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**Effects of agricultural and urban land uses on birds breeding
in forest fragments near Ottawa, Ontario**

By

Wendy Dunford, B.Sc. (honours)

**A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of
Masters of Science**

Department of Biology

Carleton University

Ottawa, Ontario

July, 2001

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"Effects of agricultural and urban land uses on
birds breeding in forest fragments near Ottawa, Ontario"
✓

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Wendy Dunford, B.Sc. (honours)

in partial fulfillment of the requirements
for the degree of Masters of Science

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Abstract

Preserving forest habitat is critical for the conservation of forest breeding birds. However, much previously forested land has already been converted to other land uses. Thus finding strategies to improve the habitat available in existing forest fragments is also important, particularly to conserve forest wildlife in human-dominated landscapes. In this thesis project, the hypothesis tested was that forest fragments of similar size, surrounding forest cover, and vegetation composition and structure are not equally suitable for forest breeding birds because of different surrounding land uses.

Birds were surveyed at a single point count site in each of 23 upland deciduous forest fragments (15.1–49.5 ha) near Ottawa, Ontario. The land use mosaic surrounding each forest fragment was determined by measuring the extent of high intensity agriculture, low intensity agriculture, urban, and deciduous forest within increasingly large buffer circles from 200 to 5000 m radius around the bird survey point. Effects of the surrounding land use mosaic on forest bird species richness and abundance, pairing success of two forest species (Ovenbird, *Seiurus aurocapillus*, and Wood Thrush, *Hylocichla mustelina*), nest success of three species (Ovenbird, Wood Thrush, and American Robin, *Turdus migratorius*), artificial nest success, and artificial nest predators were determined using PCA and regression analysis. The scale at which different land uses had the strongest relationship with response variables was determined from PCA and correlation analysis. In order to attribute differences in response variables to land use mosaics rather than merely the amount of available habitat, forest fragment area and

surrounding forest cover (7.3-27.8%) were kept relatively consistent across fragments.

Vegetation composition and structure did not differ between forest fragments.

With the goal of improving forest fragment habitat for neotropical migrant forest-interior and interior-edge species, agricultural land use in the surrounding 1-1.5 km appeared to be preferable to urban land use. Within agricultural mosaics, fragments surrounded by agriculture of a less intensive nature were more suitable to those surrounded by more intensive practices. To reduce the risk of nest predation experienced in small forest fragments, limiting urban development within 3-3.5 km of forest fragments and reducing the intensity of agricultural practices within 2.5-3 km appear to be beneficial based on the available results. More research is needed to fully understand the impact of surrounding land uses on forest birds.

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General Introduction

Deforestation has led to massive native forest loss in eastern North America, resulting in smaller forest patches amidst a mosaic of human-dominated land uses including agriculture, urban development, and commercial forestry. The field of landscape ecology encompasses the study of the effects of such spatial patterning and compositional change on organisms within a landscape. As landscape ecology is a fairly recent branch of ecology, the theoretical principles for studying the effects of different land uses on wildlife are still developing. Early landscape ecology theory focussed on patches of habitat and how species dynamics were affected by patch size and isolation (MacArthur and Wilson 1967, Levins 1970, Pickett and White 1985, Pulliam 1988). As it became evident that species dynamics could not be fully understood under a habitat vs. non-habitat dichotomy, the land between habitat patches began to merit consideration (Janzen 1983, 1986). The amount of habitat cover within a landscape was contrasted with the amount of matrix cover, where the entire matrix was considered a homogenous “other”—such as either agriculture, forestry, or suburbia. The patch versus matrix view provided the groundwork for considering forest fragmentation and loss from a landscape ecology perspective, but it failed to provide a complete understanding of the processes that occur in fragmented regions because it ignored the potential influence of mosaic landscapes composed of multiple types of land uses. Currently, landscape ecology theory is moving towards a mosaic view of the world where the amount, pattern and interaction of land uses are considered important for understanding impacts on species (Dunning et al. 1992, Wiens 1995). Within this paper, the term land use will be used to denote any type of land cover, including both natural habitat and human-dominated land covers. The

term landscape will be used to imply an areal extent that is in some way significant to the species in question.

Viewing landscapes as a mosaic of land uses enables us to understand what type of land uses cause changes to forest birds, in what amount, and if certain combinations of land use exacerbate or ameliorate adverse effects. Agricultural and urban land uses account for the majority of forest habitat conversion in eastern and southern Ontario. Understanding how the amount and intensity of these land uses impact forest birds, and at what scale, is critical for developing sustainable land use planning strategies. Results from a study based on spatially explicit computer simulations suggests that surrounding matrix quality has a moderate effect on population persistence (Fahrig 2001). Forest fragments of similar size, surrounding forest cover, and vegetative structure may not be equally suitable because of different surrounding land uses (Friesen et al. 1995); however, this hypothesis remains to be explicitly tested empirically. Unfortunately, many of the reported effects of land use composition are unclear because they are confounded by the effects of fragment area and forest cover.

Also unclear is the scale at which different land uses affect forest birds. Typically, a set distance has been selected in which to measure land use variables based upon movement distances of the species in question (Askins et al. 1987, Hinsley et al. 1995), movement distances of predators or brood parasites of the study species (Robinson et al. 1995, Burke and Nol 2000, Howell et al. 2000), or to approximate the scale at which the species perceives the landscape (Rodewald and Yahner 2000). When a multi-scale approach has been used to investigate whether various land use variables operate at similar or different scales, the landscape has been measured within two or more fixed

distances and their relative impact on the response variable compared (but see Bergin et al. 2000). This approach is not only limited by the lack of knowledge concerning movement distances and species' perceptions of landscapes, but also by the assumption that different land use processes being studied actually operate at the same specific scale that has been selected.

The purpose of this research is to test the hypothesis that forest fragments of similar size, surrounding forest cover, and vegetation will vary in forest bird species assemblages and reproductive success due to differences in the land use mosaic in which they are imbedded. More specifically, the purpose is to: 1) assess how agriculture and urban land uses affect forest breeding birds assemblages and reproductive success; 2) determine the scale at which these effects have the greatest impact; and 3) to recommend land use planning strategies that will further the conservation of forest birds.

Chapter 1: Forest Bird Assemblages

Introduction

It has been well documented that forest bird assemblages are affected by forest habitat loss. Forest interior species tend to decrease in abundance or be absent altogether from small forest fragments (Whitcomb et al. 1981, Howe 1984, Freemark and Merriam 1986, Askins et al. 1987, Blake and Karr 1987, Freemark and Collins 1992, Burke and Nol 1998, Fauth et al. 2000; although see Bender et al. 1998, Lee et al. *in press*). Similarly, some species respond negatively to landscapes with low forest cover (Askins

et al. 1987, Robbins et al. 1989, Drolet et al. 1999, Saab 1999, Drapeau et al. 2000, Howell et al. 2000). Forest birds that avoid non-forest edges are not common in forest fragments dominated by edge habitat, while other species are attracted by edge habitat and proliferate in these areas (Kroodsma 1984, Hinsley et al. 1995, Bellamy et al. 1996, Howrot and Niemi 1996, King et al. 1997, Sisk et al. 1997, Howell et al. 2000). The amount of available habitat clearly affects forest bird species; however, habitat loss implies more than just a reduction in the amount of habitat. What used to be continuous forest has been largely replaced with a multitude of human-dominated land uses, particularly agricultural and urban development. This massive land use conversion may also alter forest bird species dynamics apart from the effects of reduced habitat availability.

Neotropical migrant birds have been identified as species of concern due to both observed and anticipated population declines (Hagan and Johnston 1992, Martin and Finch 1995, Sauer et al. 2000). Forest interior and interior-edge species may be particularly vulnerable. In Britain, the breeding presence of both resident and tropical migrant forest bird species was affected by the percentage of forest perimeter adjoined by certain types of land use including agriculture and housing (Hinsley et al. 1995). The probability of Hazel Grouse (*Bonasa bonasia*, a short distance migrant) occurrence in forest fragments was related to the degree of isolation from other fragments, with the effects of isolation more pronounced in an agricultural region than a managed forest region (Aberg et al. 1995). Forest bird species were found to differ in abundance and species richness between forest fragments surrounded by grassland and those surrounded by chaparral, with characteristic assemblages found in each (Sisk et al. 1997).

Forest bird assemblages changed in species richness and abundance along a gradient from more natural to more urbanized habitats, with areas of greater urbanization supporting fewer individuals and species (Blair 1996, Bolger et al. 1997, Clergeau et al. 1998). Residential land use surrounding forest fragments has been shown to cause groups of forest bird species—notably Neotropical migrant species—to decrease in species richness and abundance (Friesen et al. 1995, Kluza et al. 2000). Blue Jays, which are considered important bird nest predators, tend to increase in abundance near urbanizing areas (Engles and Sexton 1994, Kluza et al. 2000) and there is evidence to suggest that high abundance of Blue Jays in forest fragments may deter some species from establishing territories within those fragments resulting in lower abundance for those species (Engles and Sexton 1994).

The above studies have all confounded potential land use effects by also varying bird habitat type, forest fragment area, or percent forest cover in the surrounding area. These three variables have each been shown to affect forest bird assemblages (Ambuel and Temple 1983, Askins et al. 1987, Robbins et al. 1989, Bersier and Meyer 1994, Freemark et al. 1995, Bender et al. 1998). The observed or anticipated decline of Neotropical migrant, forest interior or interior-edge species warrants further, more specific, investigation into the effects of human-dominated land uses on these species.

The purpose of this chapter is to explicitly test the hypothesis that land use composition surrounding forest fragments affects the species composition and abundance of forest birds. More specifically, the goal was to test how forest bird assemblages respond to the amount and intensity of agriculture, the amount of urban development, and the scale at which the response is most pronounced. The existing literature suggests that increased amounts of urbanization and increased amounts and intensity of agriculture surrounding forest fragments will result in lower species richness and abundance with fewer Neotropical migrant species. This is the first study to examine the forest bird

assemblage in forest fragments that differ primarily in the composition of surrounding non-forest habitat up to a distance of 5 km away.

