute topographic quadrangles, and 15' Scale = 15 degree-minute scales. Statistically significant ($P < 0.01$) correlation coefficients are indicated by bold type.

itat. This process could then manifest as a negative correlation between increasing unsuitable habitat (urban land cover) and decreasing NT-species richness. Since conservation and management strategies often concern regional diversity, understanding the spatial scale where population effects are more manifest than individual processes could be a strong indicator of the minimum habitat area requirements and reserve sizes needed to manage diversity.

Forest land cover was found to be a strong correlate with NT species, although not all of the NT species analyzed were

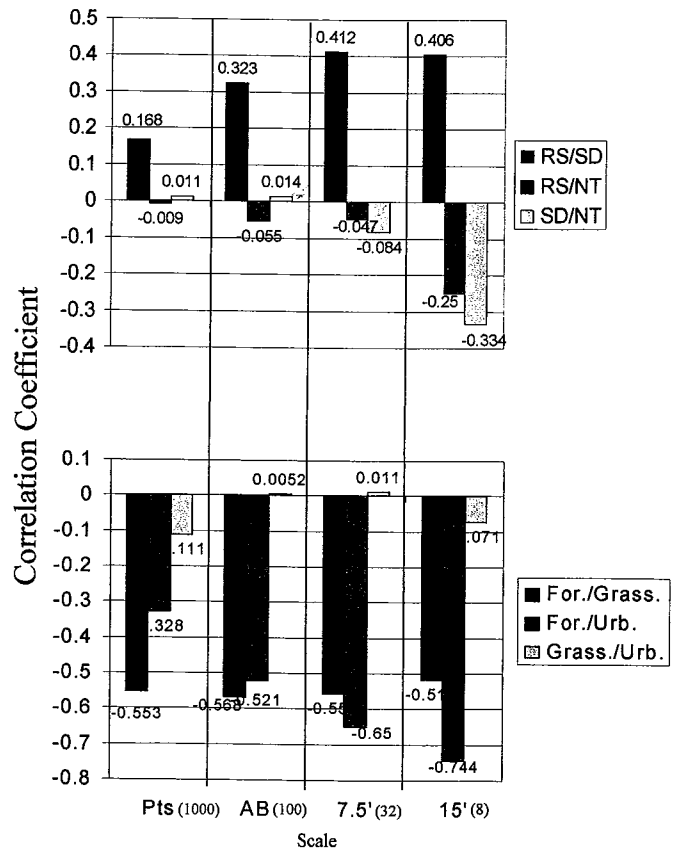


FIG. 7. Multiscale correlation coefficients, r , between the different bird groups and between the different land cover categories. Bird groups were resident species (RS), short-distant migrants (SD), and Neotropical migrants (NT). Land cover categories were forest (For.), grasslands (Grass.), and urban (Urb.). Statistically significant ($P < 0.01$) correlation coefficients are indicated by bold type.

forest breeding birds [e.g., Prairie Warbler (*Dendroica discolor*), Yellow-breasted Chat (*Icteria virens*), Blue-winged Warbler (*Vermivora pinus*), Common Yellowthroat (*Geothypis trichas*), and Chimney Swift (*Chaetura pelagica*)]. Deriving a single forest land-cover category from the satellite imagery lumped several forest habitats together. This may have contributed to the statistical association between forest and NTs. However, lumping several natural forest habitats together cannot account completely for the correlated results between NTs and forest because of the number of non-forest breeding NT species. Perhaps the amount of forest in an area is an indication of how relatively undisturbed, or urban land cover free, a particular block was. In addition, NT-richness may also represent the level of disturbance or lack of human-induced disturbance in this study area.

Both amount of habitat and its configuration in a given area affect NT diversity. The importance of forest area and configuration for many NT-species has been assessed. Studies have found that forest fragmentation is an important variable in understanding NT migrant population trends and diversity (Robinson et al., 1995; Flather and Sauer, 1996). However, in this study as in others, the amount of natural habitat appears to be a good predictor of bird diversity (Nicholson, 1991; Flather and Sauer, 1996). The relative effects of habitat fragmentation vs. overall amount of habitat need further study to better frame the spatial

scales at which relative effects of fragmentation or proportion of a habitat emerge as better predictor variables.

