THE SPATIAL IMPACT OF AN URBAN AREA ON BREEDING BIRDS

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ABSTRACT—Urbanization alters the landscape profoundly affecting plant and animal distributions and abundances. Urbanized areas negatively affect bird communities by favoring resident generalist or invasive species, in turn, reducing diversity and promoting local extinction. Even though urbanization affects biodiversity in many systems, the spatial extent to which a metropolitan area impacts biodiversity is not well characterized. The goal of the present study was to elucidate the areal extent to which an urban/suburban landscape affects avian diversity. I conducted a breeding-bird distribution study containing over 2,000 roadside survey locations in a 500,000 ha study area in north-central Tennessee, that contained areas of natural and urban (mainly the city of Nashville) land cover. Breeding bird species were divided into three guilds: those that breed and winter in the same area—residents; those that breed and winter in different but relatively close areas—short-distance migrants; and those that breed in North America and winter in Central and South America—Neotropical migrants. These data were spatially analyzed through spatial interpolation surface models: Kriging and linear surface models. Neotropical migrant richness exhibited stronger negative associations with urban land cover than either residents or short-distance migrants. The surface model for urban land cover formed urban density zones. Neotropical migrant total richness spatial patterns significantly corresponded to the urban spatial patterns. Neotropical migrant breeding bird richness was significantly less over a 150,000 ha area of urban/suburban-developed landscape, or an area 50 times larger than Nashville's downtown district. Assessment of the overall metropolitan spatial effect to diversity will provide a benchmark for areal urban/suburban impacts that can assist conservation and management strategies directed towards controlling environmental impacts of urban sprawl.

Urban areas are increasing in number and growing in population size (Hall, 1988; Geddes, 1997; Clark, 2000). Since the middle of the twentieth century the number of urban areas with greater than a million people has increased globally from 78 to over 258; 65 of these contain more than four million inhabitants (Dogan and Kasarda, 1988). Often coupled to population increases of urban areas is areal expansion. For example, in the United States over the last three decades, New York, New York, Chicago, Illinois, and Cleveland, Ohio, grew geographically by 65%, 46%, and 33%, respectively. During this same time period, however, New York and Chicago only had single-digit percent population growths and Cleveland even had a population decline (Geddes, 1997; United States Census Bureau). Furthermore, there has been a general United States trend over the last few decades toward greater population growth in metropolitan areas surrounding central cites rather than in the central cities themselves (United States Census Bureau). As a result, urban growth in the United States is predominantly a function of development in a growing metropolitan area. Within eastern North America, urban/metropolitan growth is now occurring to such a large geographic extent that some areas are being described as "City-Regions" (Geddes, 1997). For example, the third regional plan for New York considered an area of 32,500 km² where 20 million people live (Geddes, 1997).

Over the last half-century in the United States, the general process of urban development has led to a pattern of less centralized urban centers producing cities that spread out over large geographic areas (Hall, 1996; Geddes, 1997; Hudson, 2001; Ji et

al., 2001). This type of urban design is defined as "suburban" as it is transitional between densely developed and populated urban areas and rural, natural or pastoral landscapes. The result of suburban development is a "sprawling" metropolitan urban pattern (Hall, 1996; Geddes, 1997; N'Dow, 1997; Hudson, 2001). Sprawling urban growth produces patchy and fragmented landscapes composed of aging city cores, expanding suburbs, habitat fragments, and patches of farmland (Geddes, 1997; Ryznar and Wagner, 2001). Even seemingly pristine natural areas in such a suburban land cover matrix can be relatively inhospitable to wildlife as compared to similar habitat patches in more natural settings (Askins, 1995; Friesen et al., 1995). Urban and suburban growth directly impacts the native ecosystem's biodiversity by reducing, fragmenting, and changing native habitats, increasing local surface temperature and runoff, altering disturbance regimes, disrupting resource and energy flow, and affecting species composition (Wilcove et al., 1998; Kinzig and Grove, 2001; Weng, 2001a, b). The consequences of these events can virtually eliminate previously occurring ecological communities (Thomlinson and Rivera, 2000; Kinzig and Grove, 2001).

Urbanization effects on biodiversity tend to vary along an urban-to-rural land cover gradient (Ruszczyk et al., 1987; Jokimaki and Suhonen, 1993; Blair, 1996). The most profound effects on diversity occur in urban-core areas characterized by a dense, almost complete covering of hard, human-made surfaces (roofs, concrete, tarmac, or macadam) that greatly diminish plant and animal resources such as water, light, shelter, food, roosts, or nesting sites (Whitney and Adams, 1980; Mooney and Gulmon,

1983; Sisk, 1991). As a result, urban land use in the United States often results in decreased bird diversity and abundances, especially for habitat specialists many of which are Neotropical migrant breeding bird species (Emlen, 1974; Lancaster and Rees, 1979; Beissinger and Osborne, 1982; Tilghman, 1987; Diamond, 1988; Soule et al., 1988; Bolger et al., 1997; Blair, 1999). Ultimately, urbanization can lead to local avian extinctions (Diamond, 1988; Soule et al., 1988). However, apparent diversity spikes in suburban settings have been observed in some urban avian assessments (Blair, 1999).

Often urban ecological studies utilize small-scale (< 500 ha) study sites selected along an urban gradient (Tilghman, 1987; Soule et al., 1988; Blair, 1999). Urban effects on bird communities and diversity found at the relatively small spatial scales of study sites may not translate to metropolitan sprawl scales as many patterns and their underlying ecological process act and are expressed across a narrow range of scales (Levin, 1992). Even if small-scale approaches reveal urban small-scale effects on avian communities, the basic understanding of a metropolitan area's spatial impact to birds would not be elucidated. Thus, it is important for basic scientific understanding of urban effects on birds to be able to assess the area to which urban areas impact birds. This understanding in turn will have conservation relevance by framing the extent both in shape and size that metropolitan complexes can impose on avian diversity (Marzluff, 2001). Furthermore, assessing urban spatial impacts on avian diversity may help link small scale with large-scale urban biodiversity studies and provide broad-scale estimates of urban impacts on biodiversity. In turn, these type of studies may allow for better anticipation of urban settlement effects and help design and arrange conservation land within large to regional landscape planning initiatives (Marzluff, 2001; Miller et al., 2001).

The goal of the present study was to elucidate the overall spatial impact to which a city affects avian diversity. Very few studies have examined how urban areas spatially impact birds (Marzluff, 2001). To do so would require avian surveys over large-scaled areas where locations were not constrained to any particular land cover nor would be placed only along transects. Furthermore, the spatial assessment would likely require the intersection of field data, spatial analytical tools, and landscape land-cover information. To conduct this study, I classified satellite imagery, used digital image processing, integrated geographic information system (GIS) technology, conducted geostatistical and surface modeling, performed statistical tests, and collected breeding bird data from a broad-scaled study area.

METHODS

Study Area—The study area is in north-central Tennessee (Fig. 1). Tennessee is an important state to assess urban impacts to breeding birds because it is rich in breeding avian species and is undergoing population increase coupled to urban development and suburban sprawl. There are 170 confirmed breeding avian species in Tennessee, which is over 29% of the total for all of North America (Nicholson, 1997). In addition, Tennessee straddles both the Mississippi and Atlantic migration pathways; therefore, many more species pass through the state as well. The population of Tennessee increased from just over 4.8 million in 1990 to over 5.6 million people in 2000 (United States Census Bureau). The metropolitan Nashville area, occupying most of the southeastern corner of the study area, has 1.1 million people living there and was ranked 25th in population amongst United

States cities (United States Census Bureau). The other main urban centers within the study area total less than 12,000 people (Dickson) and are generally distributed throughout the study area (Fig. 1) (see Butler, 2001 for further details of the study area). Most of the study area was originally covered by forest (Braun, 1950; Clawson, 1979; Smalley, 1980; Butler, 2001).

Land Cover Classifications—I used a supervised protocol to classify land cover (Jensen, 1986) from a Landsat Thematic Mapper satellite image (August 31, 1993) (Fig. 1). Supervised classification methods incorporate field-collected land cover information to help classify raw (unclassified) "pixel" ("picture-element" of the digital satellite image) reflectance values into thematic classes, such as land cover or land use (Jensen, 1986). I used a supervised classification method because I was familiar with the study area a priori and became more familiar with its various land covers through the fieldwork (Butler, 2001).

I classified Urban from 97 study area sites. Variations in surface types (and reflectance values) characteristic of urban surfaces necessitated the use of many urban sites to classify urban areas. These sites are characterized by human-made artificial surfaces such as, tarmac, concrete, asphalt, rooftops, airport runways, railroads, and macadam (roads). I performed an accuracy assessment between the digitally classified image and ground-truthed (field-surveyed) land cover. I randomly selected 200 locations that I could relatively easily access from roads, recorded land cover and compared the field assessed land cover to the digital classifications. At a pixel resolution (a 'pixel' is 30 m on a side), 83% of the digital-site classifications corresponded with the field-collected land-cover information, or an 83% pixel accuracy (90% for urban land cover alone).