Methods

Site Selection - The study was conducted in Ontario within 75 km of the city of Ottawa, ON (45°25'00" N - 75°42'00" W). The region is dominated by agricultural and urban areas with an overall forest cover of 24%. Twenty-three mature, closed-canopy hardwood forest fragments were selected for the study based upon their size, surrounding forest and non-forest cover primarily within 2 km (Figure 1). The vegetation of all forest fragments was dominated by mature sugar maple (*Acer saccharum*), but also included ironwood (*Ostrya virginiana*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*), and American basswood (*Tilia americana*). Less abundant canopy species included eastern hemlock (*Tsuga canadensis*), white elm (*Ulmus americana*), and eastern white cedar (*Thuja occidentalis*). Habitat evaluations assessing vegetation composition and structure were conducted and found not to differ between forest fragments.

Fragments were selected to minimize variation in fragment area and percent forest cover so that any observed differences between fragments in forest bird assemblages could be attributed to differences in land use rather than habitat amount (Table 1). Thirty percent forest cover within a region is believed to represent a threshold for many forest birds where regions with less than this amount contain forest patches with lower species richness and abundance (Robbins et al. 1989, Freemark and Collins 1992). For this reason, forest fragments were selected so that forest cover within 5 km remained below 30% and thus were embedded in land use mosaics that were not dominated by forest

habitat, enabling investigation into the effects of other land use types within the mosaic.

Forest Bird Assemblage - Following the Ontario Forest Bird Monitoring Program protocol (Welsh 1995), the forest bird assemblage was characterized using 10-minute, 100 m limited distance point counts. Counts were conducted at one station per forest fragment located 100 m from a non-forest edge so that both forest interior and forest edge species would be included. Each fragment was surveyed between June 9 and June 19, 2000 and again two weeks later between June 25 and July 2, 2000. Counts were all conducted from 6:00-9:00 a.m. on mornings with little wind or rain. For each fragment, the count with the highest number of individuals was used as the abundance estimate for each species.

For statistical analysis the assemblage was first broadly characterized by total abundance and total species richness. Species were then grouped into the following categories (based on classifications by Whitcomb et al. 1981, Freemark and Collins 1992) and abundance and species richness were determined within each category: 1) migratory strategy (Neotropical migrant, short distance migrant, resident); and 2) forest spatial specialization (edge, interior-edge, interior). Lastly, the abundance of all species that occurred in four or more of the 23 fragments was analyzed to better understand how individual species influenced the observed trends within life history groupings (see Appendix 1 for a full list of species).

Land Use Variables and Scale - Using classified Landsat Thematic Mapper data (30 m resolution; classification error unknown) collected in early May 1991 (source: D. Burke OMNR, London Office) and a GIS (ArcView), land use composition was determined within a series of circles centered on the point count sites (cf. Freemark et al.

in press [landscape level analysis using focal point method]). Each circle increased in size by 200 m increments—the smallest having a radius of 200 m, the largest a radius of 5000 m (Figure 2). Four types of land use accounted for at least 90% of the total area of each circle: 1) intense agriculture (row crops such as corn and small grains); 2) less intense agriculture (pasture, hay fields, old fields); 3) urban areas (settlements and developed land, major transportation routes); and 4) forest (deciduous and mixed deciduous only). Urban areas were updated by converting 1998 air photo housing data into a polygon theme (source: I. Olthoff, Dept. of Geog., Carleton University). In general, intense agricultural practices differ from less intensive practices in three major ways (Freemark and Kirk 2001). The amount of chemical fertilizers and pesticides is greater with intensive types of agriculture. The disturbance level increases with the intensity of production due to more frequent planting, tilling and harvesting. Lastly, intense practices typically result in less heterogeneous land use mosaics with large fields of monoculture crops. Less intensive practices typically result in smaller fields with more field margins and hedgerows.

Statistical Analysis - Because land use variables were highly correlated within and between buffer circles, the four variables for the 25 circles (100 variables) were reduced using principal components analysis, PCA (PROC FACTOR METHOD=PRIN, SAS Institute 1990). Components were rotated using the PROMAX method to increase interpretability (as in Saab 1999). PROMAX is an oblique transformation which creates more meaningful, but not necessarily orthogonal and uncorrelated, principal components (SAS Institute User's Guide 1990). The reference axis correlations were examined to determine that each component described a different aspect of land use composition,

intensity, and scale.

The principal components were used as predictor variables in multiple regression with stepwise selection (PROC REG; alpha to enter: 0.1, alpha to stay: 0.1) to determine which attributes of land use composition best accounted for the variation in each bird assemblage response variable. Each multiple regression was testing an independent hypothesis about species assemblages and thus corrections for multiple testing were not necessary. Regression models were constructed in a similar manner with individual species abundances as response variables; however, these analyses were used only to understand which species might be driving the relationships between assemblage-level responses and land use composition.

To determine whether Neotropical migrant species were more sensitive to urban and high intensity agricultural land uses, a G-test was conducted comparing the numbers of Neotropical migrant species demonstrating positive, negative, or no relationships with these land uses to the number of species with other migratory strategies (short distance migrants and residents) showing positive, negative, or no relationships. A positive response was considered a significant increase in abundance with greater amounts of surrounding urbanization (positive relationship with PC2 or negative relationship with PC5) or greater intensity of agriculture (negative relationship with PC1). A negative response was considered a significant decrease in abundance with these land uses. If changes in abundance were non-significant in relation to these land uses, there was considered to be no response. This would indicate whether the nature of species' responses to land use was independent of migratory strategy. The sensitivity to urban and high intensity agriculture of forest interior and interior-edge species in comparison to

edge species was tested with the same method. These analyses were used to gain insight into the response of different life history classifications to land use composition.

In order to better understand the scale at which different forest bird life history groupings responded to different land uses, an analysis was conducted to determine the distance at which each of the four measures of land use composition explained the most variation in each response variable. A series of simple linear regressions was conducted for each type of land use with the percent cover in each buffer circle used as a predictor variable. Measures of the species assemblage were response variables. The buffer circle with the highest R^2 value indicated the distance within which that type of land use had the strongest effect on each measure of the species assemblage (Figure 3). Only regressions with $p < 0.05$ were considered to be indicating a biological response to surrounding land use. As the purpose of this analysis was to examine the pattern in the amount of variation explained across scales, corrections for multiple tests were not performed. These results were compared to PCA loadings in order to better understand issues of scale as well as to assist in the interpretation of the principal components.

Results

Land Use Variables - The proportion of each land use changed with increasing distance from the point count sites (Figure 4). In general, forest was the dominant land use up to 600 m and intense agriculture the most dominant land use from 800 m to 5000 m. The proportion of each land use within the buffer circles remained fairly consistent past 1600 m.

Using the scree plot criterion, five principal components (PCs) were found to be

meaningful, together accounting for 87.5% of the variation in the land use composition data (see Appendix 2 for the loadings of each variable). PC1, accounting for 27.0% of the total variation, described a gradient in agricultural intensity. The agricultural land around forest fragments with a negative score was dominated by higher intensity practices, while fragments with a positive score were surrounded by agricultural land of a less intensive nature. The highest loadings for more intense agriculture were from 400-600 m while the highest loadings for less intense agriculture were from 400-2600 m (Table 2), suggesting that differences in the intensity (although not necessarily the total amount) of agriculture within these distances contributed the most to the total variation in agricultural intensity across all scales.

PC2 accounted for 24.6% of the total variation and described a gradient in the amount of urban development. Fragments with a high negative score had little surrounding urban development while fragments with a high positive score were more urbanized. The percent cover of urban land use had high loadings on PC2 from 2800-3600 m (Table 2).

Accounting for 20.7% of the variation in land use variables, PC3 described the amount of forest cover surrounding each fragment. High loadings on PC3 extended from 2800-5000 m (Table 2), making PC3 a measure of forest cover at a relatively large scale. A negative score indicated lower forest cover, a positive score higher forest cover. PC4 also described the amount of forest cover and accounted for 8.4% of the total variation. Because the highest loadings were for the amount of forest within 1200 m, particularly from 1000-1200 m (Table 2), PC4 is a measure of the amount of forest immediately surrounding each fragment. Again, negative scores indicated lower forest cover, positive

scores higher forest cover. It is important to note that because the amount of forest surrounding each forest fragment did not differ substantially (Table 1) both components relating to forest cover are describing relatively small differences between mosaics.

Lastly, PC5 accounted for 6.8% of variation and described a contrast in the amount of agriculture versus the amount of urban, regardless of intensity. Fragments with a negative score had more urban (highest loading at 800 m) whereas fragments with a positive score had more agriculture (highest loadings at 600 m for intense agriculture and 4800-5000 m for less intense agriculture) (Table 2).

Reference axis correlations were low (± 0.04 to ± 0.25) between PCs except for between PC1 and PC5 (-0.32) and between PC2 and PC5 (0.33). Similar levels of correlation were found to be acceptable in other studies (Saab 1999). Correlations amongst the original variables across all scales ranged from ± 0.028 to ± 0.64 .

Total Abundance and Species Richness - A total of 33 species was detected across all point count sites (Table 3; see Appendix 1 for full species names). The total abundance and species richness of forest breeding birds were not significantly related to any PC measure of land use composition.

Abundance and Species Richness by Migratory Strategy - A total of 19 Neotropical migrant (NTM) species was detected in the study (Table 3, Appendix 1). Both the abundance and species richness of NTM species increased significantly with PC5 (Table 4, Figure 5E). That is, forest fragments within a more urbanized land use mosaic had lower abundance and species richness of NTM birds, while fragments within a mosaic dominated by agriculture had higher abundance and species richness. The amount of less intense agriculture within a distance of 200 m of the point count site was

the most highly positively correlated with NTM abundance while the amount within 1400 m was the most highly positively correlated with NTM species richness (Table 5). The amount of urban land was most negatively correlated with NTM abundance within 800 m and species richness within 1200 m (Table 5).

There were six short distance migrant (SDM) species detected in the study (Table 3, Appendix 1). SDM species richness did not vary in relation to any PC measure of land use composition. SDM abundance declined with PC3 (Table 4, Figure 5C), indicating these birds preferred fragments surrounded by relatively little forest cover. This was supported by the scale correlation analysis where the amount of forest cover within 5000 m was the most highly negatively correlated with SDM abundance (Table 5).