This study supports the value of forested land for NT richness, which has been linked to many eastern NT migrants (Whitcomb et al., 1981; Robinson et al., 1995) and also shows the negative effect urban land cover can have on species richness. If the landscape changes from forest to urban/suburban, NT species could suffer a compound effect: as forest area diminishes, NT-species richness declines, and as urban land area increases NT-species richness also decreases. The negative effect on NT species exhibited in urban and suburban areas has been observed elsewhere and has led to these landscapes being called "hostile" to avian communities (Askins, 1995).

Two broad conclusions are suggested by this study. First, some ecological patterns can be similar across spatial scales that differ by orders of magnitude. This type of scale-independent pattern is similar to patterns found in different landscapes (Milne, 1992). The investigation and separation of ecological phenomena into scale dependent and independent groups is important. If it were known that certain ecological phenomena group into scale-independent patterns, then analyses and conclusions drawn at one scale would have greater validity when extrapolated to other scales. The ability to make more accurate scale-related predictions is desirable when there may be insufficient resources and time to study a phenomenon or impact at all its relevant scales.

Second, bird and land cover patterns were expressed at smaller as well as larger scales. However, a smaller to larger trend is arbitrary and could just as accurately be interpreted as a trend from the larger to smaller scales. In general, any area that is spatially defined with boundary and location is in context to a larger landscape. Thus, patterns and processes found to occur within a small study site may not necessarily be unique to the site, but are likely influenced by larger scale processes. However, a larger region is a composite of smaller scaled, contiguous patches. Therefore, patterns expressed in large-scaled areas are influenced by the dynamics occurring within its collection of local patches. In essence, smaller scaled areas are not independent of the larger context, and the larger region is composed of and influenced by factors in the smaller subunits.

This concept of landscape patches being interrelated is similar to metapopulation theory (Levins, 1969). Metapopulations are ensembles of interacting populations. For example, by analyzing the relationship of individual populations, it was shown that a more effective method for controlling a pest species that erupts asynchronously in local patches is to apply a control synchronously over the region (Levins, 1969). Similarly, a distribution of local areas or patches can be viewed as a single larger region or a "metapatch."

Relative to the avifaunal and land cover implications of this study, not only is it important to consider the land cover conditions within smaller areas or reserves, but also the overall landscape characteristics in which they are located (Farina, 1997). Conservation or management areas that are geographically separate may not be so ecologically. Management practices incorporated in one area could affect others. For example, if a bird species in Nashville was found to be declining, one could estimate the proportionate decrease for the Nashville area. If the species was not increasing elsewhere in the state, only the relative proportionate decrease between the Nashville area and the state would be different. Even if a species was increasing elsewhere in the state, local declines would tend to decrease the effects of population increases, when population trends were as-

essed for the entire state. Furthermore, depending on the scale of the analysis, population decreases or increases could emerge for a species: opposing conclusions could be drawn on the population trend of a species if the scale of the study is not accounted for. What may seem less likely in regard to a bird species decline in Nashville is that conditions in the Ridge and Valley Province, for example, could affect bird diversity in Nashville. This could occur if a bird species source population was in the Ridge and Valley Province and its habitat there was declining. In terms of management, efforts at a local reserve could be negated by conditions occurring on a regional, state, or for Neotropical and short-distance migrant breeding birds, even continental scale. Thus, whether at local, regional, or state levels, better-coordinated management and conservation efforts among and between the state's management and conservation lands and even between public and private land sectors could manifest as more effective regional and local management and conservation goals.

For example, in this study area, Edwin Warner, Percy Warner, and Radnor Lake State Natural Area are forested parks that form a west-to-east trend on the southern edge of Nashville. As Nashville grows, they will likely continue to be surrounded by suburban sprawl, especially for Radnor Lake as this is the most easterly of the three (Radnor Lake is the small lake, due south of the 'a' in Nashville). The park is the forest patch surrounding it; Fig. 1). Radnor Lake is a wildlife refuge, whereas the Warner parks are multiuse areas. Radnor Lake's mandates regarding human-use restrictions may not realize its bird diversity conservation goals because of its landscape context, including suburban impacts such as car exhaust, road kill, noise, roaming pets, etc. Furthermore, the Warner parks geographic positions to the west of Radnor could facilitate dispersal of forest birds to Radnor Lake from nearby large forest areas, such as the Cheatham Wildlife Management Area (The large forest area between the confluence of the Cumberland and Harpeth Rivers; Fig. 1). As a result, human-use decisions considered for the Warner parks could have impacts on bird diversity in Radnor Lake by affecting dispersal between nearby avian source populations (Cheatham) to Radnor Lake via the Warner parks. This park and reserve system can be viewed as a metapatch with each entity a patch connected by their habitat similarities (forest) and possible bird source and dispersal processes. Thus, decisions enacted at one park or area could also manifest as impacts to wildlife at another. Decisions based solely on local scale circumstances may not be able to address the larger scale conditions.