Survey Location Placement and Field Methods—A major methodological goal was to randomly select each roadside point count while simultaneously obtaining a spatially regular pattern of sample sites at the study area scale. To accomplish this goal, I subdivided the entire study area into 1,152 grid cells or census blocks (CBs) with the intention of randomly locating two roadside point counts in each CB. Each CB was further subdivided into 16 'tiles', in four rows and four columns. I generated a randomly selected list of 2,500 integers between 1 and 16. The 16 tiles in the CBs were numbered from west to east with the northwest tile being '1' and the southeast tile being '16'. This grid was then overlain onto 7.5 degree-minute, United States Geological Survey topographic quadrangle maps (7.5' quads) of the study area. Roadside survey locations were found by consulting the list of random numbers and then making a mark on the 7.5' map alongside a road that was nearest to the centroid (central location of a geometric shape) of the corresponding tile. Because of the road network across the study area, some CBs either had one or zero survey locations. As a result, 1,069 of the 1,152 total CBs, or ≈ 93% were sampled. Most of the CBs that I did not sample occurred over two large lakes (southeast corner of the study area). Of the sampled CBs, 89% or 952 contained two point counts for a total of 2,021. Overall, 96% (1,940) of the roadside surveys (point counts) were conducted along secondary and tertiary roads or dirt tracks, e.g., two-lane, light-duty, minor, and dirt roads. Furthermore, to not cluster the field sampling or favor one study area portion over another in a given sampling season, each 7.5' topographic quadrangle was subdivided into six geographically equivalent areas or Atlas Blocks (Nicholson and Hamel, 1986). For every 7.5' quad, three of the Atlas Blocks, or ABs were further randomly selected so that no more than half of a 7.5' quad would be sampled in any one year.
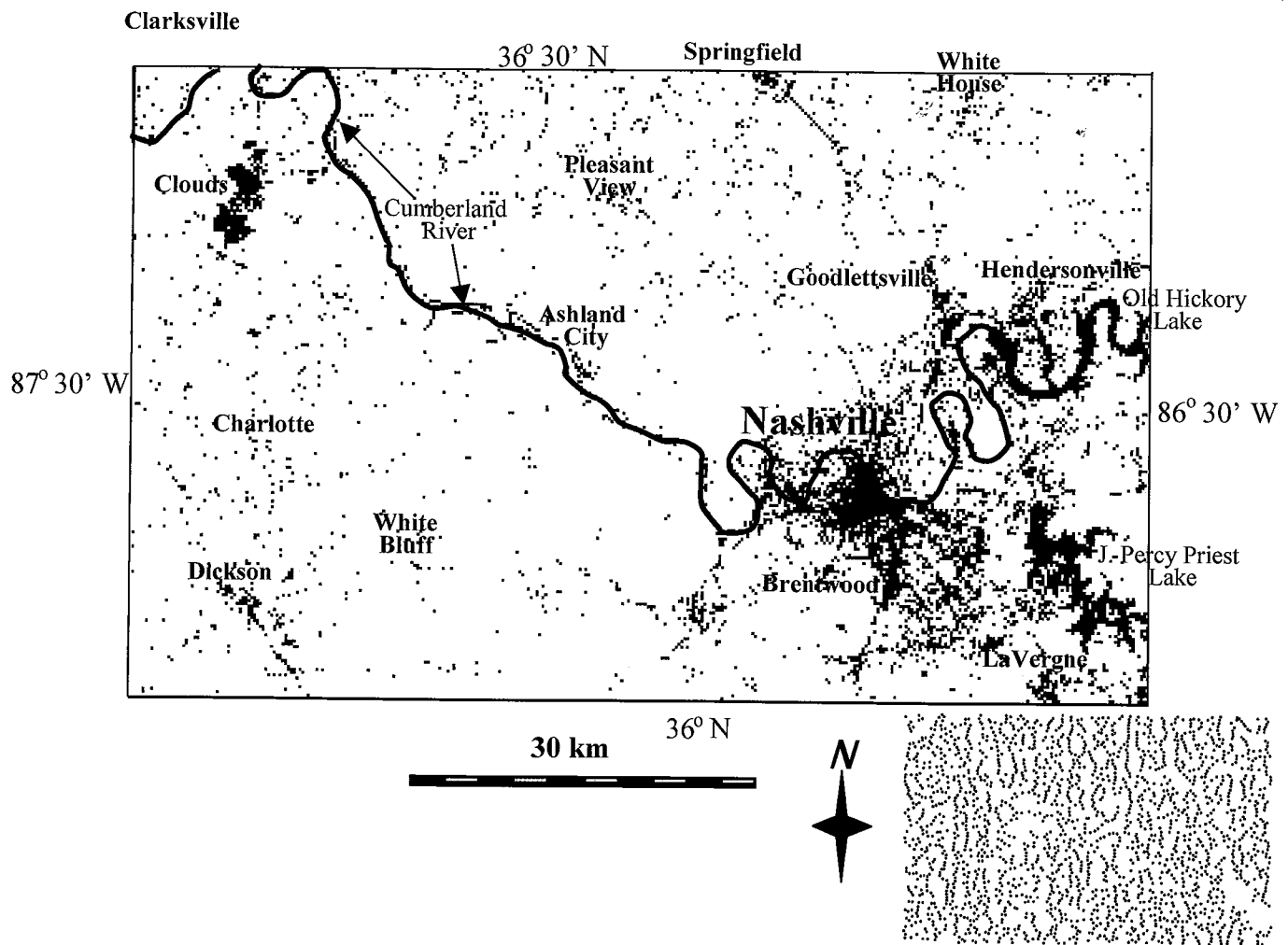
Study Area

FIG. 1.   The study area. (Inset figure is the complete distribution of roadside survey locations.).

Furthermore, the order in which the 7.5′ quads were sampled was randomly selected. All of these point locations were hand digitized into a geographic information system (Butler, 2001).

I located the mapped survey location in the field with each of the 2,021 point-counts being sampled for breeding bird richness in good weather for three or five min and were conducted from 1993–1996, between 15 May–17 July and 0500–1100 h (Butler, 2001). Survey locations (point counts) were visited once and were within 20 m from the edge of the road surface. Bird species that were either seen or heard and estimated to be within 300 m of the observer were recorded. I estimated distance by observing birds in the field and then gauging their distance by using USGS 7.5′ topographic maps. I conducted several of these distance estimation sessions at the beginning of each field season. Because of the differences in study area land cover from urban and large fields to bottomland forests, detectability of birds would vary. Bird detection distances in forests would likely be less than distances in fields and urban areas. Thus, 300 m was chosen as a best estimate to represent an overall study-area average maximum for breeding bird detection.

Recording birds from roads may impact bird detection and species composition. In other work in this area, we examined the effect roads might have on breeding bird sampling as compared to a similar number of points not constrained to roads (Butler and Eickmeier, unpublished observations). We found that possible local effects of roadside sampling decrease when the number of species, number of points and/or the spatial scale of the analysis increase. Thus, local variations that might bias avian landcover assessments at small spatial scales decrease at larger levels of investigation. This follows since local variations between point counts contribute less to diversity as the number of species, number of sample points and the size of the study area increases (Butler and Eickmeier, unpublished observations).

Breeding Bird Data—Breeding-bird data were separated into four groups: total species, resident species (RS), short-distance migrants (SD), and Neotropical migrants (NT) (Butler, 2001). RS breed and winter in the same area, SD breed in North America and generally winter in the southern half of the continent, and NT breed in North America and winter in Central and South America and the Caribbean Basin (Hamel, 1992; DeGraff and Rappole, 1995). Neotropical migrants are of special interest in urban assessments because they comprise over half of the North American breeding species and many are declining (Askins et al., 1990; Bohning-Gaise et al., 1993; DeGraaf and Rappole, 1995; Robinson et al., 1995; Flather and Sauer, 1996). Because of the breeding bird objective to this study, non-breeding migrant

species were not considered in the analyses (Butler, 2001 Appendix A). In this context, a migrant species refers to birds that migrate through the area but breed further north.

Avian Diversity—I calculated breeding-bird diversity in two ways: species richness and species diversity. Richness together with evenness describes the diversity of an area. Species richness is the number of species and evenness refers to how well each species is represented by individuals in an area. Often abundance, or number of individuals of each species, is used to estimate evenness.

Some avian studies indicate that avian diversity and density can by higher in relatively urban sites as compared to natural areas (Lancaster and Rees, 1979; Beissinger and Osborne, 1982; Jokimaki and Suhonen, 1993; Blair, 1996). This observation has generally been found to be a function of synanthropic bird species (European Starlings, House Sparrows, pigeons) that have adapted well to human-influenced systems (Beissinger and Osborne, 1982; Johnson, 2001). These bird species also are commonly found in small flocks, even in breeding season. In contrast, breeding Neotropical migrant species in this area are territorial: individuals tend to exclude other members of their species from breeding sites (except for mates). Exceptions found in this area are Chimney Swifts and some swallow species. These adaptive and behavioral differences between many Neotropical migrant species and resident, generalist synanthropic ones could bias abundance and diversity comparisons between urban/suburban sites and more natural areas.

To address this potential bias I utilized the probability-of-occurrence for each bird species as a measure of evenness. Probability-of-occurrence is the number of point-count or survey locations at which a bird species was observed within a particular site, relative to the total number of survey locations in that site. Implicit in this evenness estimator is the assumption that, within the study area, common bird species would be found at more locations than rare species. Strictly speaking this is a conditional probability. In this case, the conditional probability takes the form:

$$Ps_i(S_x) = F_i(S_x)/Nsl_x$$

where $Ps_i(S_x)$ is the probability of observing species i, in site x, $F_i(S_x)$ is the frequency of species i (number of survey locations species i was observed) in site x, and Nsl_x is the total number of survey locations is site x.

Conditional probabilities for each species were calculated and then summed into an overall probability value for the site. From these calculations, the proportion that each species' conditional probability contributed to the total probability value was computed.

These proportion calculations were then used in a relative-proportion diversity index, the Shannon H' diversity index (Magurran, 1988). The Shannon H' diversity index utilizes the number of species as well as the proportion that each species contributes to a site; it combines both species richness and species evenness (Magurran, 1988). Shannon H' is calculated by:

$$-\sum p_i \text{LN } p_i,$$

where p_i is the proportion that species i contributes to the site and LN is the natural $\log_e$. Higher values of the index represent greater diversity.

Avian Diversity as a Function of Population Density—A well understood correlate to urban land-cover density is population density. To assess a relationship between avian diversity and population density within the study area, I calculated the number of people living in selected areas within the study area as well as for the entire study area itself, from the 1990 United States Population Census (United States Census Bureau). This analysis was independent of spatial scale. Instead this scale-less assessment concentrated on the association between avian species richness as a function of a population density gradient.

Surface Modeling—One of the analytical benefits of a data set consisting of geographically referenced points is that these points can be interpolated into surfaces (Jones, 1997). Surface modeling involves a variety of techniques, but all these techniques are designed to generalize information from specific locations into local and broad trends in varying spatial phenomena (Jones, 1997). All techniques for modeling a complete surface from sample points are based on the assumption that there is local similarity (Jones, 1997). Surface modeling can be separated into two broad interpolation types: linear and non-linear (Jones, 1997; Goovaerts, 1998). Linear methods weight point locations as a function of their distance from other point locations and then estimate the surface; whereas non-linear methods (Kriging) perform a preliminary analysis of the data to determine the nature of the correlations between sample points, and then a function, such as a low-order polynomial, can be used to interpolate the surface (Jones, 1997; Goovaerts, 1998). These types of analyses provide a visual representation of spatial phenomena as well as an analytical layer in the GIS.

Each surface modeling technique utilized point-scale (36 ha) land cover and breeding bird data to create surface models from these point attributes. Point attributes refer to data that are spatially attached to a point location, e.g., elevation, soil type, land cover, or number of bird species (Jones, 1997). The 36 ha scale is the area of a circle 600 m in diameter (449 pixels) centered on the location from which I observed birds in the field. Thus, 36 ha represents the geographic sampling space (300 m maximum distance) surrounding each roadside point count. For the land cover surface models the point values were the proportion of different urban land cover pixels found in each 36 ha area and for the avian surfaces it was the number of species of each bird group per point.