Eight resident (RES) species were detected across all point count sites (Table 3, Appendix 1). The abundance of RES species declined with PC1 but increased with PC2 (Table 4, Figures 5A and 5B). That is, forest fragments surrounded by greater amounts of intense agriculture and/or highly urbanized areas had a greater abundance of resident bird species. RES species richness was not related to any PC measure of land use composition. Although there was no significant correlation with the amount of intense agriculture at any scale, the amount of less intense agriculture within 2200 m was the most negatively correlated with RES abundance (Table 5), indicating that the intensity of agricultural land within this distance is important in predicting resident abundance. The amount of urban development within 1200 m had the highest positive correlation with RES abundance (Table 5).

Abundance and Species Richness by Spatial Specialization - Eight forest interior (INT) species were detected (Table 3, Appendix 1). Neither INT species richness nor

abundance were related to any PC measure of land use composition.

A total of 13 interior-edge (I/E) species was detected (Table 3, Appendix 1). Both I/E abundance and richness increased with PC1 (Table 4, Figure 5A). That is, the number of I/E individuals and species increased with less agricultural intensity. The amount of less intense agriculture was most highly positively correlated to both I/E abundance and richness at a scale of 1400 m (Table 5). The amount of intense agriculture had the highest negative correlation with I/E species richness within a distance of 600 m (Table 5).

Twelve edge (EDG) species were detected in the study (Table 3, Appendix 1). Both EDG abundance and richness decreased with PC1 (Table 4, Figure 5A), indicating that edge species have higher abundance and species richness in forest fragments surrounded by intense agriculture. Less intense agriculture had the highest negative correlation with EDG abundance within a distance of 600 m and with EDG richness within 1000 m (Table 5). Intense agriculture was most positively correlated with EDG abundance at a scale of 1400 m and EDG species richness at 1000 m (Table 5).

Individual Species Abundance - Four species occurred in less than four (17.4%) of the 23 forest fragments and thus were not included in analyses of individual species abundance (Appendix 1). Sixteen of the remaining 29 species responded to at least one PC measure of land use composition (Table 6, Figure 5). Of these 16 species, proportionately more NTM species were negatively affected by urban and high intensity agricultural land uses than short distant migrant and resident species pooled together (G-test: $G_{(2)}=9.26$, $p<0.01$; Table 7A). Similarly, there were proportionately more forest

interior and interior-edge species in comparison to edge species negatively affected by these land uses (G-test: $G_{(2)}=14.48$, $p<0.001$; Table 7B).

Discussion

Land use composition—the amount and intensity of various human-dominated land uses—did affect forest bird assemblages in forest fragments embedded in the agricultural/urban mosaic of the Ottawa area. While there was no overall effect of land use composition on total species richness and abundance, species with different life history strategies responded differently to surrounding land uses, likely obscuring any pattern when the entire assemblage was examined. As a result, interpretation of whether particular land uses cause adverse effects on forest birds depends upon the group or species being studied. In this study, interpretation of adversity was based upon the impact on species of concern such as Neotropical migrant, forest interior or interior-edge species. This underlines the importance of considering life history groupings when conducting assemblage-level analyses.

When considered together as a life history classification, Neotropical migrant forest birds were found to increase in abundance and richness in agricultural as opposed to urban land use mosaics (PC5). Previous studies have found NTM species to be sensitive to the number of houses within 100-200 m of forest fragments (Friesen et al. 1995, Kluza et al. 2000). In contrast, resident species (when grouped together) responded positively to urbanization within 1200 m of forest fragments. The abundance of resident species increased with the amount of urbanization (PC2) and more resident species were present in fragments surrounded by an urbanized mosaic than an agricultural mosaic

(PC5). Resident species are frequent visitors of backyard bird feeders and thus have an abundant food supply throughout the year in urban areas. In addition, many resident species nest in tree or building cavities—a nesting strategy known to experience lower rates of nest predation (Martin and Li 1992). These factors could lead to higher abundances of resident bird species in more urbanized forest fragments.

With the exception of the Brown-headed Cowbird (a SDM edge species which was less abundant in urban mosaics), those individual species negatively affected by urbanization were all NTM, forest interior or interior-edge species. These individual species may be largely driving the negative responses of the NTM and interior-edge groups to urban land use mosaics. Individual species that responded positively to urbanization were all RES or SDM edge species, except for the Baltimore Oriole (a NTM edge species) and the Downy Woodpecker (a RES interior-edge species). It was likely changes in the abundance of these particular resident species which made the positive relationship between the resident species classification and urban land use significant.

The underlying factors that make forest fragments surrounded by urban areas less suitable for Neotropical migrant and interior-edge species are not well understood. A number of mechanisms have been suggested but need further investigation. These species may avoid urbanized forest fragments due to: 1) a psychological need to maintain distance from houses (Whitcomb et al. 1981); 2) changes in vegetation related to increased disturbance from human use (Matlack 1993); 3) changes in micro-climate (Saunders et al. 1991); 4) competition with, or avoidance of, urban-adapted species (e.g. resident species such as the Blue Jay) (Engles and Sexton 1994, Kluza et al. 2000); and/or 5) increased levels of nest predation (Wilcove 1985, Matessi and Bogliani 1999).

An understanding of the causal mechanisms that deter some forest birds from forest fragments within even lightly urbanized regions is essential to developing strategies for managing urban growth (see Chapter 2).

When analyzed as a group, interior-edge forest birds responded negatively to the intensity of surrounding agricultural practices. Individual species negatively affected by agricultural intensity were all classified as forest interior or interior-edge. As a group, edge species were also affected by agricultural intensity but in an opposite manner to interior-edge species. The Red-tailed Hawk was the only individual species to increase in abundance with greater agricultural intensity, perhaps due to increased hunting efficiency in large fields with less cover and little structural variation in the vegetation, particularly early in the breeding season when point counts were conducted.

Very few studies have examined the impact of agricultural intensity on forest breeding birds: as a result, theories as to why such effects occur have not been well addressed in the literature. Forest interior-edge birds may be attracted to forest fragments with more heterogeneous surroundings than are typically associated with land use mosaics dominated by intensive agricultural practices. Potentially, interior-edge species may avoid forest fragments in intense agricultural mosaics due to increased levels of adjacent disturbance from planting, tilling and chemical spraying, or due to increased competition from more abundant edge species.

Best et al. (1995) found that landscape scenarios representing a diverse mosaic of crops and natural habitats supported substantially more (93 vs. 18) breeding bird species than mosaics dominated by large, intensively managed, monoculture row crops. Lower intensity types of agriculture such as pasture, old fields, perennial crops and organic

farms provide greater regional diversity of habitat types which benefits farmland breeding birds (Best et al. 1995, Freemark and Kirk 2001) as well as forest NTM and interior-edge breeding birds (this study). Low intensity agriculture also tends to provide more hedgerows, field margins, and wind breaks which have been shown to increase avian diversity in agricultural regions (Jobin et al. 2001). Buffer strips between cultivated fields and forest fragments can help to protect forest flora and probably forest wildlife from disturbance associated with agricultural practices (Boutin and Jobin 1998).

The abundance and species richness of forest interior birds as a group did not vary in relation to land use composition at least in part because forest fragments were selected to minimize the difference in amount of forested land use. Forest interior species preferentially avoid non-forested edges (Freemark and Collins 1992, Burke and Nol 1998) and thus may be more insulated from the effects of surrounding land uses than other forest bird species. The amount and pattern of available habitat within a region is a strong determining factor of population size for interior species (Bender et al. 1998); thus, they may not be as affected by non-habitat land uses. Populations of these species may be generally low within the study fragments as they were all less than 50 hectares and forest interior species tend to be more abundant (as measured with point counts) in larger tracts of forest (Villard et al. 1993, Burke and Nol 1998, Roberts and Norment 1999). There is some debate, however, that point count measures of abundance can be misleading indicators of density. At least one study measuring true density (# of birds/ha determined across the entire area of the forest fragment) has found forest interior bird density to increase with decreasing fragment size (Lee et al. *in press*).

- As a group, short distance migrants responded negatively to the slight variation in

forest cover between land use mosaics. The underlying cause of this response may be related to the forest spatial specialization of SDM species. Species classified as SDM were comprised predominately of edge species and to a lesser extent interior-edge species. No SDM species were associated with the forest interior. Landscapes with greater forest cover tend to have less edge habitat, resulting in lower abundance of edge species—many of which are classified as SDM. Individual species affected by forest cover most often responded to the amount of forest immediately surrounding the forest fragment (within 1200 m [PC4]) as opposed to the amount within a larger mosaic of 5000 m (PC3). Species that responded negatively to the amount of forest were a mixture of all life history groupings while those that responded positively were all NTM or SDM, forest interior or interior-edge species.

Species considered to be of conservation concern such as Neotropical migrant, forest interior and interior-edge forest birds, tended to decrease in abundance within forest fragments surrounded by greater amounts of urbanization and greater intensity of agriculture. With the goal of improving forest fragment habitat for these species, agricultural land use in the surrounding 1-1.5 km appeared to be preferable to urban land use. Within agricultural mosaics, those dominated by less intense agricultural practices were more suitable than those dominated by more intensive practices.

Chapter 2: Reproductive Success

Introduction

Analyzing patterns in species richness and abundance is useful for understanding effects of different land uses and for determining which species are sensitive to particular land use attributes. However, some researchers have argued that abundance and density are misleading indicators of habitat quality and thus may also be misleading about how land use might affect the breeding success of forest birds. (Van Horne 1983, Vickery et al. 1992, Roberts and Norment 1999). As a consequence, an increasing number of studies have been examining measures of reproductive success as response variables. Pairing success of some Neotropical migrant forest interior and interior-edge species has been shown to be significantly lower in small forest fragments (Gibbs and Faaborg 1990, Van Horn et al. 1995, Burke and Nol 1998, Roberts and Norment 1999), more isolated fragments (Villard et al. 1993), and in fragments surrounded by lower forest cover (Dunford et al. *in review*). Nest predation and brood parasitism of a variety of forest species typically increase with decreasing forest fragment area (Gates and Gysel 1978, Brittingham and Temple 1983, Roberts and Norment 1999) and regional forest cover (Robinson et al. 1995, Burke and Nol 2000). Proximity to non-forested edges has also been shown to lower reproductive success (reviewed in Paton 1994). Because reproductive success varies with the amount of available habitat, it is imperative in studying the effects of anthropogenic land uses to control the amount of habitat between regions.

