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Detecting the scales at which birds respond to structure in urban landscapes

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Abstract. Little empirical information exists about how birds respond to urban landscape structure across multiple scales. We explored how the variation in percent tree canopy cover, at four different scales, affected the abundance of bird species across various urban sites in North America. Bird counts were derived from previous studies, and tree patches were measured from aerial photographs that represented areas of 0.2 km^2, 1.5 km^2, 25.0 km^2, and 85.0 km^2. At each of the four areas, we conducted regressions between bird counts and percent cover of various tree patch sizes. From these analyses, we determined the area (called the best prediction area—BPA) and the patch size (called the best patch size—BPS) that accounted for a significant amount of the variation in bird counts, beyond the variation accounted for by these parameters measured at other scales. BPA and BPS were calculated primarily to take into account the high degree of collinearity that existed among the amount of tree canopy cover measured across the four scales.

We calculated BPA and BPS values for a variety of bird species and ascertained whether larger species had relatively larger BPS and BPA values. In the spring, middle-sized to large birds (16.6 g–184.0 g) had relatively larger BPS values than did smaller birds (3.2 g–16.5 g), but in the summer, the largest birds (61.7 g–576.0 g) had small BPS values. Spring BPA values showed a similar result but summer BPA values did not. A majority of birds of all sizes had summer BPA values at the finer scales of 0.2 km^2 and 1.5 km^2. Overall, body size was an approximate predictor of the area and patch size at which a species responds to trees in a landscape, but many exceptions did occur. These exceptions could be related to a variety of factors, one being the difficulty in relating human-biased measurements to avian measurements of a landscape. The method described in this study will help researchers design multi-scale studies to address the effect of landscape pattern on different animal species.

Keywords: urban ecosystems, birds, landscape structure, scale, habitat selection

Introduction

The range of scales over which organisms respond to landscape structure is defined by the spatial extent, or largest area at which an organism responds to heterogeneity in an environment, and the spatial grain, or smallest area at which an organism responds to heterogeneity (Kotliar and Wiens, 1990; Wiens, 1990). The term "response" is defined here as the ability of an animal to utilize structural patches in a landscape (e.g., tree patches). Although extent and grain are the upper and lower boundaries of an animal's perceptive range, there probably is a hierarchy of decisions made within this range when animals select

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habitat (Johnson, 1980; Hutto, 1985; Kotliar and Wiens, 1990; Holling, 1992). Imagine a wren and a hawk flying over a landscape in search of habitat that provides foraging sites, nesting sites, and adequate protection from predators. Both birds go through a nested set of hierarchical decisions, but each bird probably responds to different landscape attributes as a function of its body size. Based on estimated home range areas (Schoener, 1968), we illustrate the different scales at which a red-tailed hawk (*Buteo jamaicensis*) and a Carolina wren (*Thryothorus ludovicianus*) may respond to structure in a landscape (figure 1). The wren operates at a finer spatial grain and extent than the hawk.

To distinguish between the different hierarchical levels of selection between grain and extent, we have adapted Johnson's (1980) concept of selection order. *First-order selection*

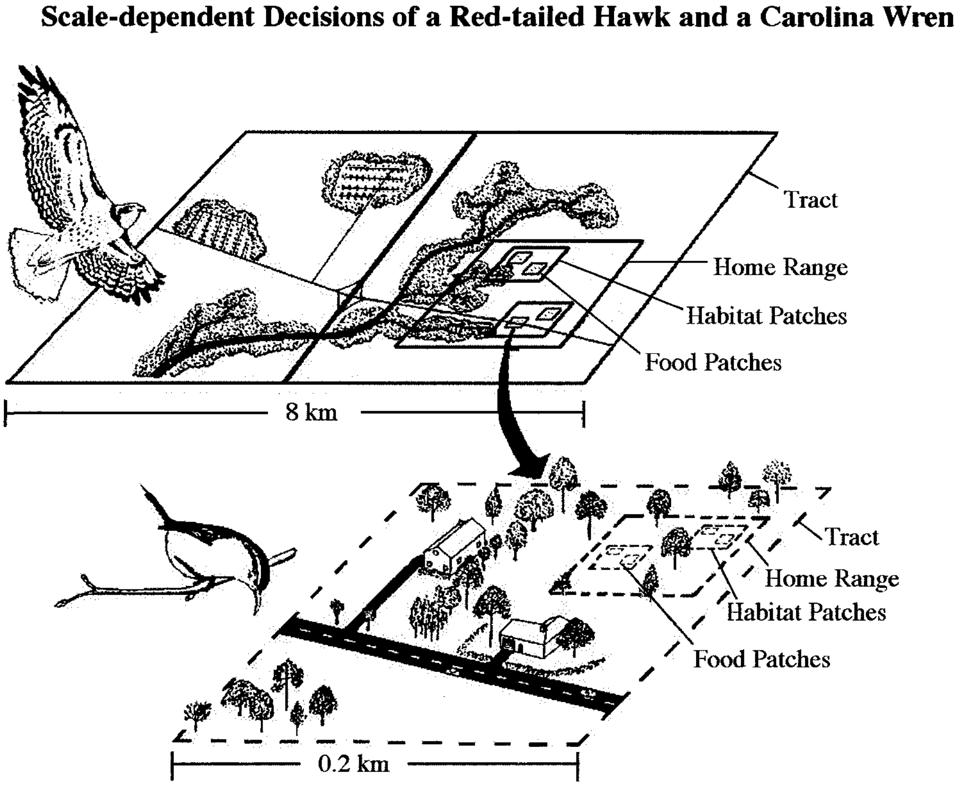

Figure 1. Different scale-dependent landscape structures responded to by a wren and a hawk. Notice that the only overlap in the types of objects sampled by the two birds is at the food patch level (fourth-order selection) for the hawk and at the tract level (first-order selection) for the wren. At the upper boundary of scales relevant to a wren, the wren searches a region (spatial extent of 0.1–0.4 km^2) to locate a tract of land (spatial area of 0.01–0.04 km^2) that has ample resources to survive harsh times; next, the wren searches this tract to establish a home range (spatial area of 1000.0–4000.0 m^2); at the next scale, the wren searches its home range for suitable foraging patches (spatial area of 100.0–400.0 m^2); then, within these foraging patches the wren locates areas (spatial area of 10.0–40.0 m^2) where food is abundant; and at the smallest scale, the wren searches these areas where food is abundant for its prey (spatial grain of 0.1–1 cm^2). The hawk has a similar nested set of hierarchical decisions, but it selects much larger areas and objects at each comparable scale (e.g., home range equals a spatial area of 2.0–4.0 km^2).

is defined here as the selection of a tract of land within a region; a *second-order selection* is the selection of a home range area, a wintering area, or a stopover site within this tract; a *third-order selection* is the usage of various habitat patches within the area; and a *fourth-order selection* is the actual procurement of food items within a habitat patch. Higher-order selections are contingent upon lower ones. For example, whether a bird utilizes a particular habitat patch is contingent on whether the bird first established a home range in a given area. Further, note that a bird probably selects a home range based on the distribution of certain sizes of patches within a specified area. Thus, it is important to know not only the scales at which a species responds to structure, but the patch sizes that it utilizes at each scale. Intuitively, birds of different sizes respond to different areas and patch sizes at each selection order, but what are the dimensions of these areas and patch sizes?

When humans alter a landscape, the way animals respond to remnant landscape structure influences whether a species is present in a given area. Fragmentation of a landscape may affect different sizes of animals in markedly different ways (Harris, 1984). For example, Morton (1990) proposed that the extinction of many mid-sized Australian mammals was due to how they responded to fragmented landscapes; their extinction was hypothesized to be a function of their size. Altered fire regimes and the introduction of rabbits reduced patch size and increased patch isolation in Australian landscapes. Presumably, small animals could still find enough resources in the remaining small patches, whereas large animals could travel among patches and utilize clusters of small patches as one big patch. However, middle-sized animals may have gone extinct because they neither could find enough resources within a small patch nor travel between patches. Thus, knowing the relevant area and patch size of different species is critical to understanding how landscape change would affect them.

Many ecologists have recognized that the range of scales relevant to animals is an important determinant in the spatial distribution and population dynamics of animals (Wiens, 1989; Levin, 1992; Wiens *et al.*, 1993). Both landscape ecologists and behavioral ecologists have identified habitat selection and movement by animals as being important in the development of ecological and theoretical models (Turner *et al.*, 1989; Bell, 1991; Hansson, 1991; Krebs and Davies, 1991; Turchin, 1991; Levin, 1992; Pulliam *et al.*, 1992; Wiens *et al.*, 1993). In general, traditional behavioral ecologists conduct research within relatively small areas whereas landscape ecologists conduct research over large areas. Behavioral ecologists have conducted empirical studies on habitat selection and movement by animals within their home range or at smaller scales (e.g., Gass and Montgomerie, 1981). However, empirical studies on how animals respond to landscape structure at broad scales, particularly second-order selection, are virtually nonexistent (Opdam, 1991; Harrison, 1992; Lima and Zollner, 1996). From both an ecological and conservation perspective, two questions about second-order selection are important to address: (1) what are the scales at which different species primarily respond to landscape structure, and (2) what patch sizes do species primarily respond to within these scales?