Different surface modeling techniques, even utilizing similar techniques but employing different functions to model the point data set, can result in different surfaces (Jones, 1997). Because this study stresses the spatial relationship between avian richness and urban land cover, utilizing only one surface interpolation technique might by chance either display strong or weak spatial relationships. Thus, to better capture spatial relationships between avian richness and urban land cover, I incorporated two different surface modeling techniques. In this way, there could be a comparison of results by the different methods. Thus, I used both linear and non-linear surface modeling techniques to interpolate the surfaces.

Linear Surface Models—The breeding bird and urban land cover surface linear models (Digital Elevation Models) were constructed by utilizing "nearest neighbor" averages (nearest neighbors is a local set of points) (Jones, 1997; Idrisi 32, 2001). The total number of points to be included in this set is balanced between including a sufficient number of points to indicate general trends but not including too many points, which could over-generalize or "smooth" the surface trends (Jones, 1997). However, to counterbalance a smoothing effect and still include a reasonably large number of points in the nearest-neighbor set, a distance-weighting variable is added to reduce the contribution of

more distant points in the nearest neighbor set. A common distance weighting procedure, and the one used here, is to weight a sample point in the nearest neighbor set inversely proportional to the square of its distance from other points in the set (Jones, 1997; Idrisi 32, 2001).

Because the number of species, an integer value, was utilized to create the avian species linear surface models, I created two different urban linear surface models. For the first surface model, the urban proportion data were subjected to a statistical clustering process. All 2,021 points were utilized in this clustering process (K-means cluster analysis, SPSS) and this technique generated six classes or clusters representing an urban land cover density gradient. The number of clusters (6) was chosen to reasonably represent an urban gradient across the study area and it followed methods used in other urban/avian studies (Blair and Launer, 1997; Blair, 1999). Once the clusters were derived, integer values were assigned to these clusters, with the cluster containing the highest average amount of urban land cover being assigned "0" and the cluster with the least average amount of urban land cover being assigned "5". When visually representing these type surface models, it is often the convention that the lowest values are displayed with darker colors, higher values lighter colors. Thus to be more consistent with the visual display properties of the avian richness surfaces, the densest urban clusters were darker than the least dense urban clusters. This linear model could then be assessed using GIS techniques.

The second urban linear model was a more continuous type representation. Instead of clusters, the proportion data were converted into percent urban data for each 36 ha site and these values were used to create a percent urban linear surface model. This model was used to statistically assess the spatial relationship between urban land cover and avian species richness.

Kriging—Kriging encompasses a variety of statistical and spatial interpolation techniques that use existing data to estimate values for unsampled areas (Goovaerts, 1997). Whereas the previous surface modeling procedure utilized linear functions to estimate surface values from point data, Kriging can utilize nonlinear functions to estimate surface values from point data (Goovaerts, 1997). The resulting Kriged surface models of breeding bird richness and urban density represent a surface of probability values. The probabilities are the likelihood of observing a particular number of bird species in an area or the expected density of urban land cover. The Kriging process generally follows a three-step approach: assessment of spatial dissimilarity (inverse of spatial similarity), model fitting, and surface interpolation.

Kriging, which is a subset of geostatistics, utilizes variogram calculations to estimate spatial dissimilarity. Variograms calculate the average degree of spatial dissimilarity between attribute values that are solely based on their membership in user-defined intervals of distance and direction (Goovaerts, 1997). The most common form of variogram calculations is the semivariogram. In this case, half the average squared differences of paired attributes are calculated (Goovaerts, 1997). As a result, variograms produce graphical representations of spatial dependency in multiple directions. From the shape of the variogram function, an appropriate mathematical model is fit, and the surface interpolation process determines a surface by fitting estimated values to the unsampled locations (Goovaerts, 1997).

A closely related function to the variogram is the correlogram (Goovaerts, 1997). The correlogram is an autocorrelation function that describes the correlation (as a correlation coefficient r) between attributes and the distances between them. I calculated the cross-correlogram function between avian richness and urban density. This method thus assessed the spatial correlation between avian diversity and urban density as a function of distance.

Spatial Autocorrelation, Statistical Inference, and GIS Functions—Spatial autocorrelation occurs when adjacent variables are either similar (positive autocorrelation) or dissimilar (negative autocorrelation) as compared to distant ones (Jones, 1997). Measures of spatial autocorrelation quantify the spatial interdependence between variables. Spatial autocorrelation has special relevance in ecological assessments because organisms are distributed over the Earth's surface and distributions are inherently spatial. Organisms are likely restricted in space because they respond to environmental factors as well as habitat types, which themselves are spatially autocorrelated (Legendre and Legendre, 1998). On the one hand, patterns that exhibit spatial autocorrelation in organismal and environmental factors help explain ecological process, but on the other hand, interrelated variables violate statistical assumptions regarding independence and thus can inflate statistical associations.

I addressed the autocorrelation of the avian and land cover variables by conducting a GIS technique called pixel thinning (Idrisi 32, 2001). First, all original images were analyzed for spatial autocorrelation (Moran's I, King's Case, Idrisi 32, 2001). Next I conducted spatial regression between the avian and urban surface images. Spatial regression is similar to regression but the paired variates are statistically assessed while incorporating their geographic locations. The regression coefficients were then transformed into correlation coefficients and then assessed for statistical significance. Since there were multiple statistical tests, Bonferoni correction of the generally accepted level of statistical significance ($P \leq 0.05$) was used. The results of this analysis would include biases influenced by autocorrelation, but would also act as a control for the other statistical trials. Both sets of surface images, linear and Kriged, were then "thinned". Thinning removes pixels from the images and then recombines the remaining pixels into a single image (Idrisi 32, 2001). The pixel thinning protocol I followed thinned the images by retaining every 200th pixel in both the X (Longitude) and Y (Latitude) directions. This degree of thinning followed from iterative thinning steps that best reduced spatial autocorrelation while simultaneously leaving a statistically robust sample size ($n = 198$). Then these thinned images were subjected to spatial regression (Idrisi 32, 2001). Statistical analyses between these new sets of images would then better reflect avian/urban land cover associations with autocorrelation bias minimized.

I used a GIS procedure called Image Overlay (Idrisi 32, 2001) to assess the relationship between breeding bird richness and amount of urban area. In this procedure different images are overlaid to produce a single image that combines the attributes of interest from the previous images. Thus, the resultant image is an analytical combination of the previous images. The urban clustered, linear image and the Neotropical migrant richness linear image were overlain and the values at each pixel location were summed to produce a single image. This image was then reclassed (Idrisi 32, 2001). Reclassifying assigns new pixel values to an image that then can be displayed as a new image.

GIS functions include the ability to create images that depict distances. I created a distance image of the study area that indicates increasing distances from urban pixels or locations. Distances were defined in meters.

Number of Species as a Function of Time—At a single point count location, three min may be too short a time period to make
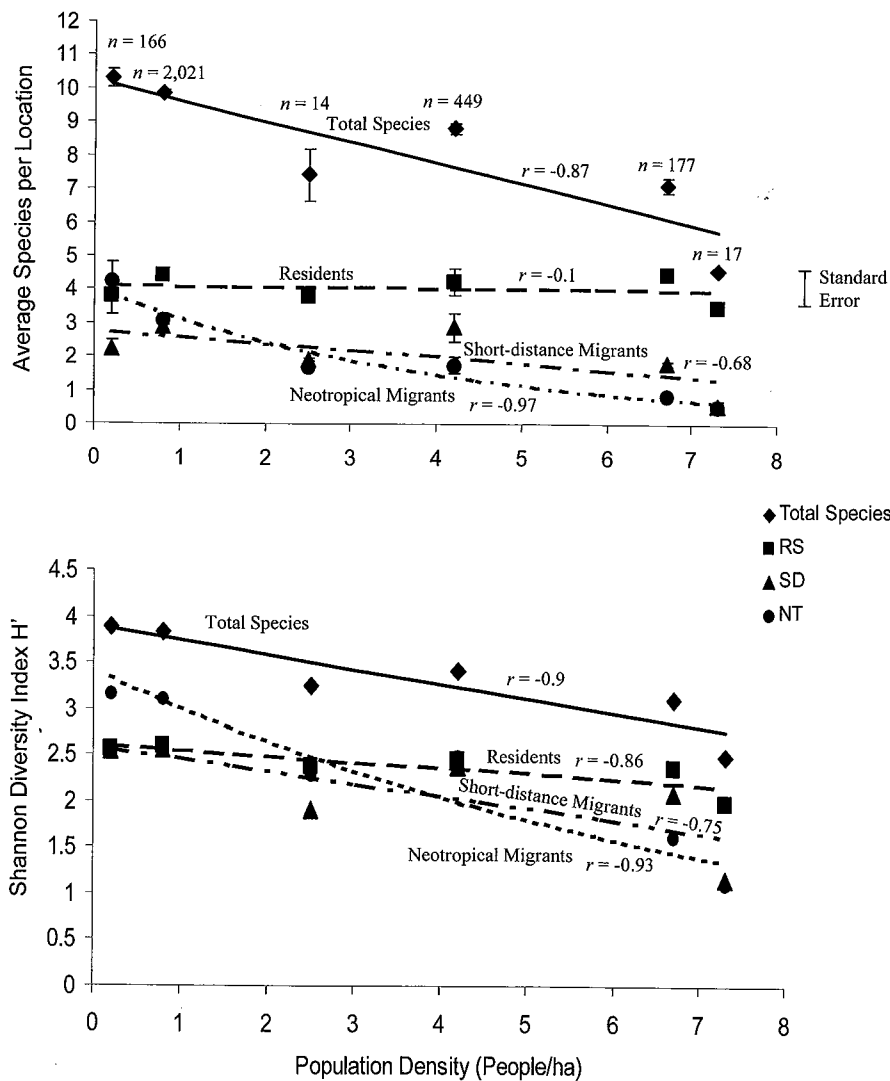
FIG. 2.　　The trends between average number of species and species diversity with population density.

accurate avian diversity assessments. However, for large areas and many point counts, three min is likely a reasonable time limit (Smith et al., 1993; Butler, 2001). To assess possible effects of point count duration on avian richness assessments, I randomly selected 300 point count locations and performed five-min point counts. In addition, I randomly selected 200 of these five min counts and calculated the number of species for the time interval between three and five min as a function of the proportion urban land cover. Then the number of species was correlated with proportion urban, at the 36 ha scale, for three and five min and the time interval between three and five min. This method would thus allow for time-based comparisons of breeding bird richness and urban land cover.

RESULTS

Avian Diversity and Population Density—There was a strong association between urban land cover density and population density in the study area. The correlation (Pearson Product Moment, PPM) between population and urban density is statistically significant ($r = 0.92$; $P < 0.01$; $d.f. = 4$). The correlations between total, resident, and short-distance average number of

species per location and population density were not statistically significant (Bonferoni correction $P \leq 0.0125$) (Fig. 2). Of these three trends, total species exhibited the strongest association ($P < 0.05$, $d.f. = 4$) and residents exhibited a virtually level trend with increasing population density (Fig. 2). Both the average number of resident and short-distance migrant species were negatively associated with population density (Fig. 2). In contrast, the average number of Neotropical migrant species per location was significantly ($P < 0.005$, $d.f. = 4$) negatively correlated with population density and was exponentially associated with population density as compared to the linear associations found in the three other bird groups (Fig. 2).