The effect of non-forest land use composition on avian reproductive success has never been examined in detail for any forest bird species. One study has shown that

whether contiguous forest was disturbed by agriculture or silviculture had no effect on Ovenbird pairing success (Rodewald and Yahner 2000). However, study plots were located more than 100 m from forest edges in contiguous forest with 45% to 82% forest cover—thus, forest would actually have been the dominant habitat in this area and other habitat types in the region could be expected to have less influence. Forests fragments surrounded by predominately agriculture as opposed to forest have been shown to have a higher incidence of forest bird nest predation (Anglestam 1986, Robinson et al. 1995) and brood parasitism by Brown-headed Cowbirds (Donovan et al. 1997). Another study measured reproductive success of American Robins in a suburban environment and compared these results to robin nesting success from rural areas found in the literature, concluding that robins can be equally if not more successful in urban settings (Morneau et al. 1995). However, the conclusion was confounded by the fact that the nesting micro-habitats between the suburban and rural environments differed drastically, making it difficult to attribute differences in success to land use.

Except for the above studies, very little research has been conducted on the effects of non-forest land use composition on nesting success of forest nesting birds. Finding and monitoring real nests is extremely labour-intensive, time consuming, and therefore costly. Using artificial nests to study factors that may affect natural bird nest predation rates has many advantages including larger sample sizes, eliminating nest searching time, avoiding potential disturbance from nest monitoring, and (by using wax or plasticine eggs) enabling identification of nest predators.

Wilcove (1985) found that predation pressure on artificial nests appeared to be more intense in forest fragments near suburban developments than in fragments in more

rural areas. However this was purely observational since no measure of urbanization was included other than "surrounded by housing developments" vs. "surrounded by agricultural fields" and no statistical testing was conducted between the two. In a study comparing artificial nest predation rates and predator assemblages in forest fragments with rural edges (created by agricultural fields, housing density of 1.7 houses/km) and forests with suburban edges (created by backyards or pasture near houses, housing density of 20 houses/km), it was found that rural forests experienced higher levels of predation than suburban forests (Danielson et al. 1997). Gering and Blair (1999) found urban environments had lower predation pressure than more natural environments. In contrast, a study in Ohio found no differences in artificial nest predation between rural and suburban forest fragments (Melampy et al. 1999).

A comparison of forest fragments in a landscape fragmented by forestry and a landscape fragmented by agriculture resulted in agricultural forest fragments exhibiting higher artificial nest predation rates and greater nest predator species richness than forestry landscapes (Bayne and Hobson 1997). In a multi-scale study of artificial nest predation on roadsides, the amount of rowcrops and alfalfa/pasture were found to be important at larger spatial scales (1600 m) (Bergin et al. 2000). Predation rate declined with increasing amount of row crops while alfalfa/pasture habitats were positively associated with nest predation (Bergin et al. 2000). This result was related to the spatial scale at which the nest predator community operates as well as the fact that rowcrops were negatively correlated with forest cover, thus those landscapes provided less nest predator habitat (Bergin et al. 2000).

Knowledge of whether the suite of nest predators differs with land use

composition provides insights into any observed changes in predation rates.

Conflicting findings on the effects of non-forest edges, forest fragment size, and amount of surrounding forest habitat on nest predation rates (Andren 1992, Paton 1994, Andren 1995) are often attributed to differences in predator assemblages (Andren 1995). The abundance and diversity of nest predators may differ between land use mosaics causing the observed differences in predation rates (Danielson et al. 1997).

The purpose of this chapter is to test the hypotheses that land use composition affects: 1) pairing success of two Neotropical migrants, the Ovenbird (a forest interior species) and the Wood Thrush (a forest interior-edge species); 2) nest success of three forest birds (Ovenbird, Wood Thrush, and American Robin, a forest edge species); 3) artificial nest success; and 4) the suite of nest predators responsible for depredating artificial nests. The scale at which these processes take place will be discussed. Correlation between the three measures of reproductive success (pairing success, natural nest success, and artificial nest success) was also examined. Based upon the existing literature, expectations were: 1) Ovenbird and Wood Thrush pairing success would be lower in fragments surrounded by more urbanized areas and higher in fragments with land use mosaics dominated by less intensive types of agriculture; 2) natural and artificial nest success would be highest in forest fragments surrounded by more urbanized areas due to low amounts of predator habitat and lowest in fragments surrounded by less intense agriculture; 3) the number of predator groups depredating artificial nests would be higher in fragments surrounded by less intense agricultural practices; and 4) natural nest success and artificial nest success would be positively correlated, but would not necessarily be correlated with pairing success.

Methods

Site Selection - This study was conducted in the same forest fragments as the forest bird assemblage research. For more information refer to Methods section in Chapter 1.

Land Use Variables and Scale - Because artificial nest transects were placed near (0 to 350 m away) point count sites, the same measures of land use composition and intensity were used across all 25 buffer circles. For information on land use variables, refer to Methods section in Chapter 1.

Pairing Success - Pairing success of Ovenbirds and Wood Thrush was determined by one or a combination of several criteria (Villard et al. 1993). Since males and females of these species are not overtly sexually dimorphic in appearance, males were considered to be paired if they engaged in non-aggressive interactions with another bird of the same species. Males were also considered paired if they were seen carrying food, feeding fledglings, or if an active nest was found within a territory. Singing males of each species were located randomly by following the sound of their song. Over several visits, individual birds were observed until determined to be paired or until a total time of approximately 60 minutes had elapsed, at which time they were considered unmated. Within each fragment the percent paired birds of each species was recorded. Pairing success was not determined for American Robin because they did not appear to be as territorial as the other two species, making detection of pair bonds difficult.

Natural Nest Success - Nests of Ovenbirds, Wood Thrush and American Robins were located by observing adult birds fly into the nest as well as by systematically searching the foliage within territories. Each nest was marked with a flag placed at least

5 m away. Nests were checked and the contents recorded approximately once a week or close to the expected fledging date (Beintema 1996). Each nest was classified as successful (fledged at least one young of the host species) or failed (no host young fledged). Failed nests were considered depredated if the nest structure, eggs, or nestlings disappeared or were found destroyed. Several criteria were used to classify the outcome of each nest (Manolis et al. 2000) and if nests could not be classified as successful or failed their fate remained unknown (Table 8). An estimate of the proportion of nests surviving each day of the nest cycle (daily survival) was determined for all species grouped together for each site using the Mayfield method (Mayfield 1961, 1975).

The Mayfield method is based on the probability of a nest surviving each day in the nesting cycle and is thus a function of time. A simple percentage of successful nests will over estimate nest success because a nest found during the first day of construction is given equal weighting to one found the day before chicks fledge (Mayfield 1961, 1975). In actuality, the first nest has a greater chance of being depredated as it has many more days which it must survive to be successful. The Mayfield estimate corrects this bias by incorporating the number of "nest days" each nest is observed ($\text{daily nest survival} = 1 - [\# \text{ failed nests} / \# \text{ nest days}]$). The length of time (in nest days) that each nest is monitored is important in the Mayfield calculation. As nests were visited only once a week, certain assumptions were made in calculating nest days. The Last Active-B method (Manolis et al. 2000) was used to determine the termination point of nest days for successful nests, failed nests, and nests of uncertain fate if this point could not be directly established (i.e. chicks fledged when nest checked). For both successful and failed nests, the midpoint between the last day the nest was checked and still active and the first day the nest was

found to be inactive (either due to fledging or failure) was used as the last nest day.

For nests of uncertain fate, the day the nest was last found to be active was used as the last nest day.

Artificial Nest Success - Forest bird nest predators and daily success rates were assessed with artificial nests each containing two wax eggs. Wax eggs were used because they hold the imprint of tooth, claw and bill marks. In each forest fragment, sixteen artificial nests (eight ground nests and eight shrub nests [placed 1.5-2 m high]) were placed along two transects 10 m apart. The transects started at the forest edge and ran perpendicularly into the forest, alternating between ground and shrub nests every 15 m (0 m through to 105 m from the forest edge). The location of each nest was marked with a flag placed 1-2 m away. Nests were set out in early June (peak incubation time for forest birds) and collected one week later (exposure period of seven days).

Nests were made from cardboard peat flower pots and were medium brown in colour. Ground nests resembled Ovenbird nests—pots were cut in half length-wise to form a dome, placed cut side down on the forest floor and covered with leaf litter. The wax eggs placed inside ground nests were of a similar size to Ovenbird eggs and painted a similar colour and pattern. While egg colour has not been conclusively shown to affect predation rates, a general recommendation in designing artificial nests is for them to as closely as possible resemble natural nests of target species (Major and Kendal 1996). Artificial shrub nests were designed to mimic robin nests more specifically than Wood Thrush nests. While nests of the two species can appear quite similar, robin nests often contain more grass and are located further out on tree branches than the nests of Wood Thrush which tend to contain more leaf litter and be positioned nearer the tree trunk

(Peck and James 1987). Peat pots were cut in half width-wise and straw-like grass was wrapped around each pot. Nests were secured to tree branches with brown string. The wax eggs placed inside tree nests were of a similar size to robin and Wood Thrush eggs and were dyed a similar colour blue.

As with natural nests, each artificial nest was classified as successful or depredated (eggs missing and/or marked). Daily artificial nest survival was calculated using a modified Mayfield estimate (Mayfield 1961, 1975). Each successful nest survived the full seven days of exposure and therefore was allotted seven nest days for the Mayfield calculation. Because artificial nests were not checked during the exposure period, those that were found to be depredated were arbitrarily allotted half of the exposure period, 3.5 nest days, for the Mayfield calculation.

Artificial Nest Predators - Nest predators were identified into groups based on the size and pattern of tooth, bill and claw marks in the wax eggs. Group identification was as follows (see Appendix 3 for genus names): 1) mouse, including mice species, voles and shrews; 2) squirrel, including red squirrels, gray squirrels, flying squirrels and chipmunks; 3) weasel, including weasel species and mink; 4) raccoon, including raccoons and skunk; 5) bird, including corvid species and other potential avian nest predators; and 6) predators that removed eggs from the nest (i.e. eggs that were missing from the nest). The number of nests depredated by each group was recorded. Unlike real eggs, many wax eggs were not actually eaten but merely chewed or pecked; thus they were left to be "depredated" by another individual. Hence, for clarity, all nests with evidence of predation by more than one predator group were discarded from the analysis of nest predators.