To address the above questions, we focused on birds that occur in North American urban landscapes because the geometry of these landscapes changes in a variety of ways from fine to broad scales, which was important to our analyses. Operationally, we measured the response of birds in terms of the number of individuals that occur in a particular area. We assumed that bird abundance was correlated to the quantity of vegetative patches in an area. In addition, the range of scales relevant to an organism may be dependent on the life history stage of that organism (Levin, 1992). During the breeding season, birds search for areas in which to nest. During the spring, however, birds that migrate long distances search for stopover sites (Moore and Simons, 1992) and resident species search for sites that permit dispersal (i.e., dispersal mediums). Because of these different life history stages, we examined separately bird survey data collected during the spring migration season and during the nesting season. Our objectives were: (1) to develop hypotheses about how large an area birds use to make a second-order selection; (2) to develop hypotheses about the patch sizes that different species responded to within an area; and (3) to ascertain whether birds of similar sizes responded to similar patch sizes at the same scales. The last objective was explored because many ecological and behavioral traits are correlated with body size (Brown, 1995), and thus size may be a useful and a simple way to gain insight about the scales at which different bird species respond to landscape structure (Wiens, 1989; Holling, 1992).

Methods

Overview

Our analyses involved four steps, which we briefly describe here. First, we obtained bird count data (#birds observed/hr) from studies conducted in various cities across North America. We separated the bird surveys into two groups: (1) surveys that were conducted during the breeding season, and (2) surveys that were conducted during the spring migration season. Second, we gathered aerial photographs of four different spatial areas representing fine to broad scales (0.2 km^2, 1.5 km^2, 25.0 km^2, and 85.0 km^2) that were positioned over the location where birds were surveyed. Within each spatial area, we measured the percent cover of small to large tree patches (partitioned into 11 patch size categories).

The third step was to determine whether the variation in percent tree cover (of any of the 11 patch size categories) could accurately predict the variation in counts for each bird species. Eleven least square linear regressions were conducted for each of the four spatial areas. We compared the regression results across the four areas to determine if a tree patch category at one scale significantly explained more of the variation in bird counts than the other scales. If so, then this scale was named the “best prediction area” (BPA). For each BPA, the 11 linear regressions were compared to determine if one patch size category significantly explained more of the variation in bird counts than the other categories. If so, this patch category was named the “best patch size” (BPS). Thus, BPA and BPS correspond to the area size and patch size that may be of primary importance during a second-order selection of habitat. The final step was to evaluate whether birds of five body-size categories had similar BPA and BPS values.

Urban bird data sets

We used bird data from a number of different published and unpublished studies (see below). Criteria for selection of a study were that it contained a comprehensive bird species list, including information to calculate the mean number of birds observed/hour for each species (i.e., total number of birds observed divided by the number of hours a transect was surveyed), spring and/or summer surveys, an adequate explanation of how birds were surveyed, and the exact locations of the survey routes. All surveys used a line-transect method (Emlen, 1974) to estimate bird abundance and diversity. Observers walked down a road and counted the number of birds seen or heard within approximately 45 meters on either side of the transect. The number of sites surveyed in each study were as follows: Amherst/Springfield, MA had four separate sites (DeGraaf and Wentworth, 1981); Austin, TX had three sites (Sexton, 1987); Blacksburg, VA had seven sites (Lucid, 1974); Chicago, IL had eight sites (Guth, 1980); Seattle, WA had six sites (Penland, 1984); and Vancouver, B.C. had seven sites from Lancaster (1976) and four sites from Weber (1972). These surveys typically consisted of multiple visits to a site over a two-year period.

The bird data were separated into two groups: (1) species counted only during the breeding season, and (2) species counted during the spring migration. The breeding season was defined as the period of time during which most spring migrants have passed through an area and the bulk of fall migrants have not started to fly south. These dates vary among cities, depending on latitude, and were either gathered directly from the reports or a local expert was contacted. A total of 31 sites were included in the breeding season data set, from Chicago, Amherst, Springfield, Austin, Blacksburg, and Vancouver. For the spring migration data set, 23 sites from Chicago, Seattle, and Vancouver were included.

Only tree canopy was readily quantifiable from aerial photographs; thus, we were interested only in those bird species that use trees for foraging or nesting. We also included species that nest or forage both in trees and on the ground or the low shrub layer. Ehrlich *et al.* (1988) was used to determine a bird's life history characteristics. Also, certain species may primarily use factors other than tree canopy to evaluate the suitability of an area. For example, cardinals (*Cardinalis cardinalis*) are known to use bird feeders in urban areas, and they may respond to the availability of feeders and not to the amount of canopy cover. A 5-year urban bird study in Amherst, MA (Goldstein *et al.*, 1986) was consulted; those species where abundance was not correlated to vegetation volume were excluded from our analyses. All bird masses (in grams) were derived from Dunning (1993); for each species, the mass was the average of reported male and female masses.

Measurement of tree patches from aerial photographs

All trees, regardless of age class or species, were used in our analyses. We centered aerial photos at three different nominal scales (1:2400, 1:24,000, and 1:40,000) over each survey site in order to measure landscape structure from small to large areas. Photos were taken during the spring/summer (i.e., leaves were on the trees), within 3 years of when the bird surveys were conducted.

Spatial area of measured tree patches. For each survey site, we measured the amount of canopy cover within four different areas from the aerial photographs. At the smallest nominal scale (1:2400), two rectangular areas were measured. The smallest area was 0.2 km^2, which encompasses the home range of all the birds in this study (Schoener, 1968). The other spatial area was 1.5 km^2. At the next nominal scale (1:24,000), the rectangular area was 25.0 km^2.

Table 1. Tree patch size categories for each of the four spatial areas (0.2 km^2 and 1.5 km^2, 25.0 km^2, and 85.0 km^2). The smallest patch size is listed for each category. Patch sizes included in each category are all tree patches that are equal to or greater than the smallest patch size (up to the smallest size in the next category).

Spatial area	Tree patch categories (m^2)										
	A	B	C	D	E	F	G	H	I	J	K
0.2 & 1.5 km^2	36.0	396.0	756.0	1116.0	1476.0	1836.0	2196.0	2556.0	2916.0	3276.0	3636.0
	L	M	N	O	P	Q	R	S	T	U	V
25.0 km^2	2499.0	2.6299 $\times 10^4$	5.0099 $\times 10^4$	7.3899 $\times 10^4$	9.7699 $\times 10^4$	1.2150 $\times 10^5$	1.4530 $\times 10^5$	1.6910 $\times 10^5$	1.9289 $\times 10^5$	2.1670 $\times 10^5$	2.405 $\times 10^5$
	W	X	Y	Z	A	B	C	D	E	F	G
85.0 km^2	6.9420 $\times 10^3$	2.0530 $\times 10^5$	4.0366 $\times 10^5$	6.0202 $\times 10^5$	8.0038 $\times 10^5$	9.9874 $\times 10^5$	1.1949 $\times 10^6$	1.3955 $\times 10^6$	1.5938 $\times 10^6$	1.7922 $\times 10^6$	1.9244 $\times 10^6$

At the largest nominal scale (1:40,000), the rectangular area was 85.0 km^2. These latter areas were chosen arbitrarily.

Patch size categories. For all aerial photos, tree patches were digitized into the Geographical Information System program Map II®and grouped into 11 tree patch categories (Table 1). The smallest patch size within each area was based on the resolution of a photograph; we selected the smallest patch that could be readily seen in a photo. From the smallest category, we increased the size range of each additional category in equal increments up to the largest category. For example, at 0.2 km^2 and 1.5 km^2, the difference between the lower and upper limit for each category was 360.0 m^2 (Table 1). However, the largest category (K) included all patches >3636 m^2, the designated lower limit.

For each of the four spatial areas, percent canopy cover represented by a tree patch size category was calculated by summing the area occupied by the range of tree patches in a category and dividing by the area of the measured rectangle.

Determining the best prediction areas and best patch sizes of birds

Step 1: linear regression. We used regression analysis to determine which spatial areas (if any) displayed a significant correlation between bird counts (dependent variable) and percent canopy cover (independent variable). For the summer analyses, only those sites that were located within the breeding range of a species (Peterson, 1980, 1990) were included. For spring analyses, sites were divided between eastern (Chicago) and western regions (Seattle and Vancouver). Some species were recorded in both eastern and western sites, but analyses were kept separate because of regional differences in bird abundances (Robbins *et al.*, 1986). Because each scale had 11 tree patch categories, we ran 11 simple linear regressions for each of the four scales. At each scale, we looked for those tree patch categories that had a significant squared correlation coefficient (r^2, $P < 0.05$). A significant result was an indication that a species may be responding to tree patches at this scale.

Step 2: best prediction area (BPA). The purpose here was to determine which of the four spatial areas best explained the variation in bird counts. If only one area had one or more tree patch categories with significant r^2 values (step 1), then this scale was the best prediction area (BPA). If several areas had significant r^2 values, then a uniqueness index test (SAS Institute, 1994) was calculated. We entered into a full, multiple regression the patch size category that displayed the highest r^2 value from each area (i.e., one patch size category for each area). The uniqueness index test compares the reduced regressions (excluding the patch size category of interest) to the full regression; if the reduced regression r^2 value dropped significantly ($P < 0.05$), then this meant that the variation of bird counts was uniquely explained by the excluded patch size category beyond the variation accounted for by the other categories. The area with a significant uniqueness value was considered the BPA.