This study supports findings in Nicholson (1991) by illustrating an opposite but coupled trend. Nicholson (1991) found increasing breeding bird species richness with increasing natural vegetation cover. This study found decreasing breeding bird species richness with increasing human-made land cover at the Atlas Block scale, a scale analyzed in both studies. Furthermore, this study found that the most affected group of birds was NT migrants. Breeding bird results from these two studies could be used as guides to link and frame predictions and hypotheses of other statewide avian studies at a number of spatial scales. Although scale-independent ecological patterns were indicated here, their relative magnitudes could change when different regions are analyzed. Further study among Tennessee's varied landscapes could better define the relative impacts different land covers have on avifauna.

This study also found breeding bird and land-cover association patterns that remained consistent across a broad range of spatial scales. Landscape and spatial ecology, with implicit consideration of scale and scaling, have begun to unravel how scale is intertwined with ecological processes. Taking scale into consideration when examining environmental systems can be crucial

in gaining further insight into the behavior of the system being studied.

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LITERATURE CITED

- ASKINS, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. *Science*, 267: 1956–1957.
- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in Eastern North America. Pp. 1–57 in *Current Ornithology*, vol. 7. (D. M. Power, ed.). Plenum, New York.
- BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 1992. Bird census techniques. Cambridge Univ. Press, Cambridge.
- BOHNING-GAISE, K., M. L. TAPER, AND J. H. BROWN. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? *Conser. Biol.*, 7:6–86.
- BRAUN, L. 1950. *Deciduous forests of North America*. Blakston, Philadelphia.
- CLAWSON, M. 1979. Forests in the long sweep of American History. *Science*, 204:1168–1174.
- COOLEY, W. W., AND P. R. LOHNES. 1971. *Multivariate data analysis*. Wiley, New York.
- DEGRAAF, R. M., AND J. H. RAPPOLE. 1995. Neotropical migratory birds: natural history, distribution and population change. Cornell Univ. Press, New York.
- FARINA, A. 1997. Landscape structure and breeding bird distribution in a sub-Mediterranean agro-ecosystem. *Landscape Ecol.*, 12:365–378.
- FLATHER, C. H., AND J. R. SAUER. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology*, 77:28–35.
- FORMAN, R. T. T. 1995. *Landscape mosaics: The ecology of landscapes and regions*. Cambridge Univ. Press, Cambridge.
- FORMAN, R. T. T., AND R. D. DEBLINGER. 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conser. Biol.*, 14:36–46.
- GUTZWILLER, K. J., AND S. H. ANDERSON. 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. *Condor*, 89(3):534–548.
- HAMEL, P. B. 1992. *The land manager's guide to the birds of the South*. Nature Conservancy, Chapel Hill, North Carolina.
- HAMEL, P. B., N. D. COST, AND R. M. SHEFFIELD. 1986. The consistent characteristics of habitats: a question of scale. Pp. 121–128 in *Wildlife 2000: modeling habitat*. Univ. Wisconsin Press, Madison, Wisconsin.
- IDRISI. 1995. IDRISI for Windows version 1.0. Clark labs for cartographic technology and geographic analysis. Clark University, Worcester, Massachusetts.
- JENSEN, J. R. 1986. *Introductory digital image processing: a remote sensing perspective*. Prentice Hall, Englewood Cliffs, New Jersey.
- LEVIN, S. A. 1992. The problem of pattern and scale in Ecology. *Ecology*, 73:1943–1967.
- LEVINS, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. America*, 15:237–240.
- MANLY, B. F. J. 1991. *Multivariate statistical methods: a primer*. Chapman & Hall, London.
- MEENTEMEYER, V., AND E. O. BOX. 1987. Scale effects in landscape studies. Pp. 15–34 in *Landscape heterogeneity and disturbance: ecological studies*. (M. Goigel Turner, ed.). Springer-Verlag, New York.
- MILNE, B. T. 1988. Measuring the fractal geometry of landscapes. *Appl. Math. Comput.*, 27:67–79.
- NICHOLSON, C. P. 1991. Geographic patterns in species occurrence of Tennessee's breeding birds. *J. Tennessee Acad. Sci.*, 66:195–198.
- NICHOLSON, C. P., AND P. B. HAMEL. 1986. *Tennessee breeding bird atlas handbook*. Tennessee Ornithological Society, Nashville, Tennessee.
- PARKER, R. E. 1991. *Introductory statistics for Biology*. Cambridge Univ. Press, Cambridge.
- RAHBEK, C., AND G. R. GRAVES. 2001. Multiscale assessment patterns of avian species richness. *Proc. Nat. Acad. Sci.*, 98(8):4534–4539.
- ROBINSON, S. K., F. R. THOMPSON III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science*, 267: 1987–1990.
- ROTENBERRY, J. T., AND S. T. KNICK. 1995. Evaluation of bias in roadside point count surveys of passerines in shrubsteppe and grassland habitats in southwestern Idaho. Pp. 99–102 in *Monitoring bird populations by point counts* (C. J. Ralph, J. R. Sauer, and S. Droege, eds.). US Dept. Agric. Gen. Tech. Report, PSW-GTR-149.
- SMALLEY, G. W. 1980. Classification and evaluation of forest sites on the Western Highland Rim and Pennyroyal. US Dept. Agric., Forest Service Gen. Tech. Report, SO-30.
- SMITH, W. P., D. J. TWEDT, D. A. WIEDENFELD, P. B. HAMEL, R. P. FORD, AND R. J. COOPER. 1993. Point counts of birds in the bottomland hardwood forests of the Mississippi alluvial valley: duration, minimum sample size, and points versus visits. US Dept. Agric. Forest Service Gen. Tech. Report, 20-274.
- TERBORGH, J. 1989. *Where have all the birds gone?: Essays on the biology and conservation of birds that migrate to the American tropics*. Princeton Univ. Press, Princeton, New Jersey.
- VIRKKALA, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. *Oikos*, 62(1):59–66.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125–205 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess, and D. M. Sharpe, eds.). Springer-Verlag, New York.
- WIENS, J. A. 1981. Scale problems in avian censusing. *Stud. Avian Biol.*, 6:513–521.
- . 1987. Spatial scaling in Ecology. *Funct. Ecol.*, 3:385–397.
- . 1989. *The ecology of bird communities: foundations and patterns*. Cambridge Univ. Press, Cambridge.
- WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos*, 48(2):132–147.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*, 66:1211–1214.