Statistical Analyses - To test hypotheses relating to the effects of surrounding land uses on measures of forest bird reproductive success, principal components of the land use variables were used as predictor variables in multiple regression with stepwise selection (PROC REG; alpha to enter: 0.1, alpha to stay: 0.1). Response variables were Ovenbird and Wood Thrush pairing success, natural nest success, artificial ground and shrub nest success, predator group richness, and predation events by each predator group. Due to low predation on shrub nests by some predator groups, the number of predation events by each predator group was combined for ground and shrub nests. A t-test was used to determine if pairing success differed between Ovenbirds and Wood Thrush (PROC T-TEST). Daily survival of natural nests was compared between Ovenbird, Wood Thrush, and American Robin with ANOVA (PROC REG), and between artificial ground and shrub nests with a t-test. Logistic regression (PROC LOGISTIC) was used to test for an effect of distance from the forest edge on ground and shrub nest survival. The predation pattern on ground and shrub nests was compared; predator group richness was compared between ground and shrub nests using a t-test, and the proportion of each nest type depredated by the different predator groups was compared using Fisher's Exact test (PROC FREQ). Fisher's Exact test was also used to investigate whether the distance of the nest from the forest edge affected the proportion of nests depredated by each predator group. To test the nature of the relationships between pairing success, natural nest success, and artificial nest success correlation analysis was used (PROC CORR).

Similar to the approach undertaken to understand the scale at which the forest bird assemblage responded to land use, an analysis was conducted in order to better understand the scale at which reproductive success was most strongly related to different

land uses. A series of simple linear regressions was conducted for each type of land use with the percent cover in each buffer circle used as a predictor variable. Pairing success of Ovenbird and Wood Thrush, natural nest success, and artificial nest success (calculated separately for ground and shrub nests) were response variables. The buffer circle with the highest R^2 value indicated the distance within which that type of land use had the strongest effect on each measure of reproductive success. Only regressions with $p < 0.05$ were considered to be indicating a biological response to surrounding land use. As the purpose of this analysis was to examine the pattern in the amount of variation explained across scales, corrections for multiple tests were not performed.

Results

Land Use Variables - For information on principal components analysis of land use variables see Results section in Chapter 1.

Pairing Success - Due to time constraints, pairing success was determined in only 17 of the 23 forest fragments. Wood Thrush were not present in 4 of the 17 fragments so pairing success for this species was determined in 13 forest fragments. In total, 53 Wood Thrush were followed, 42 of which were found to be mated. Forty-five out of a total of 81 Ovenbirds were mated. The average percent pairing success across fragments was higher for Wood Thrush than Ovenbirds (t-test: $t=2.05$, $p=0.00027$; Table 9).

Wood Thrush pairing success was not related to any measure of PC land use composition, although it is possible that the low sample size may have resulted in statistical power too low to detect a biologically significant relationship. Ovenbird pairing success decreased with PC3 but increased with PC4 (Table 10, Figures 6C and

6D). That is, the number of paired Ovenbirds was higher in forest fragments immediately surrounded by higher forest cover (up to 1200 m), but was lower in fragments with higher forest cover at a larger scale of 5000 m. The scale correlation analysis indicated that the amount of forest within 400 m was the most highly positively correlated with Ovenbird pairing success while the amount of forest within 4000 m was the most highly negatively correlated (Table 11).

Natural Nest Success - In total, 76 nests were found in 14 forest fragments. The number of nests found was low for Ovenbird (10 nests in 5 forest fragments) and Wood Thrush (25 nests in 11 fragments) and higher for American Robin (41 in 11 fragments). Mean daily nest survival did not differ significantly between the three species (ANOVA: $F_{2,24}=0.62$, $p=0.54$; Table 9). PC land use composition did not affect individual species success or the success of all species grouped together, but again the statistical power may have been too low to detect biologically meaningful relationships due to very small sample sizes.

Artificial Nest Success - More ground nests (121/184) were destroyed than shrub nests (98/184); however, daily survival did not differ between the two types of nests (paired t-test: $t_{22}=2.07$, $p=0.19$; Table 9). There was no effect of distance from the forest edge on probability of either ground or shrub nest predation (logistic regression: ground: $X^2=0.82$, $p=0.36$ $n=184$; shrub: $X^2=0.11$, $p=0.75$, $n=184$).

PC land use composition did not have a significant effect on the daily survival of artificial ground nests. Artificial shrub nest survival declined with PC2 and increased with PC3 (Table 10, Figures 6B and 6C). This suggests that artificial shrub nests had a greater chance of surviving in forest fragments surrounded by low amounts of

urbanization and higher amounts of forest within 5000 m. This was supported by the scale correlation analysis where the amount of forest cover within 5000 m was the most highly negatively correlated with artificial shrub nest survival (Table 11). Shrub nest survival was most highly negatively correlated with the amount of urban land use within 3600 m of the forest fragment (Table 11).

Artificial Nest Predators - Nineteen artificial ground nests and two shrub nests had signs of predation by more than one predator group and were thus excluded from further analyses. The number of different predator groups detected in each forest fragment (predator group richness) was higher for ground nests than shrub nests (paired t-test: $t=2.07$, $p=0.003$; Figure 7). The "missing" category was not included as a group in determining predator group richness. Ground nest predator group richness decreased with PC1 and increased with PC4 (Table 10, Figures 6A and 6D). That is, there were more types of predators depredating ground nests in forest fragments surrounded by intense agriculture than in those surrounded by less intense agricultural practices. More ground nest predators were also found in forest fragments surrounded by higher amounts of forest within 1200 m. Predator group richness for ground nests was most highly positively correlated with the amount of intense agriculture within 2600 m of the fragments, and most highly negatively correlated with the amount of less intense agriculture within 3800 m (Table 11). The amount of forest within 200 m had the highest positive correlation with ground nest predator richness (Table 11). Shrub nest predator richness was not related to PC land use composition.

For ground and shrub nests combined, wax eggs that were missing from the nest accounted for the most predation (81/198 nests). There is some evidence that most

missing eggs were taken by avian nest predators. In two instances, eggs from artificial shrub nests were found further than 10 m from the nest with peck marks; artificial eggs with marks from all other predator groups were found inside or directly beside or below nests. Of the predator species groups, the mouse group accounted for the most predation (49/198 nests) with the raccoon group a close second (40/198). Predation by the bird group (12/198), squirrel group (10/198), and weasel group (6/198) was low. The proportion of nests depredated by each group differed between artificial ground and shrub nests (Fisher's Exact test: $p < 0.0001$; Figure 8); however, because predation by some groups was low, predation events were combined between ground and shrub nests in order to make statistical analysis of land use effects more robust. The proportion of nests depredated by each predator group did not vary with distance from the forest edge (Fisher's Exact test: $p = 0.35$).

Although the amount of predation by the mouse group was high, it was not significantly related to any PC measure of land use composition. Similar to the mouse group, the raccoon group accounted for much of the predation on artificial nests but was not significantly related to PC land use composition. Predation by the squirrel group increased with PC4 (Table 10, Figure 6D), indicating that artificial nest predation by species in the squirrel group was higher in forest fragments surrounded by more forest habitat within 1200 m. The amount of predation by the weasel group decreased with PC2 (Table 10, Figure 6B), indicating that these species are either less abundant or less active in highly urbanized areas. The amount of predation by the bird group was also not related to PC land use composition. The number of nests with eggs missing increased with PC2 and decreased with PC3 (Table 10, Figures 6B and 6C). This suggests that

predation events where eggs were completely removed from the nest were more common in forest fragments surrounded by high amounts of urban and less common in fragments surrounded by higher forest cover within 5000 m.

Relationships between Measures of Reproductive Success - Wood Thrush nests were found in all but two of the 13 forest fragments in which Wood Thrush pairing success was determined. There was no correlation between the daily survival of Wood Thrush nests and Wood Thrush pairing success ($r=0.48$, $p=0.13$; Figure 9). Ovenbird nests were only found in five of the 17 sites in which pairing success was determined and there was no relationship between these two measures of reproductive success ($r=-0.56$, $p=0.32$; Figure 10).

Daily artificial nest survival (ground and shrub nests combined) was not correlated with daily nest survival of the three species combined ($r=0.13$, $p=0.65$). However, artificial shrub nest survival was positively correlated with American Robin nest survival ($r=0.6$, $p=0.051$; Figure 11).

Discussion

Many of the observed effects of land use mosaics on measures of reproductive success were contrary to initial expectations. There was a significant relationship between land use composition and Ovenbird pairing success but not Wood Thrush pairing success. There were relationships between land use composition and artificial shrub nest survival, ground nest predator group richness, and the frequency of predation by some nest predator groups but not with ground nest survival, shrub predator richness, or natural nest success.

Artificial shrub nest success was lower in forest fragments surrounded by higher levels of urbanization within 3600 m. The number of depredated nests with eggs completely removed also increased with the amount of surrounding urbanization. It is likely that shrub nest survival was largely influenced by predators that removed eggs from nests because the majority of depredated shrub nests were found with the eggs missing. Other researchers have concluded that eggs removed from artificial nests could potentially have been destroyed by avian nest predators (Yahner and Wright 1985). The Blue Jay, a noted nest predator (Wilcove 1985, Danielson et al. 1997), was found to increase in abundance with greater amounts of surrounding urbanization (Engles and Sexton 1994, Kluza et al. 2000, this study). In addition, avian predators depredate artificial shrub nests more frequently than ground nests (Bayne and Hobson 1997, Bayne et al. 1997). Thus, the pattern of eggs removed from nests appears to correspond to avian nest predators, particularly the Blue Jay. In contrast, the number of predation events by the weasel group decreased with increasing urbanization. Weasels and related species are known to be less dense in populated areas (King 1989).

Also contrary to initial predictions, forest fragments surrounded by land use mosaics with higher proportions of intense agriculture had greater predator group richness for artificial ground nests. In Iowa, Bergin et al. (2000) found that artificial nest predation was lower in intense agricultural mosaics and attributed this result to poor nest predator habitat availability in these areas. The present study indicates that many different types of artificial ground nest predators can find suitable habitat within intensely managed agricultural regions. In support of this conclusion, Bayne and Hobson (1997) found artificial ground nest predator richness to be higher in agricultural landscapes than

in forested landscapes of northern Saskatchewan. The contrast in results could be related to differences in the degree of agricultural intensity between Iowa and parts of Canada, with Iowa having far more extensively intense agricultural production.