Step 3: best patch size (BPS). The purpose here was to determine which patch size category (within an area) best explained the variation in bird counts. Only areas designated as a BPA (step 2) were used to explore the best patch sizes that birds may respond to in a landscape. If only one tree patch category had a significant r^2 value (step 1), then this category was the best patch size (BPS). If several tree patch categories had significant r^2 values, then a uniqueness index value was calculated (as explained above). The tree patch category with a significant uniqueness index value ($P < 0.05$) was considered the BPS. If the uniqueness test was not significant, all of the tree patch categories with a significant r^2 value were listed as the BPS to see how small a tree patch a species may have responded to.

Rationale for calculating BPA & BPS. BPA and BPS values were calculated using the uniqueness index so that we could compare the approximate areas and patch sizes at which species primarily responded to structure. For example, the BPS was interpreted as the range of tree patch sizes that may be most important to a species, but this does not mean that a species did not respond to the other tree patch categories with significant r^2 values. It is just that the variation of bird counts was uniquely explained by one tree patch category beyond the variation accounted for by the other predictors. Each significant regression *could not* be interpreted as the area or patch size that a species responded to in a landscape because of the potential collinearity of tree cover among different area or patch sizes. For example, the occurrence of a species at a site may truly be related to the amount of tree patches at one scale, but because of collinearity across scales, several scales may display significant r^2 values. A uniqueness index takes into account this collinearity and indicates the relative importance of each area or patch size. We examined collinearity of the independent variables in those cases where the uniqueness test was employed. We conducted simple regressions between the tree patch categories with the highest r^2 value from each scale (for BPA) and between the tree patch categories with significant r^2 values from one scale (for BPS). The resultant r^2 values of these regressions were the amounts of collinearity. If collinearity was low (0%–25%), this indicated that a species may have responded to several patch sizes or areas. If collinearity was above 25%, it was deemed suspect whether a species was truly responding to structure across all the spatial areas and patch sizes with significant regression results.

Body mass and the BPA and BPS of birds

Birds were grouped into five size categories: (1) 3.2–6.9 g, (2) 7.0–16.5 g, (3) 16.6–61.6 g, (4) 61.7–184.0 g, and (5) 185.0–576.0 g. These size categories corresponded to body-mass "clumps" found in an analysis of North American breeding birds (Hostetler, 1997). This analysis basically separates one group of species (or "clump") from the next by detecting significant gaps in a body mass distribution. These clumps theoretically represent a suite of species that respond to landscape structure at the same range of scales (Holling, 1992). We hypothesized that larger birds would have larger BPS and BPA values than smaller birds. Here, we compared the BPS and BPA values of small (category 1 & 2), middle (category 3), and large (category 4 & 5) birds. BPS and BPA values were divided into a small and a large category. Small and large BPS values were respectively tree patch categories $A - J$ and $>J$. The $A - J$ categories were arbitrarily designated as "small" because they represented less than 1/3 of the possible 33 tree patch categories. Small and large BPA values were scales 0.2 & 1.5 km^2 and 25.0 & 85.0 km^2. A one-tailed, contingency chi-square test (3×2 contingency table, $\alpha = 0.05$) was used to determine whether larger birds had larger BPS and BPA values. For the BPS comparison, if more than one patch size category was listed, we used only the smallest patch size category.

Results

Spring analyses

For each species, at each of the four spatial areas, squared correlation coefficients (r^2), and BPA and BPS values are listed in Appendix 1. Many species had significant r^2 values at one or more spatial areas and tree patch categories, which indicated that species responded to the amount of tree patches in a landscape. However, 21 of the 84 species (25.0%) lacked a significant regression at any of the four spatial areas. As an example of how to interpret Appendix 1, the magnolia warbler had significant r^2 values at 0.2 km^2 and 1.5 km^2, a significant r^2 value for tree patch category A at both areas, a BPA value of 1.5 km^2, and a BPS value of A. This indicated that this species may have primarily responded to tree patches in size category A at 1.5 km^2. This species also could have responded to structure at 0.2 km^2, but because collinearity was greater than 76% between the predictors of 0.2 km^2 and 1.5 km^2, this cannot be confidently asserted.

For the BPA comparison, of those species that displayed a significant regression (63 in all), 26 (41.0%) lacked a BPA. For these species, most of the collinearity (21 of 26 cases) existed between the independent variables at the degree of 76–100%, and all of these cases were from regressions involving the Chicago sites. Comparing species that had BPA values, larger species had larger BPA values ($X^2 = 10.8$, $P < 0.05$). In body-size categories 1 and 2, 12% of the species had a BPA of 25.0 or 85.0 km^2; in category 3, 37.5% had a BPA of 25.0 or 85.0 km^2; and in categories 4 and 5, 80% of the species had a BPA of 25.0 km^2 (Table 2). Thus, many of the larger birds primarily responded to canopy cover within larger areas.

For those species with a BPA (37 species), 10 species (27.0%) did not have a BPS. From regressions involving these species, most of the collinearity existed (9 of 10 cases) at the

Table 2. From the spring results (Appendix 1), for each body size category, the percent of species with a calculated best prediction area (BPA); n = the number of species used to calculate the percent of species in each body size category.

Body-size category		n	0.2 km^2	1.5 km^2	25.0 km^2	85.0 km^2
1	3.2–6.9 g	5	80.0			20.0
2	7.0–16.5 g	20	65.0	25.0	10.0	
3	16.6–61.6 g	8	50.0	12.5	25.0	12.5
4	61.7–184.0 g	4	25.0		75.0	
5	185.0–576.0 g	1			100.0	

Table 3. From the spring results (Appendix 1), for each body size category, the percent of species for each best patch size category (BPS).

			Best patch size category														
Body-size category		n	A	B	C	D	E	F	G	K	L	M	N	O	P	X	<u>A</u>
1	3.2–6.9 g	5	60.0		20.0											20.0	
2	7.0–16.5 g	20	55.0		10.0		10.0	5.0	10.0		10.0						
3	16.6–61.6 g	8	37.5			12.5				12.5	12.5				12.5		12.5
4	61.7–184.0 g	4	25.0								50.0		25.0				
5	185.0–576.0 g	1										100					

degree of 51–100%. Comparing species that had BPS values, larger species had larger BPS values ($X^2 = 11.2$, $P < 0.05$). In body-size categories 1 and 2, 12% of the species had a BPS > J; in category 3, 50% of the species had a BPS > J; and in categories 4 and 5, 80% of the species had a BPS > J (Table 3). Thus, larger birds primarily responded to larger patch sizes, but exceptions did occur. For example, several species in body-size categories 1 and 2 had BPS values larger than J.

Summer analyses

For each species, at each of the four areas, squared correlation coefficients (r^2), and BPA and BPS values are listed in Appendix 2. Overall, 4 of the 60 species (6.7%) lacked a significant regression at any of the four spatial areas. Appendix 2 is interpreted as explained above for Appendix 1.

For the BPA comparisons, of the 56 species that displayed a significant regression, 16 (28.6%) lacked a BPA. For these species, most of the collinearity (14 of 16 cases) existed between the independent variables at the degree of 51–100%. Comparing species that had BPA values, larger species did not have larger BPA values ($X^2 = 1.9$, $P > 0.05$). A majority of birds in all body-size categories had BPA values at 0.2 km^2 and 1.5 km^2 (Table 4). In fact, most species that had large BPA values (25.0 & 85.0 km^2) were in body-size categories 1, 2, and 3. This indicated that larger birds did not respond to landscape structure at broader scales.

Table 4. From the summer results (Appendix 2), for each body size category, the percent of species with a calculated best prediction area (BPA); n = the number of species used to calculate the percent of species in each body size category.

Body-size category		n	0.2 km^2	1.5 km^2	25.0 km^2	85.0 km^2
1	3.2–6.9 g	4	75			25
2	7.0–16.5 g	14	57	21	14	8
3	16.6–61.6 g	14	50	14	22	14
4	61.7–184.0 g	5	40	40		20
5	185.0–576.0 g	3	67	33		

Table 5. From the summer results (Appendix 2), for each body size category, the percent of species for each best patch size category (BPS).

			Best patch size category																			
Body-size category		n	A	B	C	D	E	F	G	H	I	J	K	L	O	R	T	U	V	X	Z	F
1	3.2–6.9 g	4	50		25						25											
2	7.0–16.5 g	14	50	7	7						7	7					7	7			7	
3	16.6–61.6 g	14	14									7	43	7	7	7				7		7
4	61.7–184.0 g	5					40			20			20							20		
5	185.0–576.0 g	3	33	33	33																	

For those species with a BPA (40 species), 10 species (25.0%) did not have a BPS. From regressions involving these species, all of the collinearity (10 of 10 cases) existed between the independent variables at the degree of 51–100%. Comparing species that had BPS values, larger species did not always have larger BPS values despite the significant chi-square test ($X^2 = 11.6$, $P < 0.05$). Only 25% of category 4 and 5 species had BPS values greater than J. However, 22% of category 1 and 2 species and 79% of category 3 species had BPS values greater than J (Table 5). Thus, some of the larger species responded to larger patches during the summer, but this was not the case for species in categories 4 and 5.