APPENDIX 1. Bird species observed in the present study. Each bird species is identified by American Ornithologist's Union (AOU) designation, common name, scientific name, migrant guild (RS = residents, SD = short-distant migrants, NT = Neotropical migrants), and total number of times it was observed.

AOU	Common name	Scientific name	Migrant guild	# Observed
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	RS	1345
INBU	Indigo Bunting	<i>Passerina cyanea</i>	NT	921
AMRO	American Robin	<i>Turdus migratorius</i>	SD	893
NOMO	Northern Mockingbird	<i>Mimus polyglottos</i>	RS	822
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	RS	791
EUST	European Starling	<i>Sturnus vulgaris</i>	RS	788
MODO	Mourning Dove	<i>Zenaidura macroura</i>	RS	780
TUTI	Tufted Titmouse	<i>Baeolophus bicolor</i>	RS	736
CAWR	Carolina Wren	<i>Thryothorus ludovicianus</i>	RS	705
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	RS	606
COGR	Common Grackle	<i>Quiscalus quiscula</i>	SD	587
RSTO	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	SD	586
FISP	Field Sparrow	<i>Spizella pusilla</i>	SD	578
EAME	Eastern Meadowlark	<i>Sturnella magna</i>	SD	542
CHSW	Chimney Swift	<i>Chaetura pelagica</i>	NT	494
NOBO	Northern Bobwhite	<i>Colinus virginianus</i>	RS	463
CACH	Carolina Chickadee	<i>Poecile carolinensis</i>	RS	450
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	SD	429
AMGO	American Goldfinch	<i>Carduelis tristis</i>	SD	412
RBWO	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RS	401
BGGN	Blue-gray Gnatcatcher	<i>Poliopitula caerulea</i>	NT	401
EWPE	Eastern Wood-Pewee	<i>Contopus virens</i>	NT	382
EASB	Eastern Bluebird	<i>Sialia sialis</i>	SD	378
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	SD	360
COYE	Common Yellow throat	<i>Geothlypis trichas</i>	NT	337
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	NT	257
YBCU	Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	NT	251
YBCH	Yellow-breasted Chat	<i>Icteria virens</i>	NT	248
BARS	Barn Swallow	<i>Hirundo rustica</i>	NT	247
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	NT	245
HOSP	House Sparrow	<i>Passer domesticus</i>	RS	242
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	RS	236
WEVI	White-eyed Vireo	<i>Vireo griseus</i>	NT	223
WOTH	Wood Thrush	<i>Hylocichla mustelina</i>	NT	183
HOFI	House Finch	<i>Carpodacus mexicanus</i>	RS	176
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	SD	168
ACFL	Acadian Flycatcher	<i>Empidonax virescens</i>	NT	165
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	NT	158
SUTA	Summer Tanager	<i>Piranga rubra</i>	NT	157
KILL	Killdeer	<i>Charadrius vociferus</i>	SD	130
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	SD	120
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>	RS	119
GCFL	Great Crested Flycatcher	<i>Myiarchus crinitus</i>	NT	116
PRWA	Prairie Warbler	<i>Dendroica discolor</i>	NT	107
YSFL	Northern Flicker	<i>Colaptes auratus</i>	SD	94