The avian diversity vs. population density trends exhibited similarities to the species richness trends (Fig. 2). Total, resident, and short-distance migrant species diversity linearly decline with increasing population density as before and total species is the most highly correlated group of these three (PPM, $P = 0.016$, $d.f. = 4$). Resident species diversity, however, exhibited a relatively stronger negative association with population density than did the average number of resident bird species per location did and decreased to a greater degree as compared to total and short-distance migrant species (Fig. 2). Neotropical migrant diversity

exhibited an exponentially declining trend with increasing population density and was statistically significant (PPM, $P < 0.008$, $d.f. = 4$, Fig. 2). Furthermore, the diversity of Neotropical migrant species was greater than resident and short-distance migrant species at lower population densities and less than resident and short-distance migrant species at higher population densities (Fig. 2).

Semivariograms and Cross-correlograms—All of the semivariograms contain a nugget effect (Fig. 3). A nugget effect occurs when the semivariogram function does not originate at the origin of the X-Y axes (Goovaerts, 1997). The nugget effect indicates that there is no spatial dependence or "noise" in the data. Because the point-count methods dictated that no points would be closer than 800 m, no assessment of spatial interaction at lesser distances could be calculated; thus, the semivariograms would exhibit a nugget effect of at least 800 m (Butler, 2001; Fig. 3).

Two major spatial trends emerge from the semivariogram analyses. The first is that residents and short-distance migrant species exhibited little spatial dependence at any distance (Fig. 3). Both these semivariogram functions are virtually linear and level (Fig. 3B and C). Semivariogram functions that do not initially increase, but remain virtually flat, indicate that there is little spatial dependence of the variable assessed (Goovaerts, 1997). The second trend is that both Neotropical migrant species and urban density exhibited strong spatial dependences at distances less than 10,000 m (Fig. 3D and E). These two functions resemble exponentially increasing functions with asymptotes. Where these functions reach the asymptote is called the sill; at this distance (X-axis) there is no spatial dependence (Goovaerts, 1997). The Neotropical species function reaches a sill at approximately 20,000 m; urban density at approximately 18,000 m (Fig. 3D and E). Lastly, total species appears to exhibit small spatial dependence between points at distances less than 5,000 m. At greater distances the function quickly flattens out and resembles the resident and short-distance migrant functions (Fig. 3A, B and C).

The cross-correlogram results also exhibit two major patterns (Fig. 3). The magnitude of the correlation values for residents and short-distance migrants with urban land cover are generally an order of magnitude less than the correlation values for both total and Neotropical migrant species (Fig. 3). These results indicate that residents and short-distance migrants generally tend to exhibit less spatial association with urban land cover as compared to Neotropical migrant species as well as when all species were combined (Fig. 3). At distances less than ≈ 30,000 m, Neotropical migrant species richness was negatively associated with urban land cover and at distances greater than ≈ 30,000 m, Neotropical migrants were positively correlated with urban land cover in the study area (Fig. 3D).

Urban Density and Avian Richness Surface Modeling—For both the Kriged and elevation (linear) surface models similar patterns emerge for avian richness and urban density (Fig. 4). Generally there were fewer total species in the southeastern portion of the study area than elsewhere (Fig. 4A). Resident species were found less often in the central portion of the study area (Fig. 4B). Both total and resident species tended to exhibit a mosaic pattern of species richness where species rich areas were interspersed with species poor ones (Fig. 4A and B). In contrast, the short-distance migrant surface models contain larger areas of similar richness patches than the resident image (Fig. 4C). In this case, zones of relatively low short-distance migrant richness oc-cur in the southeastern and south-central portions of the study area (Fig. 4C).

The most distinct pattern between relatively species poor and species rich zones is found on the Neotropical migrant surface images (Fig. 4D). In these surface models, large zones with relatively few Neotropical migrant species are observed over much of the southeastern portion of the study area (Fig. 4D). In addition, low Neotropical migrant species zones occur in the southwestern corner and along the northern edge of the study area (Fig. 4D). In contrast, relatively rich Neotropical migrant species zones occur over much of the central portion of the study area (Fig. 4D).

The urban surface images reveal that urban land cover predominates in the southeastern corner of the study area as well as forming smaller patches over much of its eastern portion with other smaller clusters found throughout the remainder of the study area, especially the southwest corner (Dickson) (Fig. 4E).

The urban clusters that resulted from the cluster analysis were (1) between 90 and 100% (Most Urban) urban land cover ($n = 15$ point counts); (2) the Highly Urban (60–89% urban) zone contained 36 point counts; (3) between 40 and 59% urban (Urban zone) contained 65 point counts; (4) between 10–39% urban (Suburban) contained 228 point counts; (5) the Low Urban zone (3–9% urban) contained 281 point counts, and (6) the Rural zone contained 1,396 points counts and was less than 3% urban land cover.

The urban surface image that resulted from the statistical clustering procedure exhibits distinct urban density zones (Fig. 4F). The 'Most Urban' zone formed two major clusters: one was Nashville's central city core area and a second area northeast of this downtown area and totaled 1,715 ha (Fig. 4F). The 'Highly Urban' zone covered a total area of 6,807 ha and was closely associated with the 'Most Urban' areas (Fig. 4F). The 'Urban' zone covered a total area of 13,137 ha and tended to border the previous two zones as well as being found in the Study Area's southeastern, southwestern and northern portions (Fig. 4F). The 'Suburban' zone covered 43,817 ha and is found throughout the southeast corner of the study area as well as the southwest and in small patches throughout the study area (Fig. 4F). The 'Low Urban' zone covered 96,986 ha and is located at the outskirts of the previous zones as well as forming small disjunct patches (Fig. 4F). Finally, the 'Rural' zone covered 331,939 ha. Although this zone was almost completely missing from the southeastern corner of the study area, it comprises the vast majority of the central and western portions (Fig. 4F).

A general difference between the Kriged surface and linear interpolated elevation models is that the Kriged images tended to represent larger zones of similar species richness, or were more homogeneous than the elevation models (Fig. 4A–F). This condition resulted from the Kriging statistical process of deriving the surface functions. The statistical procedures in the Kriging process calculated decimal portions for avian species probabilities. Since decimal or fractional predictions of species are not biologically appropriate, all values in this process were rounded to integer values. As a result, this process tended to produce larger, or smoother surfaces in the Kriging method than in the linear interpolation method. However, the general patterns between these two surface modeling techniques are reasonably similar (Fig. 4A–F).