Discussion

The regression analyses at each of the four scales were useful in determining the spatial areas and patch sizes relevant to different species when they make a second-order selection. The BPS and BPA values indicate the areas and the tree patch sizes that species may primarily respond to in an urban landscape. Significant results among area or patch sizes, outside of BPA or BPS values, may indicate that species are responding to structure at other scales, but because of the high degree of collinearity among the predictors, it could not be determined if a species truly responded to structure at multiple scales. As noted earlier, the BPS and BPA values are useful because these measures take into account collinearity among the predictors.

We recognize that because bird data were taken from different studies from a wide variety of locales, many biases might exist in the data. However, we purposely included a variety of sites in the hopes of obtaining landscape structure that was geometrically different from one scale to the next. Although we controlled for a few biases, we could not control for them all. For example, although analyses were done separately for eastern and western sites, bird abundances could differ among sites within regions. Also, some species that nest early may have nested during the spring season and produced fledged offspring that are highly mobile during the summer. These biases may not only influence BPA and BPS values in unpredictable ways, but they are possible reasons for why many species did not have significant r^2 values at any scale. Other reasons include observer biases in the survey data, the influence of other biotic factors (e.g., interspecific competition), and probably the most important reason, the certainty that each species responds to landscape characteristics other than tree patches (e.g., density of buildings). Finally, species composition of tree patches (e.g., conifers vs. deciduous), which could not be measured from aerial photographs, could influence which avian species occur in a patch. Previous research, though, indicates that vegetation structure is the primary variable that affects bird species distributions (e.g., DeGraaf *et al.*, 1991; Blair, 1996). Despite these potential biases, the analyses in this study did provide preliminary BPA and BPS estimates for some species. However, results should be viewed as hypotheses or guidelines for future research.

Spring and summer results

Analyses of avian body size categories revealed that many species conformed with our expectation that larger species generally would have larger BPS and BPA values, but there were several exceptions. Although many ecological, behavioral, and physiological traits are correlated to body size (Schoener, 1968; Peters, 1983; Calder, 1984; Schmidt-Nielson, 1984), exceptions to any ecological correlate are the norm. In addition to the above discussed factors that could affect BPS and BPA results, below, we discuss why results did or did not fit our hypotheses.

Best patch sizes (BPS). In the spring, a majority of middle-sized to large birds (body-size categories 3, 4 and 5) and a minority of small birds (categories 1 and 2) responded to large tree patches. This result is consistent with the hypothesis that the sizes of objects utilized by organisms are a function of their body size (Holling, 1992). However, counts of several of the small species were correlated to the percent cover of relatively large tree patches. This could be an example of where human measurements of the landscape do not adequately represent what the birds are utilizing on a daily basis. These species may be utilizing small tree patches only when these patches are surrounded by other trees (figure 2). Thus, these small, embedded patches could be regarded as the “true” BPS.

During the summer, middle-sized birds (body-size category 3) had larger BPS values than the smaller birds (categories 1 and 2). However, a majority of the largest species (category 4 and 5 birds) were found to be associated with small tree patches in the landscape. In this size category, several birds (e.g., band-tailed pigeons, northwestern crows, and American crows) use tree canopy to roost and sometimes to forage, but much of their foraging activity occurs on the ground (Ehrlich *et al.*, 1988). Perhaps these birds are primarily selecting areas with lots of scattered tree patches and open foraging areas. A “patch” to these species may be a combination of tall trees and open areas. Our measurements of canopy cover could not account

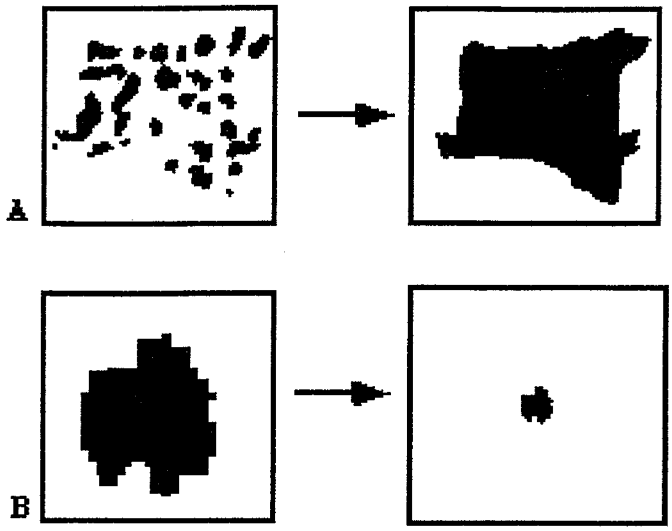

Figure 2. Representation of two possible perceptions of the landscape by birds: (A) a group of patches that actually are utilized as one big patch, and (B) one big patch that actually is utilized as one little patch.

for the possibility that clusters of canopy patches may actually be the "patch" that birds utilize on a daily basis (figure 2). If one were to "blur" an image to a point where clusters of patches become single patches, then analyses might show that the BPS may be much larger.

Best prediction area (BPA). During the spring, a majority of category 3, 4, and 5 species and a minority of category 1 and 2 species responded to the amount of tree patches within large scales (25.0 km^2 and 85.0 km^2). This is consistent with the hypothesis that larger birds would respond primarily to structure within larger spatial areas than smaller birds and is somewhat analogous to the observation that large birds have large home ranges (Schoener, 1968).

During the summer, though, results were not consistent with this hypothesis. A majority of species in all body-size categories had a BPA at 0.2 km^2 and 1.5 km^2. In fact many species in the smaller body-size categories (1, 2 and 3) had significant r^2 values at 25.0 km^2 and 85.0 km^2. One explanation for these results is that while patch size may be directly correlated to body size (Holling, 1992), area size (e.g., home range) may be dependent on other factors such as trophic status, food type, and productivity in a landscape (Harestad and Bunnell, 1979). These factors may play a dominant role during the summer but not the spring. For both small and large birds in this study, perhaps sufficient resources (e.g., food) in urban areas are available at 0.2 km^2 and 1.5 km^2. Food may be so concentrated that both small and large species can utilize tree patches within the same area. Alternatively, the scales used in this study may be too coarse for the summer analyses. Analyses using scales around 0.2 km^2 and 1.5 km^2 may tease out differences between the various sizes of birds. Further, large birds may respond to small tree patches distributed over a large area, and these patches may not be captured in broad-scale aerial photographs because of resolution problems (see next section).

Although this study explored the relationship between body size and BPS and BPA values, body size is probably one of several factors that affect BPS and BPA. In addition to body-size, life history characteristics may be a prominent factor that influences the scale at which species respond to urban landscape structure. For example, the yellow warbler (9.5 g) responded to much larger tree patches in the summer (category U) than in the spring (category C) whereas the red-breasted nuthatch (9.8 g) responded to smaller tree patches in the summer (category C) than in the spring (category L). Certain species seem to require large tree patches for successful reproduction (e.g., Gibbs and Faaborg, 1990; Hoover *et al.*, 1995), and this may be the case with the yellow warbler but not the red-breasted nuthatch. Perhaps, this is due to their different foraging and nesting strategies. The yellow warbler is a foliage gleaner and builds an open cup nest whereas the red-breasted nuthatch is a bark gleaner and a cavity nester (Ehrlich *et al.*, 1988).

In summary, the results indicate that body-size could be used as an indicator of the BPA and BPS of a variety of species when they make a second-order selection, but it is not a perfect indicator. In particular, one must pay attention to the life history characteristics of a species and to the season in which the measurements were done.

Problems with measuring the scales relevant to birds

Researchers have long recognized that scale is an important variable in many ecological studies (Allen and Starr, 1982; O'Neill *et al.*, 1986; Addicott *et al.*, 1987; Meentemeyer and Box, 1987). This study attempted to determine the areas and patch sizes used by different species of birds when they make a second-order selection. However, we encountered some difficulties in measuring landscape structure and analyzing/interpreting the correlation of landscape data with bird counts. The problems fall into three categories: (1) measuring landscape structure from aerial photographs at different scales, (2) statistical difficulty in estimating the BPS and BPA of different bird species in heterogeneous landscapes, and (3) the possibility that the landscape mosaic affects avian response and utilization of a landscape.

Aerial photographs. Any aerial photograph is defined both by its spatial area (or window size) and its resolution (or pixel size). However, the spatial area and resolution of an aerial photograph may not be appropriate to use when determining the spatial area and patch size that animals use to evaluate landscape structure. Aerial photos taken at high altitudes cover large spatial areas, but the resolution of an aerial photo is low; consequently, small objects in the photo disappear and groups of small objects fuse into a single object. In part, the pattern in the landscape changes as a function of a photo's resolution. The spatial area that larger birds in this study use to evaluate landscape structure may be quite large. However, the size of objects to which these large birds respond may be much smaller than the resolution of typical high-aerial photography. This might have been the case with size category 4 and 5 birds (summer), where larger spatial areas failed to reveal high squared correlation coefficients. It could be that these large birds may choose home range areas based on the number of small trees distributed over a large spatial area. Aerial photos at the larger nominal scales (e.g., 1:24,000 and 1:40,000) would not detect these small trees.