APPENDIX 1. Continued.

AOU	Common name	Scientific name	Migrant guild	# Observed
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	NT	93
NOPA	Northern Parula	<i>Parula americana</i>	NT	81
BLGR	Blue Grosbeak	<i>Guiraca caerulea</i>	NT	78
OROR	Orchard Oriole	<i>Icterus spurius</i>	NT	77
KEWA	Kentucky Warbler	<i>Oporornis formosus</i>	NT	69
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	RS	68
PUMA	Purple Martin	<i>Progne subis</i>	NT	64
YTWA	Yellow-throated Warbler	<i>Dendrioca dominica</i>	NT	56
RODO	Rock Dove	<i>Columba livia</i>	RS	42
NRWS	Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	NT	42
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	NT	42
AMKE	American Kestrel	<i>Falco sparverius</i>	SD	40
TUVU	Turkey Vulture	<i>Cathartes aura</i>	SD	37
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	RS	33
RSHA	Red-shouldered Hawk	<i>Buteo lineatus</i>	SD	29
BEKI	Belted Kingfisher	<i>Ceryle alcyon</i>	SD	27
HOWR	House Wren	<i>Troglodytes aedon</i>	NT	26
RTHU	Ruby-throated Hummingbird	<i>Archilochus colubris</i>	NT	25
YTVI	Yellow-throated Vireo	<i>Vireo flavifrons</i>	NT	25
GRHE	Green Heron	<i>Butorides virescens</i>	SD	23
BWVA	Blue-winged Warbler	<i>Vermivora pinus</i>	NT	22
BCNH	Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>	SD	21
WEWA	Worm-eating Warbler	<i>Helminthos vermivorus</i>	NT	21
CAGO	Canada Goose	<i>Branta canadensis</i>	SD	19
LOSH	Loggerhead Shrike	<i>Lanius ludovicianus</i>	SD	13
DICK	Dickcissel	<i>Spiza americana</i>	NT	13
PIWA	Pine Warbler	<i>Dendrioca pinus</i>	NT	12
HOWA	Hooded Warbler	<i>Wilsonia citrina</i>	NT	12
GBHE	Great Blue Heron	<i>Ardea herodias</i>	SD	8
RTHA	Red-tailed Hawk	<i>Buteo jamaicensis</i>	SD	8
CONI	Common Nighthawk	<i>Chordeiles minor</i>	NT	7
CLSW	Cliff Swallow	<i>Hirundo pyrrhonota</i>	NT	7
LOWA	Louisiana Waterthrush	<i>Seiurus motacilla</i>	NT	7
SOSP	Song Sparrow	<i>Melospiza melodia</i>	SD	7
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	NT	6
BAOR	Baltimore Oriole	<i>Icterus glabula</i>	NT	6
BAOW	Barred Owl	<i>Strix varia</i>	RS	5
YEWA	Yellow Warbler	<i>Dendroica petechia</i>	NT	4
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	NT	4
CAEG	Cattle Egret	<i>Bubulcus ibis</i>	SD	3
BLVU	Black Vulture	<i>Coragyps atratus</i>	SD	3
SSHA	Sharp-shinned Hawk	<i>Accipiter striatus</i>	SD	3
BWHA	Broad-winged Hawk	<i>Buteo platypterus</i>	NT	3
AMBI	American Bittern	<i>Butorides lentiginosus</i>	SD	2
PRWA	Prothonotary Warbler	<i>Protonotaria citrea</i>	NT	2
GRSP	Grasshopper Sparrow	<i>Ammodramus savannarum</i>	NT	2