Artificial nest predator richness was found to be higher for ground nests than shrub nests. Ground nests tend to be depredated by a variety of mammalian predators while shrub nests tend to mainly be depredated by avian predators and squirrels (Bayne and Hobson 1997, Melampy et al. 1999). In this study, group richness of shrub nest predators did not vary with land use composition, likely because the majority of shrub nests were depredated by unknown predators (the “missing” group).

Another unexpected result was that even the small changes in forest cover between land use mosaics in this study affected the frequency of predation by some nest predators. Artificial ground nest predator richness was higher in slightly more forested regions, as was the frequency of predation by the squirrel group—offering further support that ground nests are most often depredated by mammalian predators that utilize both intense agricultural and forest habitats. The number of nests with eggs missing decreased with greater surrounding forest cover indicating that these predators are not forest specialists and likely utilize non-forest habitat.

While Wood Thrush pairing success was not related to any measure of land use composition, Ovenbird pairing success varied with the amount of forest habitat within the land use mosaic. Pairing success was higher in fragments immediately embedded (within 1200 m) in higher forest cover but lower in mosaics with more forest habitat at a larger scale of 5 km. This is contrary to the findings of other researchers who found either no relationship between the amount of forest cover and Ovenbird pairing success

(Burke and Nol 1998) or the exact opposite relationship (pairing success increased with lower forest cover within 1 km; Rodewald and Yahner 2000). The current result suggests that female Ovenbirds respond to the amount of available habitat at a relatively small scale and may select breeding habitat at a scale of 1-1.5 km.

Again contrary to expectations, the pairing success of both Wood Thrush and Ovenbirds was not correlated with the nesting success of each species. This is most likely due to the fact that the sample size of nests was too small to accurately determine rates of nest success, but could also be related to different habitat and land use mosaic characteristics affecting female habitat selection and nesting success in different ways and at different scales.

Artificial nest success was evaluated against natural forest bird nests. There was no correlation between daily survival of the two types of nests potentially calling into question the validity of artificial nest experiments. Indeed, comparison between artificial and natural nests must be treated with caution. For artificial nests to estimate patterns of natural nest predation and identify natural nest predators, it is imperative that artificial nests resemble natural nests as closely as possible from the predators perspective (size, shape, colour, smell, location, etc.) (Major and Kendal 1996, Ortega et al. 1998, Wilson et al. 1998).

In this study, three species of forest bird nests (Ovenbird, Wood Thrush, and American Robin) were pooled together due to low nest numbers. The three species have different life history strategies which could confound simple correlations. Artificial ground nests were designed to mimic Ovenbird nests in size, shape, location, and appearance of eggs. When compared to natural Ovenbird nest success there was no

relationship; however this was based on a sample size of only ten natural Ovenbird nests within five forest fragments. Any potential patterns between artificial ground nests and natural Ovenbirds nests may not have been detected with such a low sample size, and when compared to all natural nests combined may have been obscured by differing patterns in Wood Thrush and robin nests. When daily success of only robin nests was compared to daily success of only shrub nests there was a positive correlation. Thus with an adequate sample size to compare against, artificial nests very closely resembling natural nests can indeed display similar patterns of success as natural nests.

In a study using a paired design of natural and artificial Wood Thrush nests, Wilson et al. (1998) found that the condition of natural and artificial nests after predation differed. Natural nests tended to remain intact after predation whereas artificial nests tended to be torn apart, potentially indicating that a different suite of predators may depredate the two types of nests. There are several inherent differences between natural and artificial nests that may attract different nest predators. Artificial nests have no “real bird clues” for predators to follow such as parental activity, smell, nestling begging calls, but tend to be placed in more open, visible locations (Wilson et al. 1998). This may result in artificial nests having a bias towards visually oriented predators such as birds and away from olfactory and auditory oriented predators such as mammals (Willebrand and Marcstrom 1988, Paton 1994, Wilson et al. 1998). Although artificial nests in the current study resembled natural nests, they were not necessarily placed in the same microhabitat as natural nests, and thus likely differed in height, tree or shrub species, visibility, and density.

Hence, the observed effects of land use composition on artificial nest success and

artificial nest predators must be treated as preliminary. Based on these preliminary findings, it appears that increasing urbanization within 3-3.5 km and agricultural intensity within 2.5-3 km of forest fragments could potentially have adverse affects on forest bird reproductive success. Further research is needed to determine the impact of surrounding land uses on natural forest bird nesting success in addition to comparisons between natural and artificial nests.

Conclusion: Land Use Planning and Forest Bird Conservation

Unquestionably, preserving forest habitat is the most critical strategy for the conservation of forest breeding birds; however, much previously forested land has already been converted to other land uses. Thus finding strategies to improve the habitat available in existing forest fragments is also critical. Maintaining low intensity land uses such as pasture, hay fields, or old field and limiting urban development within 1- 3.5 km of forest fragments would help to make this habitat more suitable for bird species of concern such as Neotropical migrant and forest interior-edge species as well as to potentially limit nest predation rates (Table 12). The increasingly intensified human use of lands surrounding remnant forest fragments could potentially be a contributing factor to observed or anticipated population declines of these species, although more research needs to be conducted before conclusive statements can truly be made.

Based upon the preliminary results of this study, it appears that land use planning could play an important role in forest bird conservation. Only four percent of Canadian land is currently fully protected in habitat reserves (Soule and Terborough 1999).

Reserves tend to be large unbroken tracts of land (which are absolutely essential). It is unprotected and largely fragmented habitat, however, which contains the majority of species (Soule and Terborough 1999). There is a need to have small privately owned forest fragments protected through land use planning policy and regulation.

Implementing a small scale biosphere reserve plan around forest fragments could aid in achieving this goal. The concept of biosphere reserves was developed by the United Nations Education, Scientific and Cultural Organization's Man in the Biosphere (UNESCO/MAB) project in 1974 to promote the conservation of ecosystems through ecologically sustainable resource practices (Francis and Munro 1994). A biosphere reserve involves three areas of zonation: 1) a core area (in this case a forest fragment) intended to be protected; 2) a buffer zone (i.e. low intensity land use) extending in all directions around the core that will help to protect the core but also allow limited resource use; and 3) a transition zone (i.e. other land uses) within which the full range of human uses can occur (Batisse 1996). This would involve zoning the land extending 1-3.5 km in diameter around forest fragments for less intensive types of land use only. More disruptive and intense land uses such as large monoculture row cropping and urban development would be delegated to land located further from forest habitat (Figure 12).

Briefly outlined below are three land use planning strategies or changes to existing policy that could help support a forest fragment biosphere reserve strategy. As an incentive for landowners to comply with this land use zonation system, a program similar to the United States Conservation Reserve Program could be adopted. The Conservation Reserve Program is part of the Conservation Title of the Food Security Act of 1985 (Napier 1990). The intent of the program is soil conservation on highly erodible

farm land; landowners who enroll land in the program that qualifies as highly erodible are paid an annual rent from the government to retire the land from production (Napier 1990). In a biosphere reserve system for forest fragments, a federal benefits program could be established to encourage farmers to farm less intensively near forest habitat. Adopting the concept of “Smart Growth” would also aid in implementing the idea of biosphere reserves surrounding forest fragments. Some principles of Smart Growth include decreasing urban sprawl by encouraging people to live in cities and nearby their work, and decreasing traffic congestion and air pollution by increasing public transportation. Adopting Smart Growth as a planning initiative would help to prevent urban development in rural areas, preserving farm land and natural areas. Finally, having land use planning decisions made and enforced at a provincial rather than municipal level would help to make a forest fragment biosphere reserve system fair and consistent across regions.

Although reforestation may be occurring in parts of eastern North America, this newly created, often commercially-based forest habitat does not ecologically replace mature hardwood forests. As suitable forest habitat slowly diminishes and concern about Neotropical migrant forest interior and interior-edge birds rises (Hagan and Johnston 1992, Martin and Finch 1995) it may become imperative to develop strategies for maintaining the quality of existing forest fragment habitat. Low levels of urbanization and a greater proportion of less intensively farmed agricultural land surrounding forest fragments could help to improve habitat quality for forest birds residing in fragmented landscapes.

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Table 1. Forest fragment size and % cover of land uses surrounding bird survey sites averaged across all 25 buffer circles. Buffer circles extended from a radius of 200 m to 5000 m surrounding each fragment, increasing by 200 m increments. The median and range for each type of land use, across all buffer circles and fragments, is also shown. IA = intensive agriculture, LA = less intensive agriculture (see methods, Chapter 1, for descriptions).

Fragment	Size (ha)	% forest	% IA	% LA	% urban
1	47.4	18.3	48.4	27.3	0.0
2	33.1	17.9	53.6	22.4	0.3
3	35.2	23.2	35.0	29.1	0.2
4	40.6	22.9	40.7	21.1	0.5
5	37.1	28.0	32.6	26.0	1.2
6	33.2	23.1	31.9	25.2	4.8
7	19.5	20.9	37.4	20.4	0.1
8	40.6	24.5	12.7	39.0	0.1
9	34.4	21.5	39.5	25.6	0.4
10	21.6	17.5	54.1	19.0	3.3
11	21.7	26.8	25.5	21.8	9.1
12	32.2	14.7	29.5	10.8	37.2
13	49.5	22.7	26.8	26.6	19.2
14	23.9	19.5	50.4	17.7	4.6
15	33.9	23.5	65.7	8.2	0.1
16	20.1	23.7	44.3	11.8	10.3
17	17.5	17.2	40.0	21.4	0.0
18	26.9	12.5	47.0	19.6	0.3
19	47.0	25.0	30.8	19.8	0.8
20	23.1	23.6	44.3	13.5	9.0
21	15.1	24.9	30.6	18.2	11.5

Table 1. con't

Fragment	Size (ha)	% forest	% IA	% LA	% urban
22	23.3	19.8	58.9	13.3	0.0
23	29.6	22.2	40.2	23.1	0.7
Median	27.2	17.6	39.8	21.8	0.4
Range	15.1 -	3.9 -	0 -	0 -	0 -
	49.5	100.0	76.9	67.2	51.4

Table 2. PCA loadings of each land use variable for all 25 buffer circles. Only those loadings with a weight greater or equal to ± 0.5 are shown. IA = intensive agriculture, LA = less intensive agriculture, F = forest, U = urban. The number following each land use abbreviations indicates the radius of the buffer circle.