The only way to remedy this situation would be to piece together a number of aerial photos taken at the nominal scale of 1:2400 to represent a large spatial area (e.g., 25.0 km^2).

BPS and BPA estimates. BPS and BPA were estimated in order to compare the scales that are most relevant to different species. However, even if we could estimate BPS or BPA, we could not rule out the possibility that other patch categories or scales (with significant r^2 values) were also important in attracting certain species. Collinearity in most cases was fairly high, as is likely the case for any study that compares the spatial geometry of several different landscapes. The best way to determine the BPS of birds is to select several different sites where the percent cover of landscape structure, within a given spatial area, is similar but the patch sizes are totally different. For BPA, one would have to compare sites with similar landscape patterns at all scales except for the one of interest, or at the very least, collinearity across scales should be below 50%. In this study, we attempted to minimize collinearity by choosing sites from a variety of studies, but collinearity was still high. We found that collinearity above 50%, in most cases, prevented us from calculating a BPS or BPA.

Measurements of structure. In our study, we only selected one landscape feature (canopy cover) for our analyses because of the complexity of measuring and analyzing the data across scales. As mentioned earlier, other landscape features that surround the measured tree patches (i.e., the landscape mosaic) could play an important role in determining whether a species forages or nests in a given site (e.g., Litwin and Smith, 1992; Pearson, 1993). The landscape matrix may adversely affect species because of increased populations of predators (Andren, 1992), but in other cases, the proximity of certain landscape features may positively influence the abundance of species found in a local habitat. For example, Szaro and Jakle (1985) found that several species of birds were absent from desert scrub when surveys were conducted farther away from a riparian habitat.

Although beyond the scope of this study, the urban landscape mosaic could have affected whether birds utilize tree patches of different sizes. We selected sites from a variety of studies with the hope that the effects of the landscape mosaic would be random, but this may have not been the case for all species. Species that are adversely affected by an adjacent landuse (e.g., high density development) may only utilize tree patches of a larger size (if at all) when surrounded by this adjacent landuse category. Conversely, a species that is positively affected by an adjacent landuse may utilize tree patches of a smaller size when this landuse was present.

Summary and future avian research in urban areas

Results indicated that many bird species, when making a second-order selection, responded to urban tree patches at broad scales from 0.2 km^2 to 85.0 km^2. This demonstrates that many birds may respond to landscape structure at much broader scales than what has been measured in most urban habitat selection studies (e.g., DeGraaf *et al.*, 1991; Blair, 1996). In addition, body size was an approximate indicator of the scales at which different bird species respond to landscape structure. However, the correlations found in this study do not necessarily mean causation. Multiple lines of evidence are needed and as mentioned previously, the results in this study should be used as guidelines for future research. The methodology outlined in this study will aid researchers to conduct multi-scale analyses, which will ultimately help determine the primary scale at which birds make first-, second-, third-, or fourth-order selections.

In particular, to determine how landscape features affect the distribution of birds in urban environments, it is of primary importance to know the scales at which different avian species make a second-order selection, especially because second-order selections constrain higher-order selections made at more limited scales. A variety of human decisions impact the landscape at fine to broad scales and these decisions would affect different avian species, depending on the scales at which each species responds to landscape structure (Hostetler, 1999). Homeowners, developers, and city planners are usually constrained by the amount of area available for vegetation when designing landscapes. Generally, homeowners operate at fine scales whereas developers and city planners operate at increasingly broader scales. If one knew the scales at which different birds respond to landscape structure, then for each species, one could target the amount of area needed to be designed to attract a given species. For example, the results from this study suggest that the design of several homeowner backyards may affect whether a Golden-crowned Kinglet (*Regulus satrapa*) establishes a home range, but a city planner's design of a large portion of a city may affect whether the Red-bellied Woodpecker (*Melanerpes carolinus*) establishes a home range in a neighborhood. Any development is defined both by its area and the sizes of structural objects (e.g., tree patches) found within the landscape, and to design urban landscapes for birds, we must first understand the connection between the scales at which a species responds to landscape structure and the scales at which humans impact the landscape.

Future urban habitat selection studies should be expanded to include species with different life history characteristics (e.g., ground gleaners) and to include avian communities in many different types of urban landscapes (e.g., arid environments, estuaries, savannahs, and rain forests). One should pay attention to the species (especially trophic status) included in a study and to the level of the decision hierarchy upon which the study focuses (first-, second-, or third-order selection). In particular, the possible influences of the landscape mosaic should be considered. If anything, the results indicate that caution should be used in the interpretation of urban habitat selection studies that examine the correlation between the distribution of species and the amount of structure at *one scale*. The distribution of a species may be primarily related to structure at other scales, especially broader ones. Habitat selection studies should empirically explore the potential influence of structure at multiple scales.

Appendix 1

For each species from the spring surveys, at the four areas, squared correlation coefficients (r^2), patch sizes that had significant r^2 values ($P < 0.05$); BPA and BPS values are listed. Dark borders separate the five body size categories; na = negative correlations. If several patch size categories had significant r^2 values at a given scale, then only the highest r^2 value is listed. Blank spaces in the BPS and BPA columns mean that none of the scales had a significant r^2 value; a question mark indicates that the uniqueness test was not significant among the regressions; a ( ) in the BPS column indicates the smallest patch category used in the BPS and bird size category comparison. For BPA and BPS where a uniqueness test was employed, collinearity among the two highest predictors is reported.

Common name	Latin name	Sites**	Mass (grams)	r^2 (0.2 km^2)	Patch size (0.2 km^2)	r^2 (1.5 km^2)	Patch size (1.5 km^2)	r^2 (25.0 km^2)	Patch size (25.0 km^2)	r^2 (85.0 km^2)	Patch size (85.0 km^2)	BPA (km^2)***	BPS***
Rufous Hummingbird	Selasphorus rufus	W	3.3	0.30*	A	0.09		0.10		na		0.2	A
Bushtit	Psaltriparus minimus	W	5.3	0.29*	K	0.45*	KBC	0.42*	MNP	0.56*	WX	85^b	X^c
Golden-crowned Kinglet	Regulus satrapa	W	6.2	0.41*	AE	0.18		0.02		na		0.2	A^b
Golden-crowned Kinglet	Regulus satrapa	E	6.2	0.28		0.27		na		na			
Ruby-crowned Kinglet	Regulus calendula	W	6.7	0.33*	AF	0.17		na		na		0.2	$?(A)^c$
Ruby-crowned Kinglet	Regulus calendula	E	6.7	0.07	B	0.15	B	0.01		0.01			
Wilson's Warbler	Wilsonia pusilla	W	6.9	0.59*	CDF	0.51*	BFI	0.17		0.17		0.2^b	C^b
Wilson's Warbler	Wilsonia pusilla	E	6.9	0.28		0.25		na		na			
American Redstart	Setophaga ruticilla	E	8.3	0.10		0.09		0.01		0.10			
Black-throated Gray Warbler	Dendroica nigrescens	W	8.4	0.43*	AF	0.21		na		na		0.2	A^b
Brown Creeper	Certhia americana	E	8.4	0.23	B	0.25	B	na		na			
Magnolia Warbler	Dendroica magnolia	E	8.7	0.76*	A	0.93*	A	na		na		1.5^d	A
Black-throated Green Warbler	Dendroica virens	E	8.8	0.44	C	0.73*	A	na		na		1.5	A
Townsend's Warbler	Dendroica townsendi	W	8.9	0.26*	F	0.10		0.14		0.17		0.2	F

Winter Wren	Troglodytes troglodytes	W	8.9	0.44*	AF	0.22		0.06		na		0.2	A[b]
Orange-crowned Warbler	Vermivora celata	W	9.0	0.38*	BK	0.35*	BHK	0.30*	L	0.15		?[a]	
Yellow Warbler	Dendroica petechia	W	9.5	0.42*	CF	0.11		0.27*	U	0.27*	B	0.2[a]	?(C)[c]
Yellow Warbler	Dendroica petechia	E	9.5	0.29		0.25		na		na			
Chestnut-sided Warbler	Dendroica pensylvanica	E	9.6	0.96*	G	0.75*	HJK	0.64*	L	0.73	X	0.2[c]	G
Chestnut-backed Chickadee	Poecile rufescens	W	9.7	0.22		0.20		0.80*	LM	0.24*	X	25[b]	L[b]
Blackburnian Warbler	Dendroica fusca	E	9.8	0.61		0.95*	G	na		na		1.5	G
Red-breasted Nuthatch	Sitta canadensis	W	9.8	0.52*	K	0.54*	K	0.80*	LMN	0.21		25[b]	L[b]
Bewick's Wren	Thryomanes bewickii	W	9.9	0.24*	K	0.50*	EIK	0.40*	LMP	0.15		1.5[b]	?(E)[c]
Tennessee Warbler	Vermivora peregrina	E	10.0	0.45	C	0.61	A	na		na			
Least Flycatcher	Empidonax minimus	E	10.3	0.66*	K	0.64*	K	0.53		0.64*	A	?[d]	
Canada Warbler	Wilsonia canadensis	E	10.4	0.68*	C	0.52		0.01		0.05		0.2	C
MacGillivray's Warbler	Oporornis tolmiei	W	10.4	0.50*	DGH	0.54*	BFH	0.18		na		?[a]	
Black-capped Chickadee	Poecile atricapillus	W	10.8	0.57*	ABE	0.40*	BGK	0.34*	L	0.15		0.2[a]	?(A)[b]
Black-capped Chickadee	Poecile atricapillus	E	10.8	0.66*	K	0.86*	HJK	0.98*	LMV	0.99*	WYG	?[d]	

(*Continued on next page.*)

(*Continued*).