Species Richness and Urban Zone Associations—Statistical analysis between the average number of species and average percent of urban land cover in each of the six urban clusters or zones
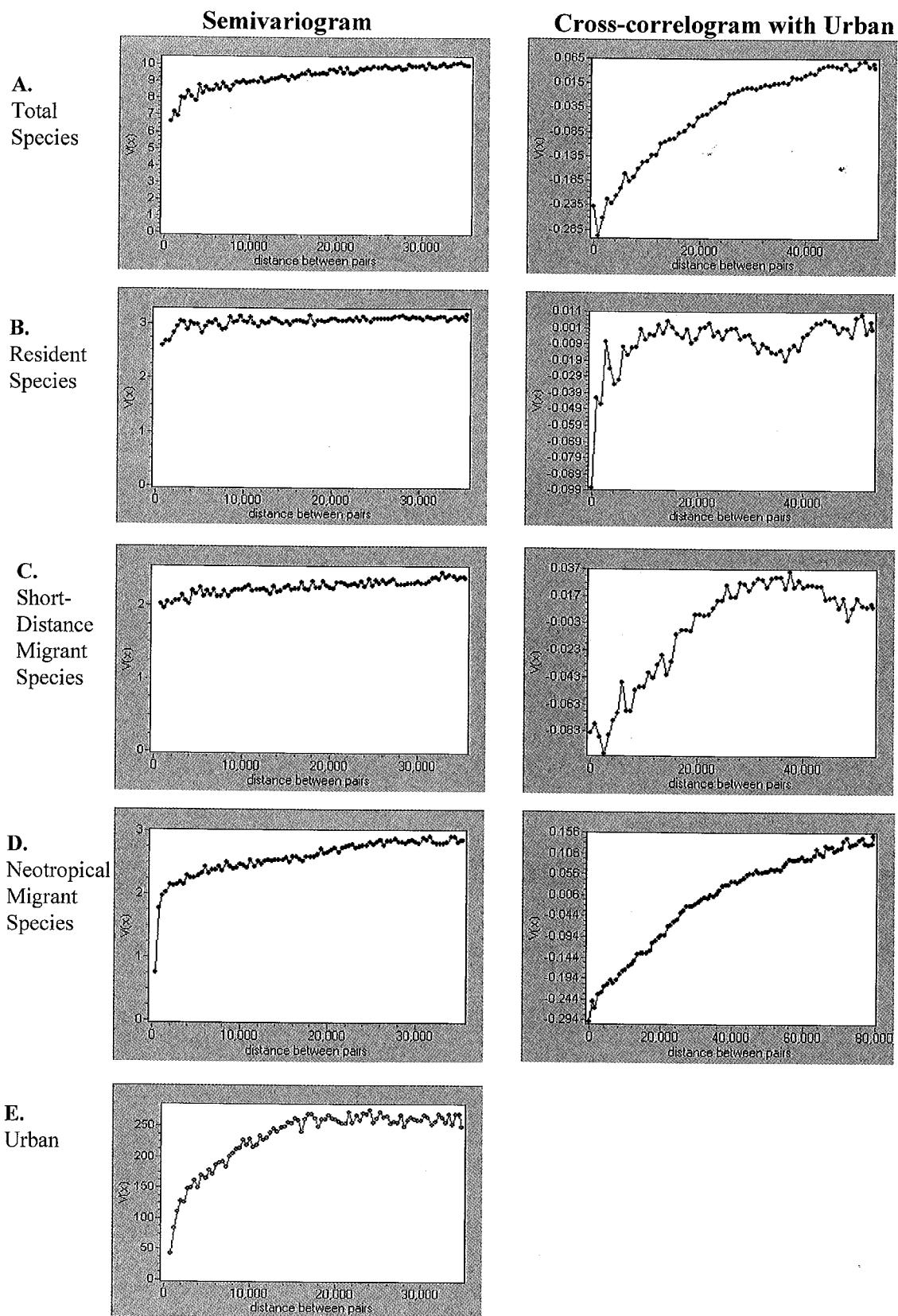
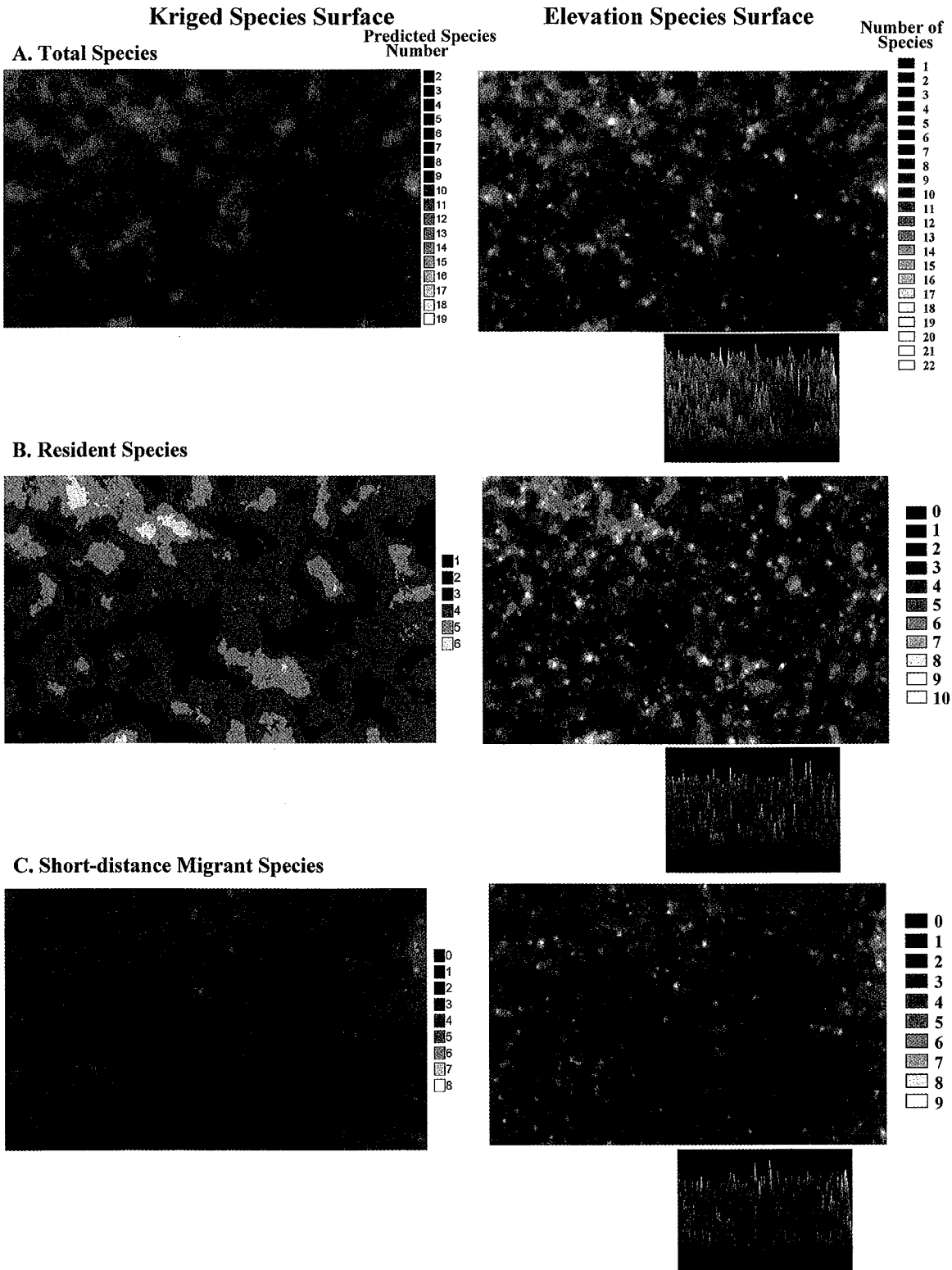FIG. 3.   Semivariogram and cross-correlogram results.

FIG. 4.   Kriged and linear elevation surface models for breeding bird richness, percent urban land cover, and urban land cover density clusters. These figures show similar zones (urban land cover density or avian species richness) by using a gray-scale color code. For all the avian surface models, zones where fewer species were observed are denoted with darker gray tones and zones with more species are coded with lighter gray tones. For the percent urban land cover surfaces, the darker the color the lower the percent of urban land cover in the area, but to be more visually consistent with the elevation models, the urban land cover cluster surface image shows denser urban areas with darker gray tones and less dense areas with light gray tones. A three-dimensional topographic relief image inset is displayed beneath each linear (elevation) surface. These relief images are displayed as if the observer is viewing the study area from the south and is 35° above the horizon.
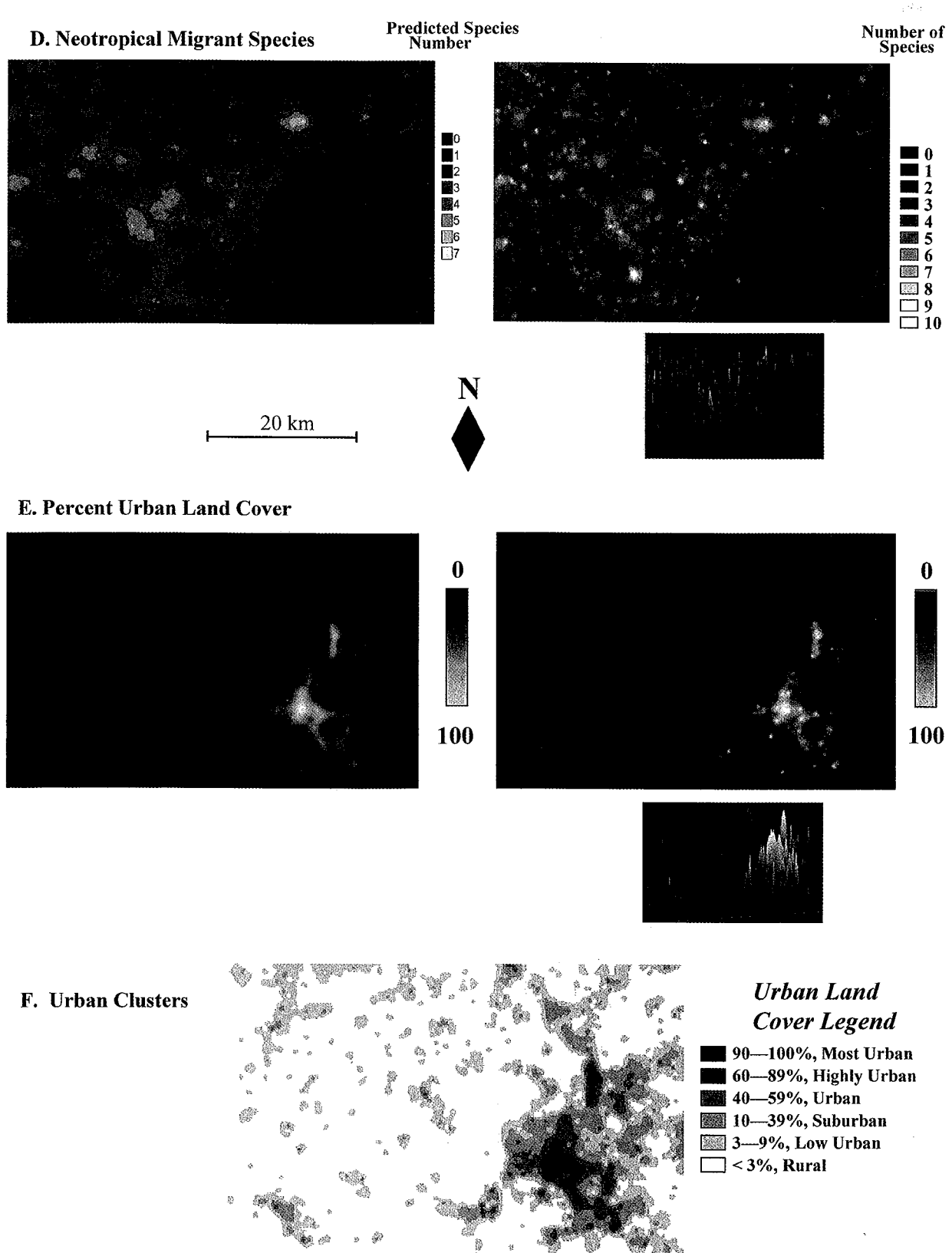
D. Neotropical Migrant Species   **Predicted Species Number**   **Number of Species**

E. Percent Urban Land Cover

F. Urban Clusters   *Urban Land Cover Legend*

90—100%, Most Urban
60—89%, Highly Urban
40—59%, Urban
10—39%, Suburban
3—9%, Low Urban
< 3%, Rural

FIG. 4.   Continued.

resulted in all species groups exhibiting significant negative trends with increasing urban land cover (PPM, $P < 0.005$, $d.f.$ = 4, Fig. 5). The main difference between the bird groups is that Neotropical migrant species exhibited an exponentially declining association with increasing urban land cover density whereas all other groups exhibited linear relationships (Fig. 5). In fact, average Neotropical migrant richness declined by 87.2% from the least urban to most urban clusters, whereas, total species declined
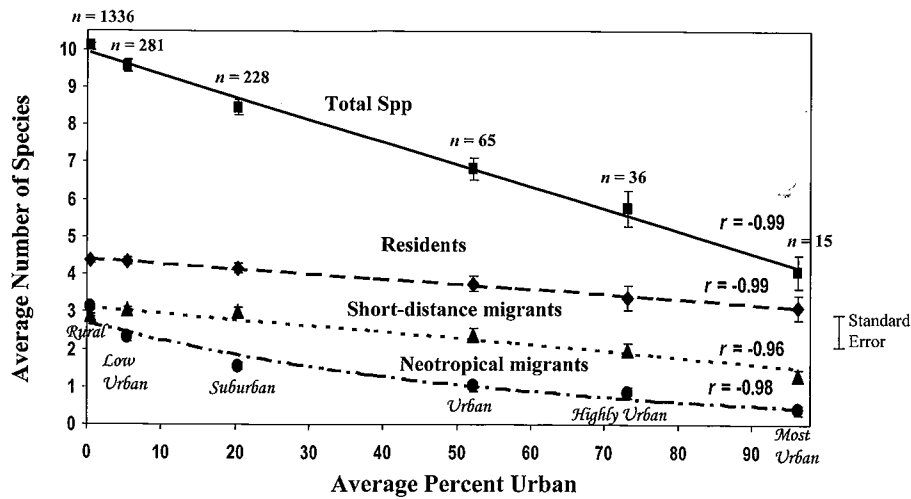
FIG. 5.   Trends between the average number of species and average percent urban for the urban clusters derived from the K-means clustering analysis.