	PC1 loading	PC1 loading	PC2 loading	PC3 loading	PC4 loading	PC5 loading					
IA200	-0.504	LA200	0.606	U1200	0.534	F1600	0.583	F200	0.532	IA400	0.514
IA400	-0.709	LA400	0.916	U1400	0.620	F1800	0.685	F400	0.854	IA600	0.602
IA600	-0.766	LA600	0.972	U1600	0.724	F2000	0.781	F600	0.899	IA800	0.593
IA800	-0.666	LA800	0.975	U1800	0.821	F2200	0.854	F800	0.883	IA1000	0.523
IA1000	-0.682	LA1000	0.993	U2000	0.901	F2400	0.912	F1000	0.916	LA4000	0.528
IA1200	-0.697	LA1200	0.990	U2200	0.948	F2600	0.971	F1200	0.910	LA4200	0.582
IA1400	-0.676	LA1400	0.971	U2400	0.978	F2800	1.018	F1400	0.868	LA4400	0.613
IA1600	-0.665	LA1600	0.932	U2600	0.997	F3000	1.036	F1600	0.671	LA4600	0.650
IA1800	-0.669	LA1800	0.965	U2800	1.008	F3200	1.041	F1800	0.574	LA4800	0.677
IA2000	-0.619	LA2000	0.994	U3000	1.012	F3400	1.034			LA5000	0.674
IA2200	-0.664	LA2200	0.996	U3200	1.011	F3600	1.026			U400	-0.563
IA2400	-0.627	LA2400	0.975	U3400	1.009	F3800	1.025			U600	-0.578
IA2600	-0.595	LA2600	0.929	U3600	1.004	F4000	1.013			U800	-0.646

Table 2. con't

	PC1 loading	PC1	PC1 loading	PC2 loading	PC2	PC2 loading	PC3 loading	PC3	PC3 loading	PC4 loading	PC4	PC4 loading	PC5 loading
IA2800	-0.565	LA2800	0.881	U3800	0.999	F4200	0.994	U1000	-0.558				
IA3000	-0.562	LA3000	0.817	U4000	0.994	F4400	0.971	U1200	-0.503				
IA3200	-0.575	LA3200	0.761	U4200	0.991	F4600	0.958						
IA3400	-0.584	LA3400	0.712	U4400	0.989	F4800	0.945						
IA3600	-0.591	LA3600	0.654	U4600	0.986	F5000	0.938						
IA3800	-0.589	LA3800	0.576	U4800	0.984								
IA4000	-0.585			U5000	0.982								
IA4200	-0.576												
IA4400	-0.564												
IA4600	-0.546												
IA4800	-0.531												
IA5000	-0.522												

Table 3. Species richness and abundance across fragments (n=23). The breakdown of migratory classifications by spatial specialization classifications and vice versa is also given. See results section, Chapter 1, for abbreviations.

Variable	Total #	Mean ($\pm$ SE)	Species Classification Breakdown
TOT richness	33	12.8 (0.06)	NTM: 57.6%, SDM: 18.2%, RES: 24.2% INT: 24.2%, I/E: 39.4%, EDG: 36.4%
TOT abundance	419	18.2 (0.09)	NTM: 51.3%, SDM: 24.1%, RES: 24.6% INT: 16.5%, I/E: 39.6%, EDG: 43.9%
NTM richness	19	6.8 (0.06)	INT: 42.1%, I/E: 36.8%, EDG: 21.0%
NTM abundance	215	9.3 (0.08)	INT: 32.1%, I/E: 47.0%, EDG: 20.9%
SDM richness	6	2.8 (0.04)	INT: 0.0%, I/E: 33.3%, EDG: 66.7%
SDM abundance	101	4.4 (0.06)	INT: 0.0%, I/E: 15.8%, EDG: 84.2%
RES richness	8	3.2 (0.05)	INT: 0.0%, I/E: 50.0%, EDG: 50.0%
RES abundance	103	4.5 (0.06)	INT: 0.0, I/E: 47.6%, EDG: 52.4%
INT richness	8	2.3 (0.05)	NTM: 100.0%, SDM: 0.0%, RES: 0.0%
INT abundance	69	3.0 (0.06)	NTM: 100.0%, SDM: 0.0%, RES: 0.0%
I/E richness	13	5.4 (0.05)	NTM: 53.8%, SDM: 15.4%, RES: 30.8%
I/E abundance	166	7.2 (0.07)	NTM: 60.8%, SDM: 9.6%, RES: 29.5%
EDG richness	12	5.1 (0.05)	NTM: 33.3%, SDM: 33.3%, RES: 33.3%
EDG abundance	184	8.1 (0.07)	NTM: 24.4%, SDM: 46.2%, RES: 29.3%

Table 4. Multiple regression results of the effects of surrounding land uses on forest bird species assemblages. See methods section, Chapter 1, for abbreviations and description of PC's.

Variable	F (df)	R ²	P	intercept	PC	slope
TOT abundance					none	
TOT richness					none	
NTM abundance	6.35 (1,21)	0.19	0.020	9.35	PC5	1.67
NTM richness	6.08 (1,21)	0.19	0.022	6.83	PC5	0.86
SDM abundance	6.91 (1,21)	0.21	0.016	4.39	PC3	-0.87
SDM richness					none	
RES abundance	3.65 (2,20)	0.19	0.045	4.48	PC1	-0.77
					PC2	0.64
RES richness	3.29 (1,21)	0.09	0.084	3.21	PC5	-0.41
INT abundance					none	
INT richness					none	
I/E abundance	3.2 (1,21)	0.10	0.074	7.22	PC1	1.04
I/E richness	5.95 (1,21)	0.18	0.024	5.39	PC1	0.75
EDG abundance	10.62 (1,21)	0.30	0.0038	8.04	PC1	-1.49
EDG richness	9.43 (1,21)	0.28	0.0058	5.13	PC1	-0.69

Table 5. Scale of land use effects on forest bird assemblages as indicated by the buffer circle distance (200-5000 m) with the highest R^2 value ($p < 0.05$). Blank cells indicate $p > 0.05$ across all 25 buffer circles. See results section, Chapter 1, for abbreviations.

Variable	Forest		IA		LA		Urban	
	dist.	R^2	dist.	R^2	dist.	R^2	dist.	R^2
TOT abundance								
TOT richness								
NTM abundance					200	0.24	800	0.27
NTM richness					1400	0.27	1200	0.35
SDM abundance	5000	0.24						
SDM richness								
RES abundance					2200	0.20	1200	0.25
RES richness								
INT abundance								
INT richness								
I/E abundance					1400	0.22		
I/E richness			600	0.18	1400	0.37		
EDG abundance			1400	0.21	600	0.32		
EDG richness			1000	0.19	1000	0.29		

Table 6. Multiple regression results of the effects of surrounding land uses on individual forest bird species abundances. See Appendix 1 for species abbreviations. See methods, Chapter 1, for description of PC's.

Species	F _(df)	R ²	p	intercept	PC	slope
RTHA	11.93 _(1,21)	0.33	0.0024	0.22	PC1	-0.32
BBCU	6.48 _(3,19)	0.43	0.0033	0.17	PC1	0.23
					PC2	-0.19
					PC5	0.23
YBSA	11.24 _(1,21)	0.32	0.003	0.52	PC1	0.43
DOWO	15.56 _(2,20)	0.57	<0.0001	0.48	PC2	0.25
					PC4	-0.44
HAWO					none	
NOFL	5.12 _(1,21)	0.16	0.034	0.17	PC4	0.17
EAWP					none	
LEFL	5.67 _(2,20)	0.30	0.011	0.43	PC3	0.35
					PC4	-0.32
GCFL					none	
BLJA	5.81 _(1,21)	0.18	0.025	1.04	PC2	0.041
AMCR					none	
BCCH					none	
WBNU					none	
VEER	3.25 _(1,21)	0.09	0.086	0.39	PC1	0.24
WOTH					none	

Table 6. con't

Species	F _(df)	R ²	p	intercept	PC	slope
AMRO	3.46 _(2,20)	0.18	0.051	1.65	PC2	0.24
					PC3	-0.23
REVI					none	
CSWA					none	
BTNW	4.01 _(1,21)	0.12	0.058	0.22	PC4	0.17
BAWW	7.4 _(1,21)	0.22	0.013	0.3	PC5	0.24
OVEN					none	
NOWA					none	
SCTA					none	
NOCA					none	
RBGR	4.91 _(2,20)	0.26	0.018	0.52	PC4	0.23
					PC5	0.24
COGR	6.35 _(1,21)	0.19	0.02	0.23	PC5	-0.25
BHCO	8.03 _(2,20)	0.39	0.0028	1.43	PC3	-0.76
					PC5	0.57
BAOR	8.01 _(2,20)	0.39	0.028	0.22	PC2	0.24
					PC5	-0.31
AMGO	4.38 _(1,21)	0.13	0.049	0.39	PC5	-0.24

Table 7. Comparison of regression results for species response to surrounding urban and agricultural land uses for A) Neotropical migrants versus species with other migratory strategies (short distant migrants and residents) and B) forest interior and interior-edge species versus edge species. See methods, Chapter 1, for definition of responses.

A) Migratory Strategy

Response	Neotropical migrants	Other
Positive	1	7
Negative	6	1
No response	8	6

B) Spatial Specialization

Response	Forest interior and interior-edge	Edge
Positive	1	6
Negative	8	0
No response	9	5

Table 8. Criteria for determining fate of Ovenbird, Wood Thrush, and American Robin nests. If one or more of these criteria could not be established, then the nest fate remained unknown.