Common name	Latin name	Sites**	Mass (grams)	r^2 (0.2 km^2)	Patch size (0.2 km^2)	r^2 (1.5 km^2)	Patch size (1.5 km^2)	r^2 (25.0 km^2)	Patch size (25.0 km^2)	r^2 (85.0 km^2)	Patch size (85.0 km^2)	BPA (km^2)***	BPS***
Pacific-slope Flycatcher	Empidonax difficilis	W	10.9	0.44*	AF	0.21		na		na		0.2	A[b]
Cape May Warbler	Dendroica tigrina	E	11.0	0.29		0.25		na		na			
White-eyed Vireo	Vireo griseus	E	11.4	1.0*	FHI	0.96*	FI	na		0.37		?[d]	
Yellow-bellied Flycatcher	Empidonax flaviventris	E	11.6	0.56		0.77*	HJK	0.96*	LMV	0.99*	WYG	?[d]	
Warbling Vireo	Vireo gilvus	W	12.0	0.45*	ACF	0.24*	A	0.10		0.15		0.2[b]	?(A)[c]
Yellow-rumped Warbler	Dendroica coronata	W	12.6	0.38*	A	0.15		0.19		na		0.2	A
Yellow-rumped Warbler	Dendroica coronata	E	12.6	0.57		0.48		0.01		0.03			
Bay-breasted Warbler	Dendroica castanea	E	12.6	0.88*	EHI	0.93*	EFI	na		0.26		1.5[d]	?(E)[d]
Western Wood-Pewee	Contopus sordidulus	W	12.8	0.43*	AF	0.21		na		na		0.2	?(A)[d]
American Goldfinch	Carduelis tristis	W	12.9	0.30*	AF	0.16		na		na		0.2	A[b]
American Goldfinch	Carduelis tristis	E	12.9	na		na		na		0.02			
Blackpoll Warbler	Dendroica striata	E	13.0	0.98*	EHI	0.90*	EFI	na		0.41		?[d]	
Willow Flycatcher	Empidonax traillii	W	13.4	0.44*	A	0.21		na		na		0.2	A
Kentucky Warbler	Oporornis formosus	E	14.0	0.57		0.45		0.67*	NV	0.69*	BEG	?[d]	

Eastern Wood-Pewee	Contopus virens	E	14.1	0.77*	FGK	0.86*	HJK	0.72*	LM	0.73*	WX	?[d]	
Indigo Bunting	Passerina cyanea	E	14.5	0.95*	FK	0.99*	HJK	0.88*	LMV	0.91*	WYG	?[d]	
Pine Siskin	Carduelis pinus	W	14.6	0.44*	ABE	0.22		0.48*	LM	0.12		?[b]	
Solitary Vireo	Vireo solitarius	W	16.6	0.63*	GK	0.60*	HK	0.64*	NQ	0.04		?[b]	
Red-eyed Vireo	Vireo olivaceus	W	16.7	0.72*	DFH	0.79*	BFJ	na		na		1.5[c]	?(D)[c]
Red-eyed Vireo	Vireo olivaceus	E	16.7	0.92*	FK	0.90*	HKJ	0.62		0.93*	WXA	?[d]	
Yellow-throated Vireo	Vireo flavifrons	E	18.0	0.46	G	0.23	J	0.36	N	0.32	B		
Dark-eyed Junco	Junco hyemalis hyemalis	W	19.6	0.50*	AF	0.26*	A	0.03		na		0.2[d]	A[b]
Dark-eyed Junco	Junco hyemalis hyemalis	E	19.6	na		0.04		na		na			
Tree Swallow	Tachycineta bicolor	W	20.1	na		na		na		0.27*	A	85	A
White-breasted Nuthatch	Sitta carolinensis	E	21.1	0.57		0.77*	JK	0.99*	LMV	0.99*	YBK	?[d]	
Downy Woodpecker	Picoides pubescens	W	27.0	0.14		0.17		0.17		0.05			
Downy Woodpecker	Picoides pubescens	E	27.0	0.90*	FK	0.95*	HJK	0.87*	LM	0.98*	WXA	?[d]	
Western Tanager	Piranga ludoviciana	W	28.1	0.22		0.11		0.20		0.13			
Swainson's Thrush	Catharus ustulatus	E	30.8	0.09		0.06		0.01		0.02			

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Common name	Latin name	Sites**	Mass (grams)	r^2 (0.2 km^2)	Patch size (0.2 km^2)	r^2 (1.5 km^2)	Patch size (1.5 km^2)	r^2 (25.0 km^2)	Patch size (25.0 km^2)	r^2 (85.0 km^2)	Patch size (85.0 km^2)	BPA (km^2)***	BPS***
Hermit Thrush	Catharus guttatus	W	31.0	0.34*	A	0.12		0.13		na		0.2	A
Hermit Thrush	Catharus guttatus	E	31.0	na		na		0.01		0.02			
Veery	Catharus fuscescens	E	31.2	0.57		0.23		0.36		0.31			
Cedar Waxwing	Bombycilla cedrorum	W	31.9	0.20		0.25*	J	0.23*	S	na		?[b]	
Cedar Waxwing	Bombycilla cedrorum	E	31.9	0.29		0.23		na		na			
Olive-sided Flycatcher	Contopus cooperi	W	32.1	0.56*	DGK	0.50*	IK	0.33*	P	na		0.2[b]	K[b]
Great Crested Flycatcher	Myiarchus crinitus	E	33.5	0.58		0.77*	JK	0.99*	LMV	0.99*	YG	?[d]	
Baltimore Oriole	Icterus galbula	E	33.8	0.70*	GH	0.89*	HJK	0.98*	LM	0.99*	YG	?[d]	
Townsend's Solitaire	Myadestes townsendi	W	34.0	0.44*	AF	0.22		na		na		0.2	A[b]
Red Crossbill	Loxia curvirostra	W	36.5	0.21		0.20		0.86*	LM	0.20		25	L[b]
Gray Catbird	Dumetella carolinensis	E	36.9	0.58		0.53		0.53		0.62			
Eastern Kingbird	Tyrannus tyrannus	E	39.5	1.0*	EHI	0.96*	FI	na		0.37		?[d]	
Black-headed Grosbeak	Pheucticus melanocephalus	W	44.5	0.53*	K	0.52*	K	0.80*	NPR	0.09		25	P[b]
Rose-breasted Grosbeak	Pheucticus ludovicianus	E	45.6	0.81*	FK	0.73*	FHK	0.44		0.82*	A	?[d]	

Yellow-bellied Sapsucker	Sphyrapicus varius	E	50.3	0.57		0.77*	HJK	0.99*	LMV	0.99*	YG	?[d]	
Black-billed Cuckoo	Coccyzus erythropthalmus	E	51.1	0.57	G	0.77*	HJK	0.99*	LMV	0.99*	YG	?[d]	
Yellow-billed Cuckoo	Coccyzus americanus	E	64.0	0.65*	G	0.52		0.73*	NOV	0.72*	YEG	25[b]	?(N)[c]
Hairy Woodpecker	Picoides villosus	E	66.3	0.57	H	0.77*	HJK	0.99*	LM	0.99*	YBG	?[d]	
Brown Thrasher	Toxostoma rufum	E	68.8	0.32	C	0.26	K	0.50	P	na			
Red-headed Woodpecker	Melanerpes erythrocephalus	E	71.6	0.98*	FHI	0.96*	I	na		0.37		?[d]	
Varied Thrush	Ixoreus naevius	W	78.4	0.58*	ADF	0.22		na		na		0.2	?(A)[c]
Steller's Jay	Cyanocitta stelleri	W	106.0	0.27*	B	0.24*	J	0.71 *	L	0.09		25[b]	L
Northern Flicker	Colaptes auratus	W	132.0	0.41*	I	0.23*	I	0.41*	L	0.15		25[b]	L
Northern Flicker	Colaptes auratus	E	132.0	0.71*	H	0.72*	HK	0.68*	AK	0.68*	CFK	?[d]	
Northwestern Crow	Corvus caurinus	V	391.5	0.90*	BDE	0.96*	J	na		na		?[d]	
American Crow	Corvus brachyrhynchos	S	448.0	0.56		0.64		0.74*	M			25	M

* $P < 0.05$.
**E = Chicago (6 sites), W = Seattle (6 sites) & Vancouver (11 sites), V = Vancouver only (11 sites), S = Seattle only (6 sites).
***a = 0–25%, b = 26–50%, c = 51–75%, d = 76–100%.