59.6%, short-distance migrants 56.3%, and residents only declined 28.2% (Fig. 5).

Spatial Statistics—Virtually all of the surface models exhibited spatial autocorrelation where values for the surface variables tended to be clustered in space (Table 1). The full, or non-thinned images were autocorrelated to a greater degree than the thinned images and the magnitude of Moran's I coefficients between the Kriged and linear surfaces were relatively similar (Table 1). In addition, the Moran's I values among the surface variables for both the full Kriged and linear surfaces were relatively similar (Table 1). The thinned surfaces exhibited much less autocorrelation than the full images; often the magnitudes were less than half the full images (Table 1). The two surface variables with the highest degree of autocorrelation in the thinned images were Neotropical migrant richness and urban (Table 1). Resident species exhibited the least level of autocorrelation in the thinned surfaces (Table 1).

Results of the spatial regressions between the full, not thinned, Kriged and linear avian species and urban percent land cover images reveal that both total and Neotropical migrant species were the most highly correlated with urban land cover (Table 2). Given the sample size of over eight million pixels, even very small correlation magnitudes would be needed for statistical significance; as a result, all the spatial regressions of the full surface images were statistically significant (Bonferoni correction, $P \leq 0.0125$, Table 2).

Even though the correlation coefficient magnitudes remain virtually identical for the spatial regressions between the avian species and urban land cover thinned surfaces as compared to the full surface regressions, not all of these spatial regressions were statistically significant ($P \leq 0.0125$, Table 2). Spatial regressions between resident species and urban land cover were not significant (Table 2). Short-distance migrant species and urban land cover for the thinned images were statistically significant (Table 2). However, as compared to both total and Neotropical migrant species and urban land cover, the magnitude of the short-distance correlation coefficients was less than half (Table

TABLE 1.   Autocorrelation (Moran's I) of the different surface models. Thinned surfaces represent a lag factor of 200.

	Moran's I		Moran's I
Kriged surfaces		Linear surfaces	
Total	1.5	Total	1.56
Resident	1.49	Resident	1.57
Short-distance	1.52	Short-distance	1.42
Neotropical	1.54	Neotropical	1.65
Urban	1.55	Urban	1.4
Thinned kriged surfaces		Thinned linear surfaces	
Total	0.4	Total	0.19
Resident	0.2	Resident	0.09
Short-distance	0.3	Short-distance	0.11
Neotropical	0.62	Neotropical	0.39
Urban	0.6	Urban	0.62

TABLE 2   Spatial regression analyses between number of species and proportion of urban land cover (regression coefficients, R^2, were converted to correlation coefficients, r).

	Between the linear species and urban surfaces ($n = 8 \times 10^6$)	Between the kriged species and urban surfaces ($n = 8 \times 10^6$)
Total species	$r = -0.43, P < 0.001$	$r = -0.59, P < 0.001$
Residents	$r = -0.09, P < 0.001$	$r = -0.11, P < 0.001$
Short-distance	$r = -0.21, P < 0.001$	$r = -0.21, P < 0.001$
Neotropical	$r = -0.45, P < 0.001$	$r = -0.55, P < 0.001$
	Between the thinned linear species and urban surfaces ($n = 198$)	Between the thinned kriged species and urban surfaces ($n = 198$)
Total species	$r = -0.41, P < 0.001$	$r = -0.54, P < 0.001$
Residents	$r = -0.09, P < 0.2$	$r = -0.08, P > 0.2$
Short-distance	$r = -0.2, P < 0.01$	$r = -0.22, P < 0.01$
Neotropical	$r = -0.44, P < 0.001$	$r = -0.54, P < 0.001$

2). The thinned total and Neotropical migrant species richness surfaces were significantly correlated with the thinned urban land cover surface (Table 2). The thinned Kriged urban surface tended to be a better predictor of total and Neotropical migrant richness than the thinned linear urban surface (Table 2).

Image Overlays—Because the results of the surface modeling and spatial statistics indicate that Neotropical migrants are the most strongly associated (negatively) with urban land cover as compared to the other bird groups, the linear Neotropical migrant and urban clustered surfaces were overlaid (Fig. 6). This resulted in a surface image with values ranging from 0 (Most Urban zone plus zero Neotropical migrant species) to 15 (Rural zone plus ten Neotropical migrant species) (Fig. 6A). The southeastern corner of the study area contains the greatest amount of darker colored zones (low Neotropical richness plus high urban density) (Fig. 6A). The rest of the image is generally a mosaic of zones representing pixel values ranging from six and seven to 15 (Fig. 6A). Reclassifying this image so that all zones between zero and six become one zone resulted in an image that exhibited large areas of the southeast as well as around other urban clusters where low numbers of Neotropical migrant species were associated with relatively high urban density areas (Fig. 6B). This last result indicated a total amount of area, 156,807 ha, with relatively low Neotropical migrant richness and the location and shape of this area corresponded with the urban zones from Low to Most urban (Fig. 6B and 4F).

Neotropical Migrant Species Richness Predicted Image— The Kriged Neotropical migrant species and urban percent surfaces were spatially regressed to produce an image predicting areas of Neotropical migrant richness as a function of urban density (Fig. 7). The main pattern of this image is the large area of two or fewer Neotropical migrant species corresponding to the urban areas and three or more species of Neotropical migrants (average of all counts = 3) tend to occur in the non-urbanized study area locales (Fig. 7). This result indicates that 146,713 ha of the study area was relatively low in Neotropical migrant breeding bird richness as a result of urban land cover (Fig. 7).

Distance Image—The distance image that resulted indicates increasing distances in meters from urban areas in the study area. Notably, because of the multinucleate nature of urban centers, e.g., towns, cities, or suburbs, there are very few locales in the study area that are more than 13 km from any urban nucleus (Fig. 8).

Species Richness versus Time and Urban Land-cover Density—For all three time intervals, three min, five min, and from three to five min, the number of Neotropical migrant species was significantly negatively associated with increasing proportion of urban land cover (PPM; $P \leq 0.004$, Bonferoni correction; Fig. 9; Table 3). For all three time frames the association between Neotropical migrant species richness and urban land cover was very similar (Fig. 9; Table 3). For both residents and short-distance migrants, as the time frame changed so did the association patterns. Residents and short-distance migrants had either negative or positive associations or significant or non-significant associations as well (Table 3).

DISCUSSION

Breeding bird richness was negatively associated with amount of urban land cover, particularly for Neotropical migrant breeding bird species. It appears that urban land cover can negatively affect Neotropical migran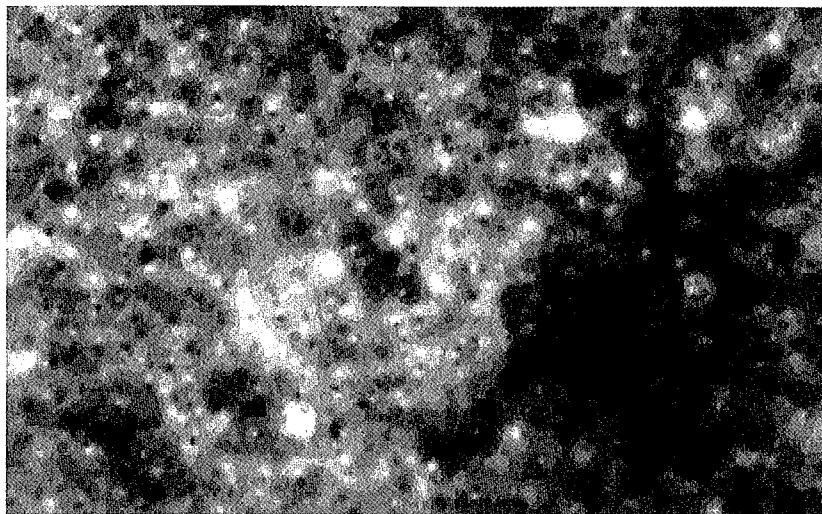t breeding bird richness for up to 20 km. Neotropical migrant richness was negatively associated and spatially coupled to the distribution and density of urban land cover: relatively low numbers of Neotropical migrant breeding birds corresponded to urban areas even where urban land cover density was as low as 10% of the local land cover. From two different assessments, an area of approximately 150,000 ha, or virtually one-third the study area, exhibited relatively low Neotropical-richness. Furthermore, relatively low Neotropical migrant breeding bird richness covered the surrounding urban/suburban area that was over 60 times larger than the intensely urbanized city center of Nashville, 1,715 ha vs. ≈ 120,000 ha. Thus, the urban spatial effect to Neotropical migrant breeding bird diversity extends into the surrounding suburban landscape matrix, and the extent to which this occurs may occupy up to two-orders of magnitude more area than a central business district (Figs. 4 and 7). The spatial extent to which low numbers of breeding Neotropical migrant bird species was found as a function of metropolitan development illustrates the importance of including geographic location as a variable in conservation assessments of avian/land cover trends (Cooper, 2002).

The urban spatial effect observed here is an overarching and broad-scale condition that is likely similar to road effect (Forman and Deblinger, 2000). If roads can impact an area greater than their road surface area alone, then many roads in close proximity to each other as well as with other patches of artificial, impervious surfaces collectively would spatially impact their surroundings to a degree greater than the total impervious surface area alone.
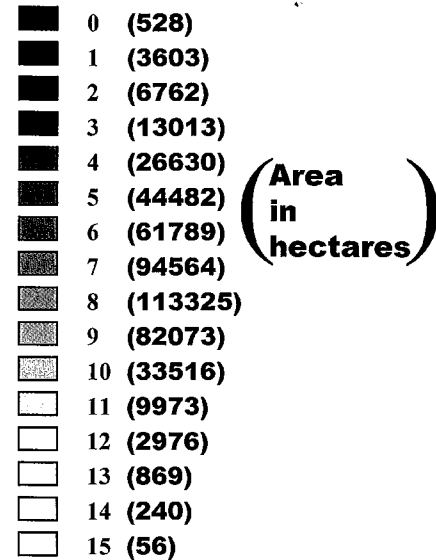
Not only did Nashville exhibit a spatial impact on breeding bird diversity, but also some of the smaller towns in the study area did as well (most notably in the southwest corner). Thus, urban effects on avian diversity are not necessarily just a function of large urban centers. Therefore, instead of just one large, main urban center presenting a front of expanding suburban development within a region, there could be a number of urban/suburban development fronts all spreading out geographically. This type of development pattern could eventually surround existing natural landscapes and isolate them (Askins, 1995). As a result, natural areas can be impacted from a number of directions and addressing conservation concerns in only one urbanized area may not alleviate development pressures on a remaining natural site. Thus, what may appear to be a reasonably large patch of suitable habitat for many Neotropical migrant breeding birds, may be distant enough from one urban center but not from another. Many small development centers distributed throughout a region could effectively reduce the distance between habitat patches and affect avian diversity (Fig. 8).