Appendix 2

For each species from the summer surveys, at the four areas, squared correlation coefficients (r^2), patch sizes that had significant r^2 values; BPA, and BPS values are listed. Dark borders separate the five body size categories; na = negative correlations. If several patch size categories had significant r^2 values at a given scale ($P < 0.05$), then only the highest r^2 value is listed. Blank spaces in the BPS and BPA columns mean that none of the scales had a significant r^2 value; a question mark indicated that the uniqueness test was not significant among the regressions; a ( ) in the BPS column indicates the smallest patch category used in the BPS and bird size category comparison. For BPA and BPS where a uniqueness test was employed, collinearity among the two highest predictors is reported.

Common name	Latin name	Sites**	Mass (grams)	r^2 (0.2 km^2)	Patch size (0.2 km^2)	r^2 (1.5 km^2)	Patch size (1.5 km^2)	r^2 (25.0 km^2)	Patch size (25.0 km^2)	r^2 (85.0 km^2)	Patch size (85.0 km^2)	BPA (km^2)***	BPS***
Ruby-throated Hummingbird	Archilochus colubris	abcu	3.2	0.23*	DG	0.14	K	0.40*	LMN	0.70*	YB	85[b]	C[b]
Rufous Hummingbird	Selasphorus rufus	v	3.3	1.0*	GI	0.38*	K	0.45*	RU	0.45*	B	0.2[b]	I[b]
Bushtit	Psaltriparus minimus	v	5.3	0.64*	A	0.15		na		na		0.2	A
Golden-crowned Kinglet	Regulus satrapa	v	6.2	0.64*	AE	0.31		na		na		0.2	A[b]
American Redstart	Setophaga ruticilla	ac	8.3	0.64*	H	0.20	D	0.61*	V	1.0*	ZF	85[b]	?(Z)[c]
Blue-winged Warbler	Vermivora pinus	ac	8.4	0.50*	K	0.67*	K	0.77*	PRU	0.78*	D	?[c]	
Brown Creeper	Certhia americana	v	8.4	0.64*	AE	0.31		0.01		na		0.2	A[b]
Brown Creeper	Certhia americana	a	8.4	1.0*	DGH	0.99*	CDE	0.58		1.0*	YEF	?[d]	
Yellow Warbler	Dendroica petechia	abc	9.5	0.11		0.01		0.45*	UV	0.08		25	?(U)[c]
Red-breasted Nuthatch	Sitta canadensis	v	9.8	0.65*	A	0.31		na		na		0.2	A
Red-breasted Nuthatch	Sitta canadensis	a	9.8	0.93*	CH	0.66		0.73		0.77		0.2	?(C)[c]
Bewick's Wren	Thryomanes bewickii	v	9.9	0.64*	A	0.30		na		na		0.2	A
Carolina Chickadee	Parus carolinensis	bu	10.2	0.46*	E	0.69*	HJ	0.05		na		1.5[b]	J[b]

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(*Continued*).

Common name	Latin name	Sites**	Mass (grams)	r^2 (0.2 km^2)	Patch size (0.2 km^2)	r^2 (1.5 km^2)	Patch size (1.5 km^2)	r^2 (25.0 km^2)	Patch size (25.0 km^2)	r^2 (85.0 km^2)	Patch size (85.0 km^2)	BPA (km^2)***	BPS***
Least Flycatcher	Empidonax minimus	ac	10.3	0.14		0.30		1.0*	T	0.55*	Y<u>BE</u>	25[b]	T
Black-and-white Warbler	Mniotilta varia	abcu	10.8	0.16		0.41*	A	na		na		1.5	A
Black-capped Chickadee	Poecile atricapillus	ac	10.8	0.73*	K	0.88*	K	0.79*	LQ	0.49*	Y<u>BC</u>	?[c]	
Black-capped Chickadee	Poecile atricapillus	v	10.8	0.45*	I	0.32		0.35*	GJ	0.17		0.2[b]	I
American Goldfinch	Carduelis tristis	abc	12.9	na		na		0.05		0.02			
American Goldfinch	Carduelis tristis	v	12.9	0.45*	A	0.17		na		0.04		0.2	A
Blackpoll Warbler	Dendroica striata	a	13.0	0.99*	DGH	0.88		0.78		0.94*	Z<u>F</u>	?[d]	
Willow Flycatcher	Empidonax traillii	abc	13.4	0.16		0.35*	A	na		0.02		1.5	A
Willow Flycatcher	Empidonax traillii	v	13.4	1.0*	BDH	0.84*	BDH	0.06		na		0.2[d]	?(B)[d]
Eastern Wood-Pewee	Contopus virens	abcu	14.1	0.22*	K	0.19*	K	0.16		0.11		?[d]	
Indigo Bunting	Passerina cyanea	abcu	14.5	0.18*	D	0.23*	H	0.51*	LM	0.44*	WY<u>B</u>	?[d]	
Pine Siskin	Carduelis pinus	v	14.6	0.43*	AE	0.23		0.20		0.10		0.2	?(A)[c]
Red-eyed Vireo	Vireo olivaceus	abc	16.7	0.46*	FI	0.44*	GHI	0.04		0.01		?[d]	

Eastern Phoebe	Sayornis phoebe	abcu	19.8	0.22*	K	0.39*	K	0.16		0.11		1.5[c]	K
Tree Swallow	Tachycineta bicolor	ac	20.1	0.03		0.05		0.59*	NOR	0.49*	BG	?[c]	
Tree Swallow	Tachycineta bicolor	v	20.1	na		na		0.26		0.30			
Carolina Wren	Thryothorus ludovicianus	bu	21.0	0.53*	EJ	0.49*	JK	0.05		0.25		?[b]	
White-breast Nuthatch	Sitta carolinensis	abcu	21.1	0.47*	K	0.37*	K	0.55*	QRU	0.12		25[a]	R[b]
Tufted Titmouse	Baeolophus bicolor	abcu	21.6	0.48*	JK	0.35	K	0.07		0.12		0.2	J[c]
Purple Finch	Carpodacus purpureus	v	24.9	0.64*	FK	0.31		0.21		na		0.2	K[b]
Downy Woodpecker	Picoides pubescens	abc	27.0	0.39*	I	0.38*	GHK	0.39*	L	0.02		?[c]	I
Downy Woodpecker	Picoides pubescens	v	27.0	0.64*	AE	0.32		na		na		0.2	A[b]
Western Tanager	Piranga ludoviciana	v	28.1	0.44*	A	0.10		0.01		na		0.2	A
Scarlet Tanager	Piranga olivacea	abc	28.6	0.64*	K	0.43*	K	0.66*	R	0.22*	C	0.2[b]	K
Swainson's Thrush	Catharus ustulatus	a	30.8	0.99*	FK	0.74		0.99*	LQ	0.60		?[d]	
Hermit Thrush	Catharus guttatus	a	31.0	0.81		0.98*	K	0.95*	P	1.0*	D	?[d]	
Cedar Waxwing	Bombycilla cedrorum	abc	31.9	0.63*	K	0.28*	F	na		0.05		0.2	K
Cedar Waxwing	Bombycilla cedrorum	v	31.9	na		na		na		na			

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Common name	Latin name	Sites**	Mass (grams)	r^2 (0.2 km^2)	Patch size (0.2 km^2)	r^2 (1.5 km^2)	Patch size (1.5 km^2)	r^2 (25.0 km^2)	Patch size (25.0 km^2)	r^2 (85.0 km^2)	Patch size (85.0 km^2)	BPA (km^2)***	BPS***
Great Crested Flycatcher	Myiarchus crinitus	abcu	33.5	0.37*	I	0.40*	IJK	0.08		0.21*	C	?[a]	
Baltimore Oriole	Icterus galbula	abc	33.8	0.62*	K	0.83*	K	0.39*	L	0.07		1.5[c]	K
Gray Catbird	Dumetella carolinensis	abc	36.9	0.54*	K	0.2		0.45*	QV	0.71*	BEF	85[b]	F[b]
Eastern Kingbird	Tyrannus tyrannus	abcu	39.5	0.37*	BI	0.34*	GH	0.05		0.01		?[c]	
Eastern Towhee	Pipilo erythrophthalmus	abc	40.5	0.15		0.18		0.34*	OV	0.11		25	?(O)[c]
Black-headed Grosbeak	Pheucticus melanocephalus	v	44.5	na		na		0.05		0.41*	XA	85	?(X)[d]
Rose-breasted Grosbeak	Pheucticus ludovicianus	abc	45.6	0.68*	BI	0.70*	GHI	0.13		0.11		?[c]	
Wood Thrush	Hylocichla mustelina	abc	47.4	0.32*	K	0.46*	K	0.26*	RU	0.23*	K	0.2[a]	K
Black-billed Cuckoo	Coccyzus erythropthalmus	abc	51.1	0.16		0.27*	J	0.51*	LMN	0.53*	XBE	25[b]	L[b]
Red-bellied Woodpecker	Melanerpes carolinus	abcu	61.7	0.12		0.26*	IJ	na		0.30*	XZE	85[b]	?(X)[c]
Yellow-billed Cuckoo	Coccyzus americanus	abcu	64.0	0.19*	FI	0.41*	EIJ	na		0.30*	XAE	1.5[b]	?(E)[c]
Hairy Woodpecker	Picoides villosus	abc	66.3	0.34*	K	0.58*	K	0.30*	LU	0.15		1.5[b]	K
Brown Thrasher	Toxostoma rufum	abc	68.8	0.05		0.05		0.18		0.16			

Red-headed Woodpecker	Melanerpes erythrocephalus	bcu	71.6	0.46*	CDE	0.31*	BCF	0.01		0.01	0.2^{b}	E^{b}
Northern Flicker	Colaptes auratus	abc	132.0	0.40*	K	0.42*	HJK	0.41*	L	0.16	$?^{c}$	
Northern Flicker	Colaptes auratus	v	132.0	1.0*	ADH	0.83*	FHJ	0.06		na	0.2^{b}	H^{c}
Band-tailed Pigeon	Columba fasciata	v	342.5	0.73*	ABF	0.46*	AB	na		na	0.2^{b}	$?(A)^{c}$
Northwestern Crow	Corvus caurinus	v	391.5	0.74*	BDH	0.84*	BFJ	0.01		na	1.5^{b}	$?(B)^{d}$
American Crow	Corvus brachyrhynchos	a	448.0	0.93*	C	0.52		0.75		0.64	0.2	C

*$P < 0.05$.
**c = Chicago (8 sites), v = Vancouver (11 sites), u = Austin (3 sites), a = Amherst/Springfield (4 sites), b = Blacksburg (7 sites).
***a = 0–25%, b = 26–50%, c = 51–75%, d = 76–100%.

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References

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. and Soluk, D.A. (1987) Ecological neighborhoods: scaling environmental patterns. *Oikos* **49**, 340–346.

Allen, T.F.H. and Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Complexity.* University of Chicago Press, Chicago.

Andren, H. (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perpective. *Ecology* **73**, 794–804.

Bell, W.J. (1991) *Searching Behaviour: The Behavioural Ecology of Finding Resources.* Chapman and Hall, New York.

Blair, R.B. (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications* **6**(2), 506–519.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.

Calder, W.A.I. (1984) *Size, Function, and Life History*. Cambridge University Press, Cambridge, MA.

DeGraaf, R.M. and Wentworth, J.M. (1981) Urban bird communities and habitats in New England. *Transactions of the North American Wildlife Conference* **46**, 396–412.

DeGraaf, R.M., Geis, A.D. and Healy, P.A. (1991) Bird population and habitat surveys in urban areas. *Landscape and Urban Planning* **21**, 181–188.

Dunning, J.B. (1993) *CRC Handbook of Avian Body Masses.* CRC Press, Boca Raton, FL.

Ehrlich, P.R., Dobkin, D.S. and Wheye, D. (1988) *The Birders Handbook: A Field Guide to the Natural History of North American Birds*. Simon & Schuster, New York.

Emlen, J.T. (1974). An urban bird community in Tucson Arizona: derivation, structure, regulation. *Condor* **76**, 184–197.

Gass, C.L. and Montgomerie, R.D. (1981) Hummingbird foraging behavior: decision-making and energy regulation. In *Foraging Behavior: Ecological, Ethological, and Psychological Approaches* (A.C. Kamil and T.D. Sargent, ed.), pp. 150–194. Garland Press, New York.

Gibbs, J.P. and Faaborg, J. (1990) Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. *Conservation Biology* **4**(2), 193–196.

Goldstein, E.L., Gross, M. and DeGraaf, R.M. (1986) Breeding birds and vegetation: a quantitative assessment. *Urban Ecology* **9**, 377–385.

Guth, R.W. (1980) *Ecology of Urban Communities in the Chicago Area*. Ph.D. Dissertation, Northwestern University, Chicago, Illinois.

Hansson, L. (1991) Dispersal and connectivity in metapopulations. *Biological Journal of the Linnaeus Society* **42**, 89–103.

Harestad, A.S. and Bunnell, F.L. (1979) Home range and body weight—a reevaluation. *Ecology* **60**, 389–402.
Harris, L.D. (1984) *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press, Chicago, Illinois.
Harrison, R.L. (1992) Toward a theory of inter-refuge corridor design. *Conservation Biology* **6**, 293–295.
Holling, C.S. (1992) Cross-scale morphology, geometry and dynamics of ecosystems. *Ecological Monographs* **62**, 447–502.
Hoover, J.P., Brittingham, M.C. and Goodrich, L.J. (1995) Effect of forest patch size on nesting success of Wood Thrushes. *The Auk* **112**, 146–155.
Hostetler, M.E. (1997) *Avian Body-size Clumps and the Response of Birds to Scale-dependent Landscape Structure in Suburban Habitats*. Ph.D. Dissertation, University of Florida, Gainesville, FL.
Hostetler, M.E. (1999) Scale, birds, and human decisions: a potential for integrative research in urban ecosystems. *Landscape and Urban Planning* **45**, 15–19.
Hutto, R.L. (1985) Habitat selection by nonbreeding landbirds. In *Habitat Selection in Birds* (M.L. Cody, ed.), pp. 455–476. Academic Press Inc., New York.
Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.
Kotliar, N.B. and Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**, 253–260.
Krebs, J.R. and Davies, N.B. (1991) *Behavioural Ecology: an Evolutionary Approach*. Blackwell Scientific Publications, Boston.
Lancaster, R.K. (1976) *Bird Communities in Relation to Structure of Urban Habitats*. M.S. Thesis, University of British Columbia, Vancouver, B.C.
Levin, S.L. (1992) The problem of pattern and scale in ecology. *Ecology* **73**, 1943–1967.
Lima, S.L. and Zollner, P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Tree* **11**, 131–135.
Litwin, T.S. and Smith, C.R. (1992) Factors influencing the decline of Neotropical migrants in a northeastern forest fragment: isolation, fragmentation, or mosaic effects? In *Ecology and Conservation of Neotropical Migrant Landbirds* (J.M. Hagan III and D.W. Johnston, ed.), pp. 483–496. Smithsonian Institution Press, Washington, D.C.
Lucid, V.J. (1974) *Bird Utilization of Habitat in Residential Areas*. Ph.D. Dissertation, Virginia Polytechnic Institute & State University, Blacksburg, Virginia.
Meentemeyer, V. and Box, E.O. (1987) Scale effects in landscape studies. In *Landscape Heterogeneity and Disturbance* (M.G. Turner, ed.), pp. 15–24. Springer-Verlag, New York.
Moore, F.R. and Simons, T.R. (1992) Habitat suitability and stopover ecology of neotropical landbird migrants. In *Ecology and Conservation of Neotropical Migrant Landbirds* (J.M. Hagan III and D.W. Johnston, ed.), pp. 345–355. Smithsonian Institution Press, Washington, D.C.
Morton, S.R. (1990) The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society* **16**, 201–213.
O'Neill, R.V., DeAngelis, D.L., Waide, J.B. and Allen, T.F.H. (1986) *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, NJ.
Opdam, P. (1991) Metapopulation theory and habitat fragmentation: a review of holartic breeding bird studies. *Landscape Ecology* **5**, 93–106.
Pearson, S.M. (1993) The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology* **8**, 3–18.
Penland, S.T. (1984) *Avian Responses to a Gradient of Urbanization in Seattle, Washington*. Ph.D. Dissertation, University of Washington, Seattle, Washington.
Peters, R.H. (1983) *The Ecological Implication of Body Size*. Cambridge University Press, Cambridge.
Peterson, R.T. (1980) *A Field Guide to Eastern Birds*. Houghton Mifflin Company, Boston, MA.
Peterson, R.T. (1990) *A Field Guide to Western Birds*. Houghton Mifflin Company, Boston, MA.
Pulliam, H.R., Dunning Jr., J.B. and Liu, J. (1992) Population dynamics in complex landscapes. *Ecological Application* **2**, 165–177.
Robbins, C.S., Bystrack, D.A. and Geissler, P.H. (1986) *The Breeding Bird Survey: Its First Fifteen Years*, 1965–1979. U.S. Department of Interior, Fish & Wildlife Service, Washington, D.C. Resource Publication 157.
SAS Institute (1994) *A Step-by-Step Approach to Using the SAS System*. SAS Institute Inc., Cary, NC.

Schmidt-Nielson, K. (1984) *Scaling, Why Is Size So Important?* Cambridge University Press, Cambridge.

Schoener, T.W. (1968) Sizes of feeding territories among birds. *Ecology* **49**, 123–141.

Sexton, C.W. (1987) *A Comparative Analysis of Urban and Native Bird Populations in Central Texas*. Ph.D. Dissertation, University of Texas, Austin, Texas.

Szaro, R.C. and Jakle, M.D. (1985) Avian use of a desert riparian island and its adjacent scrub habitat. *Condor* **87**, 511–519.

Turchin, P. (1991) Translating foraging movements in heterogeneous environments into spatial distribution of foragers. *Ecology* **72**, 1253–1266.

Turner, M.G., O'Neill, R.V., Gardner, R.H. and Milne, B.T. (1989) Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* **3**, 153–162.

Weber, W.C. (1972) *Birds in Cities: A Study of Populations, Foraging Ecology and Nest-sites of Urban Birds*. Ph.D. Dissertation, University of British Columbia, Vancouver, B.C.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology* **3**, 385–397.

Wiens, J.A. (1990) On the use of 'grain' and 'grain size' in ecology. *Functional Ecology* **3**, 385–397.

Wiens, J.A., Stenseth, N.C., Van Horne, B. and Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos* **66**, 369–380.