The growth of multiple urban centers in the United States is even more widespread than indicated in the present study (United States Census Bureau). As a result, the additive spatial effect of urban areas in large tracts of North America could significantly impact native avian diversity. A possible method to assess very large-scale effects of urban growth and development on diversity could be to analyze the spatial relationship between the 'lightprint' of urban areas and animal diversity. The lights from even small urban areas can be recorded by Earth-orbiting platforms (for an example, see the image adapted in Weier, 2000). The glow at night from urban areas corresponds to urban density and development pattern. By utilizing the boundaries different urban density light intensities represent, avian diversity across a light-intensity gradient from which regional-scale impacts of urbanization could be assessed. Furthermore, the present study indicates
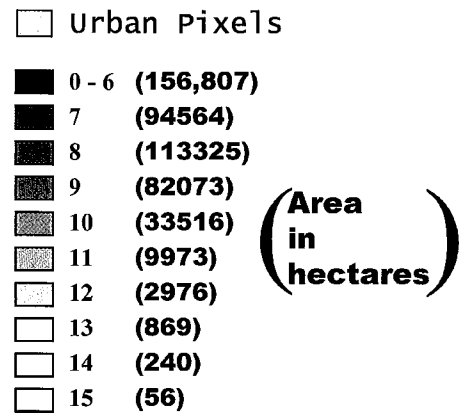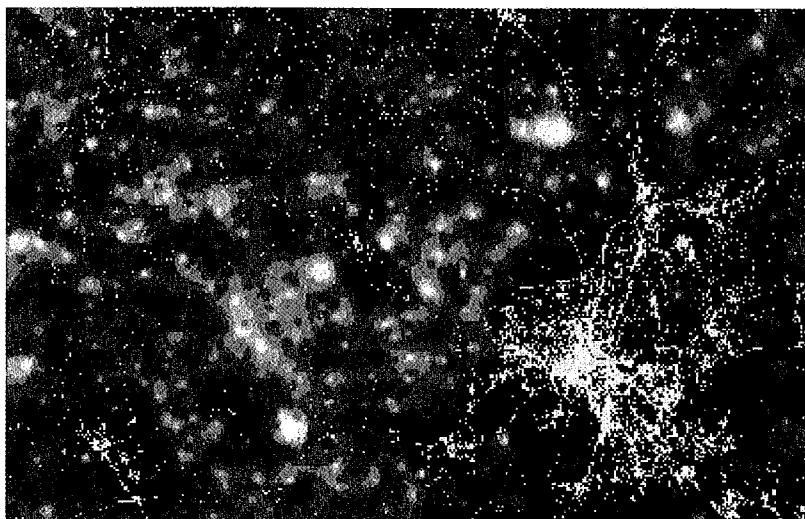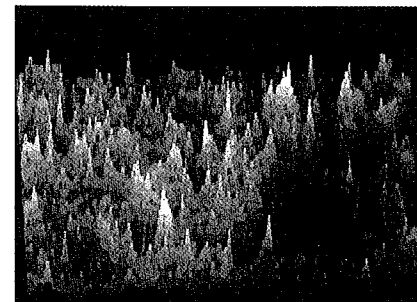
A.

Urban plus Neotropical richness zones

■	0	(528)
■	1	(3603)
■	2	(6762)
■	3	(13013)
■	4	(26630)
■	5	(44482)
■	6	(61789)
■	7	(94564)
■	8	(113325)
■	9	(82073)
■	10	(33516)
□	11	(9973)
□	12	(2976)
□	13	(869)
□	14	(240)
□	15	(56)

(Area in hectares)

N

B.

Urban Pixels

■	0 - 6	(156,807)
■	7	(94564)
■	8	(113325)
■	9	(82073)
■	10	(33516)
■	11	(9973)
□	12	(2976)
□	13	(869)
□	14	(240)
□	15	(56)

(Area in hectares)

30 km

FIG. 6.   Image overlays. (A) This image is an additive image of the Neotropical richness and urban cluster linear surface models. (B) This image combines all values from zero to six from the previous image into one category with an overlay of the distribution of urban pixels derived in the land cover classification process. The three-dimensional image inset is a topographic relief image of the combined and reclassified Neotropical migrant species richness/Urban density surface models. This relief image is displayed as if the observer is viewing the study area from the south and is 35° above the horizon.
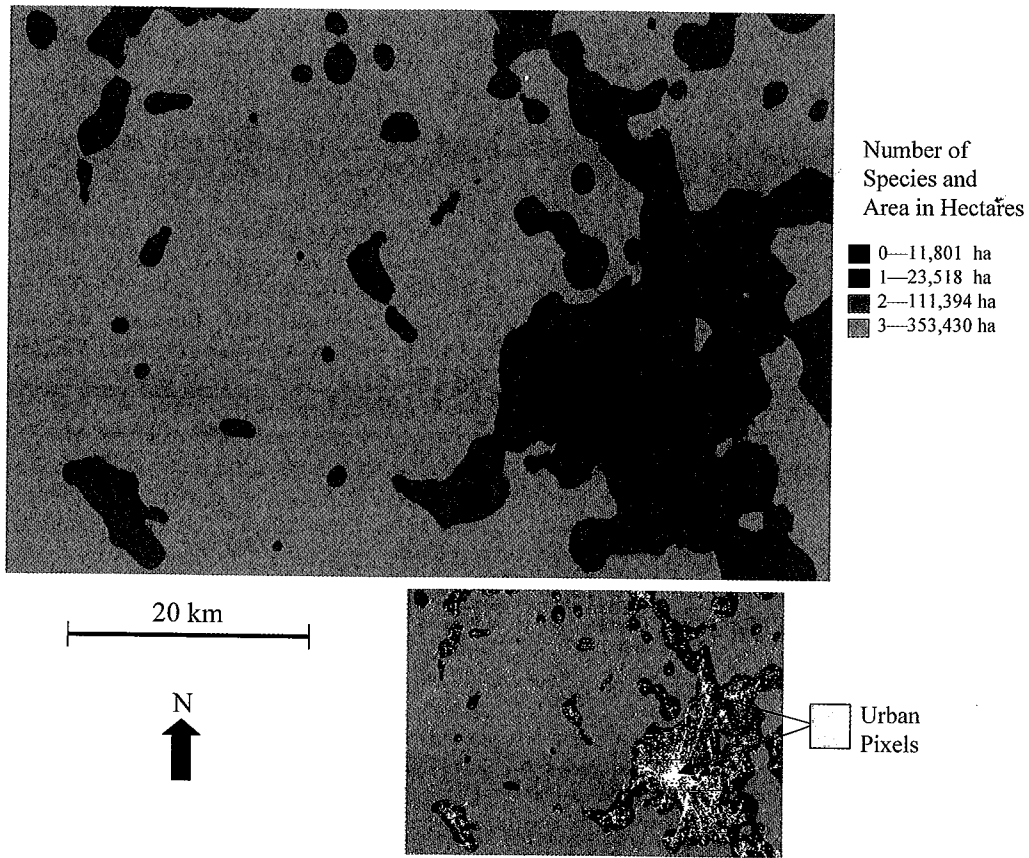
FIG. 7.   The surface image of predicted Neotropical migrant species numbers as a function of urban land cover. The image inset is the same image with the distribution of urban pixels overlaid onto it.
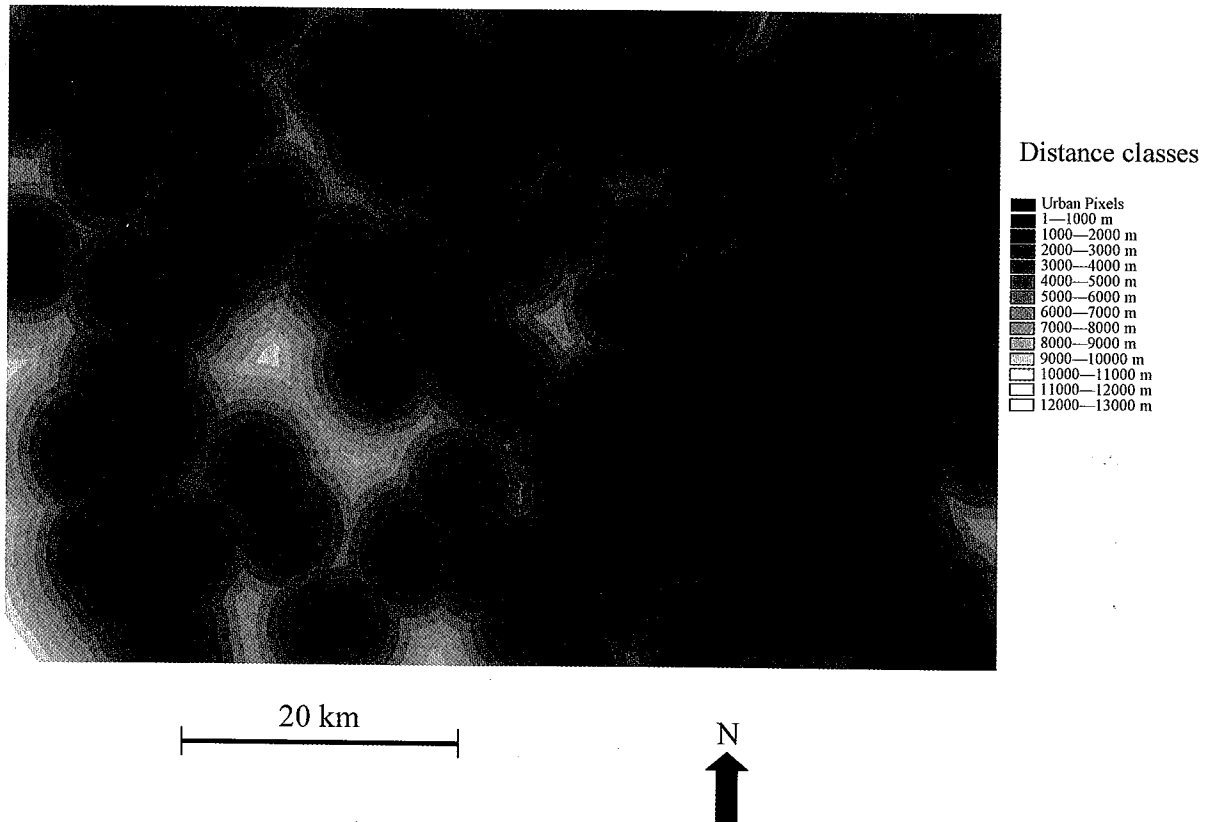

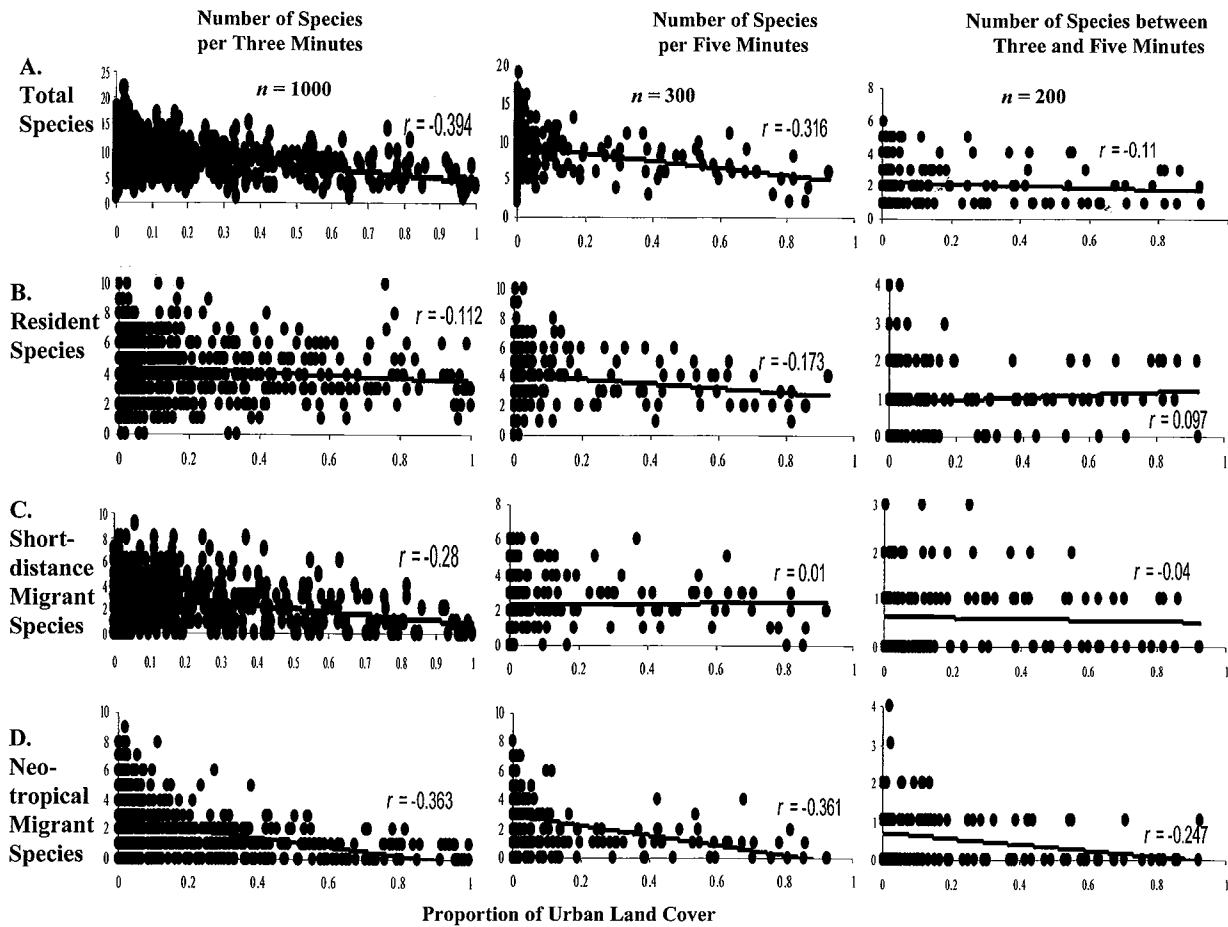FIG. 8.   Distance image. The concentric zone color pattern indicates distances away from urban areas.

FIG. 9.   Trend results of the number of species observed in three, five and between three and five min as a function of urban land cover.

a strong relationship between population density and avian diversity. Thus, utilizing census data could indicate large-scale trends in avian diversity patterns.

Even though the present study revealed a negative trend between breeding bird richness as a function of urban density, other studies have found that suburban sites can be relatively more avian diverse than both natural and dense urban sites (Blair, 1999). Two possible factors, as indicated in this study, could influence such results. First, urban negative impacts to avian diversity are not necessarily a smooth, continuous effect that radiates out equally in all directions from the central city core (Fig. 4). Rather, patches or intrusions of relatively species rich areas can occur and remain in and around a metropolitan area (Fig. 4).

Thus, if one selects only one or a small number of sites to assess urban gradient effects on avian diversity, by chance seemingly 'good' examples of each urban class, even if randomly selected, may contain a higher avian diversity as compared to the bulk of the metropolitan area. Secondly, most sites that are chosen to assess urban gradient effects on biodiversity are relatively small, often less than 500 ha (Emlen, 1974; Beissinger and Osborne, 1982; Tilghman, 1987; Smith and Schaefer, 1992; Catteral et al., 1998; Blair, 1999). As indicated in the present study and previous studies (Bolger et al., 1997; Cam et al., 2000), urban effects on avian diversity can be much more broad-scaled in nature. One of these broad-scale effects is, in Eastern North America, that Neotropical migrant breeding avian richness decreases as a func-

TABLE 3   Correlation coefficient r (Pearson's Product Moment) between number of species and proportion of urban land cover for three different time frames.

	Number of species 3 minutes ($n = 1000$)	Number of species 5 minutes ($n = 300$)	Number of species between 3 and 5 minutes ($n = 200$)
Total	$r = -0.394, P < 0.001$	$r = -0.316, P < 0.001$	$r = -0.11, P < 0.05$
Resident	$r = -0.112, P < 0.001$	$r = -0.173, P < 0.01$	$r = 0.097, P > 0.1$
Short-distance	$r = -0.28, P < 0.001$	$r = 0.01, P > 0.2$	$r = -0.04, P > 0.2$
Neotropical	$r = -0.363, P < 0.001$	$r = -0.361, P < 0.001$	$r = -0.247, P < 0.001$

tion of urban land cover density (Cam et al., 2000; Butler, 2001). What had not been assessed is the overall area to which an urban area impacts avian diversity, especially Neotropical migrant breeding bird richness.

Another factor involved in interpreting urban effects on avian diversity is that, regardless of the scale of the study, study site boundaries are often arbitrarily chosen (Emlen, 1974; Beissinger and Osborne, 1982; Tilghman, 1987; Smith and Schaefer, 1992; Catteral et al., 1998; Blair, 1999). Arbitrary in that sites along an urban gradient are defined, randomly or otherwise, in which bird/urban interactions are assessed, or researchers define the scale of the study usually through some topographic or hydrographic feature (Blair, 1999; Cam et al., 2000). However, urban effects on biotic populations are not solely limited to such boundary delineations. Urban effects manifest through complex social and physical interactions (Dogan and Kasarda, 1988; Geddes, 1997; N'Dow, 1997). Thus, to more fully understand urban impacts on biodiversity small-scale assessments need to be complemented by broad-scaled or overarching studies, especially when attempting to ascertain spatial and boundary effects to biodiversity. The present study was novel in that it derived urban and avian richness boundaries through analyses of empirical measurements: urban data from reflectance values, and avian data from field assessments. These data in combination with a large sample size rendered quantitatively derived boundaries depicting the extent to which an urban area negatively affected Neotropical migrant breeding bird richness.

"Footprint" analysis is a method to assess the geographic impact of urban areas (Wackernagel and Rees, 1997). The urban footprint is the total area estimated to sustain a particular urban population and utilizes calculations of living standards, technological and industrial productivity, and overall population size (Wackernagel and Rees, 1997). However, this type of urban-geographic impact only provides an areal, per capita estimate of a particular human population's resource impact. The shape and geographic location of the urban impact is not revealed; whereas, in the present study not only was an areal estimate of an urban area impact quantified, but also the location and shape of this impact was revealed. For conservation measures, the degree to which an urban area impacts diversity is important, but assessing its location, size and shape could greatly focus conservation actions to more precisely mitigate urban impacts on diversity.

Each city or town would have its own shape and geographic area and their impacts on the native ecosystem may vary depending on the type of native ecosystem or biome in which they developed. However, two characteristics of cities occur independent of their location and the native ecosystem they are replacing. First, urban areas are similar (Manrubia et al., 1999) in that they contain human-made impermeable surfaces: concrete, roofs, macadam, etc. Notably, the land-cover densities of these surfaces range from monolithic in "downtown" areas to more sparse in suburban settings. Secondly, urban impacts to avian diversity, or biodiversity in general, extend beyond their densest urban centers. Therefore, measuring the first characteristic will likely provide a minimal spatial estimate for the urban impact. Elucidating the spatial effect will help to define the overall metropolitan impact on the native ecosystem it is replacing. This effect is not limited to the largest urban centers, as indicated in the present study. Even towns with populations between 10,000 and 12,000 people spatially impacted Neotropical migrant breeding bird diversity (Fig. 7). Thus, cities, both large and small, can spatially impact breeding avian richness patterns to an area relatively

much larger than their "downtown" area alone, and this effect could be termed the Metropolitan Area Effect (MAE). This effect is similar to a city footprint (Marzluff, 2001). However, the spatial impact is larger than the area the city itself occupies. Urban-growth effects on diversity can have both local and regional consequences and in turn conservation initiatives require the simultaneous consideration of local to regional plans.

Understanding and estimating the MAE will be useful based on the following two reasons. First, present knowledge of the urban spatial impact on diversity can be used as baseline data from which future estimates of urban spatial effects can more accurately be made. Second, it can aid regional-scale conservation and management plans by locating and quantifying the spatial extent of urban areas and how their future growth patterns would encroach on surrounding natural areas.

Assessing urban gradient effects on biodiversity requires broad scale approaches that reveal urban impacts. The effects of urbanization could form a framework from which more general questions of ecological interest and application could better be answered (McDonnel and Pickett, 1990). Ecological patterns and their underlying processes are known to occur and act differently at different spatial scales (Wiens, 1987; Levin, 1992). Thus, to assess the overarching geographic impact of large to regional scaled environmental impacts (urban development), studies should be conducted at relevant broad or urban sprawl scales. If ecological phenomena occur at particular scales, then subdividing urban areas to evaluate diversity may only be revealing small-scale effects; whereas, cities can sprawl over hundreds of thousands of hectares (Geddes, 1997).

Broad or large-scale studies complement our understanding of human-induced environmental impacts, e.g., climate change, habitat loss, population growth and urbanization. These impacts act and are expressed across a wide range of scales. Their multiscale nature necessitates the design and implementation of multiple and broad-scaled studies to aid in better understanding impacts to diversity both presently and in the future and locally as well as regionally (Levin, 1992; Butler, 2001).

ACKNOWLEDGEMENTS

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