Evidence for nest success

Chicks fledged when nest checked

Chicks bulging from nest/stretching wings at last visit

Feather development at last visit indicates chicks ready to fledge

Nest empty, rim of nest flattened and feces on rim or outside nest

Nest empty, fledglings seen or heard nearby

Evidence for nest failure

Nest empty before fledging possible

Broken eggs, dead chicks, scattered feathers in or near nest

Nest destroyed

Eggs never hatched

Nest abandoned (no eggs ever laid or eggs cold/chicks dead but unharmed)

Table 9. Summary of reproductive success data. For pairing success variables, total # indicates the number of birds followed while total # successful indicates the number of paired birds. For nest variables, total # indicates the number of nests and total # successful the number of nests fledging at least one host young (or the number of nests without marked or missing eggs for artificial nests). See Appendix 1 for species codes.

Variable	Total #	Total # Successful	Mean ($\pm$ SE)	# Fragments
WOTH pairing success	53	42	80.6 (4.8)	13
OVEN pairing success	81	45	50.2 (5.4)	17
AMRO daily nest survival	41	22	0.96 (0.01)	11
WOTH daily nest survival	25	13	0.89 (0.09)	11
OVEN daily nest survival	10	4	0.85 (0.05)	5
artificial ground nest daily survival	184	121	0.85 (0.01)	23
artificial shrub nest daily survival	184	98	0.88 (0.02)	23

Table 10. Multiple regression results of the effects of surrounding land uses on Ovenbird and Wood Thrush pairing success, natural nest survival, artificial nest survival, artificial nest predator richness, and artificial nest predator groups. See methods section, Chapter 2, for explanation of predator groups. See methods section, Chapter 1, for description of PC's.

Variable	F _(df)	R ²	p	intercept	PC	slope
OVEN pairing success	5.58 _(2,14)	0.36	0.016	50.36	PC3	-10.31
					PC4	10.67
WOTH pairing success					none	
daily survival – natural nests					none	
daily survival - ground nests					none	
daily survival - shrub nests	5.98 _(2,20)	0.31	0.0092	0.88	PC2	-0.037
					PC3	0.046
predator richness - ground nests	7.09 _(2,20)	0.36	0.0047	1.91	PC1	-0.41
					PC4	0.46
predator richness - shrub nests					none	
mouse group					none	
raccoon group					none	
squirrel group	4.39 _(1,21)	0.13	0.048	0.48	PC4	0.31
weasel group	6.04 _(2,21)	0.19	0.023	0.22	PC2	-0.25
bird group					none	
missing eggs	6.83 _(2,20)	0.35	0.0055	3.43	PC2	1.51
					PC3	-1.44

Table 11. Scale of land use effects on Ovenbird and Wood Thrush pairing success, natural nest survival, artificial nest survival, and artificial nest predator richness as indicated by the buffer circle distance (200-5000 m) with the highest R^2 value ($p < 0.05$). Blank cells indicate $p > 0.05$ across all 25 buffer circles.

Variable	Forest			IA			LA			Urban		
	dist.	R^2	dist.	dist.	R^2	dist.	dist.	R^2	dist.	dist.	R^2	dist.
OVEN pairing success	400	0.29										
	4000	0.32										
WOTH pairing success												
Natural nest daily survival												
Ground nest daily survival												
shrub nest daily survival	5000	0.40							3600	0.12		
Ground nest predator richness	200	0.37	2600	0.20	3800	0.17						
shrub nest predator richness												

Table 12. Summary of significant relationships ($p < 0.1$) between land use variables and forest bird species assemblages, reproductive success, and artificial nest predator richness. Numbers in brackets indicate the scale at which the most variation in each response variable was explained as determined by R^2 analysis. Variables are ordered by increasing scale of response. See results, Chapter 1, for assemblage abbreviations. See Appendix 1 for species codes.

Response	Forest	Intensive Agriculture	Less Intensive Agriculture	Urban
Positive	ground predator richness (200 m)	EDG richness (1000 m)	NTM abundance (200 m)	RES abundance (1200 m)
	OVEN pairing success (400 m)	EDG abundance (1400 m)	NTM richness (1400 m)	
		ground predator richness (2600 m)	I/E richness and abundance (1400 m)	
Negative	OVEN pairing success (4000 m)	I/E richness (600 m)	EDG abundance (600 m)	NTM abundance (800 m)
	SDM abundance (5000 m)		EDG richness (1000 m)	NTM richness (1200 m)
	shrub nest daily survival (5000 m)		RES abundance (2200 m)	shrub nest daily survival (3600 m)
			ground predator richness (3800 m)

Figure 2.

Figure 3.

Figure 5 A) PC1

Figure 5 B) PC2

Figure 5 C) PC3

Figure 5 D) PC4

Figure 5 E) PC5

Figure 6 A) PCI

Figure 6 B) PC2

Figure 6 C) PC3

Figure 6 D) PC4

Figure 7

Figure 8

Figure 9

Figure 10

Appendix 1. Species code, common name, and scientific name of the thirty-three forest bird species included in analyses. Each species is classified by migratory strategy and forest spatial association. The percent of sites (n=23) in which each species was detected and the mean abundance across the sites in which they occurred is also shown. NTM = Neotropical migrant, SDM = short distant migrant, RES = resident, INT = forest interior, I/E = forest interior-edge, EDG = forest edge.

Species Code	Common Name	Scientific Name	Migratory Strategy	Spatial Specialization	% of sites	mean abundance
RTHA	Red-tailed Hawk	<i>Buteo jamaicensis</i>	RES	EDG	17.4	1.25
BBCU	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	NTM	I/E	17.4	1.00
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	SDM	I/E	39.1	1.33
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	RES	I/E	39.1	1.22
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	RES	I/E	30.4	1.00
NOFL	Northern Flicker	<i>Colaptes auratus</i>	SDM	I/E	17.4	1.00
EAWP	Eastern Wood Peewee	<i>Contopus virens</i>	NTM	EDG	78.3	1.61
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	NTM	I/E	30.4	1.43
GCFL	Great-crested Flycatcher	<i>Myiarchus crinitus</i>	NTM	I/E	52.2	1.00
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	RES	EDG	69.6	1.81
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	RES	EDG	47.8	1.45
BCCH	Black-capped Chickadee	<i>Parus atricapillus</i>	RES	I/E	43.5	1.70
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>	RES	I/E	56.5	1.08
VEER	Veery	<i>Catharus fuscescens</i>	NTM	INT	30.4	1.28
WOTH	Wood Thrush	<i>Hylocichla mustelina</i>	NTM	I/E	60.9	1.36
AMRO	American Robin	<i>Turdus migratorius</i>	SDM	EDG	100	1.65
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	NTM	I/E	100	1.87
YWAR	Yellow Warbler	<i>Dendroica petechia</i>	NTM	EDG	4.3	1.00
CSWA	Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	NTM	EDG	39.1	1.11
BTBW	Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	NTM	INT	4.3	1.00

Appendix 1. con't

Species Code	Common Name	Scientific Name	Migratory Strategy	Spatial Specialization	% sites	mean abundance
BTNW	Black-throated Green Warbler	<i>Dendroica virens</i>	NTM	INT	21.7	1.00
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	NTM	INT	30.4	1.00
AMRE	American Redstart	<i>Setophaga ruticilla</i>	NTM	INT	4.3	1.00
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	NTM	INT	95.6	1.54
NOWA	Northern Waterthrush	<i>Seiurus noveboracensis</i>	NTM	INT	17.4	1.25
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	NTM	I/E	4.3	1.00
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	NTM	INT	26.1	1.17
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	RES	EDG	17.4	1.00
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	NTM	I/E	47.8	1.09
COGR	Common Grackle	<i>Quiscalus quiscula</i>	SDM	EDG	17.4	1.25
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	SDM	EDG	69.6	2.06
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	NTM	EDG	17.4	1.25
AMGO	American Goldfinch	<i>Carduelis tristis</i>	SDM	EDG	34.8	1.12

Appendix 2. Principal component loadings for each land use across all 25 buffer circles.

Bold type indicates original variables that loaded heavily (a loading greater than ± 0.5)

on a particular component. PC's were rotated using the PROMAX method (SAS

Institute, 1990). IA = intensive agriculture, LA = less intensive agriculture, F = forest,

U = urban. The number following each land use abbreviations indicates the radius of the buffer circle.

Variable	PC1	PC2	PC3	PC4	PC5
F200	-0.134	-0.188	-0.316	0.532	-0.160
F400	-0.070	-0.007	-0.348	0.854	0.105
F600	-0.063	0.033	-0.037	0.899	0.102
F800	-0.182	0.121	0.163	0.883	0.090
F1000	-0.177	0.118	0.261	0.916	0.092
F1200	-0.089	0.049	0.350	0.910	0.078
F1400	-0.103	0.032	0.473	0.868	0.012
F1600	0.009	0.121	0.583	0.671	0.068
F1800	-0.006	0.071	0.685	0.574	0.058
F2000	-0.050	0.023	0.781	0.488	0.054
F2200	-0.067	-0.032	0.854	0.419	0.035
F2400	-0.109	-0.043	0.912	0.353	0.037
F2600	-0.126	-0.069	0.971	0.284	0.018
F2800	-0.129	-0.112	1.018	0.215	-0.021
F3000	-0.105	-0.147	1.036	0.166	-0.047
F3200	-0.080	-0.181	1.041	0.126	-0.042
F3400	-0.045	-0.204	1.034	0.098	-0.030
F3600	-0.018	-0.226	1.026	0.054	-0.028
F3800	-0.018	-0.251	1.025	0.004	-0.051
F4000	-0.012	-0.279	1.013	-0.072	-0.072
F4200	-0.004	-0.294	0.994	-0.129	-0.074
F4400	0.005	-0.299	0.971	-0.159	-0.065
F4600	0.017	-0.287	0.958	-0.166	-0.051
F4800	0.035	-0.267	0.945	-0.171	-0.049
F5000	0.043	-0.261	0.938	-0.186	-0.050
IA200	-0.504	0.037	0.440	-0.118	0.309
IA400	-0.709	-0.017	0.264	-0.283	0.514
IA600	-0.766	-0.153	0.081	-0.271	0.602
IA800	-0.666	-0.164	-0.153	-0.307	0.593
IA1000	-0.682	-0.194	-0.198	-0.284	0.523
IA1200	-0.697	-0.210	-0.288	-0.239	0.433
IA1400	-0.676	-0.198	-0.394	-0.224	0.373
IA1600	-0.665	-0.266	-0.379	-0.141	0.194

Appendix 2. con't

Variable	PC1	PC2	PC3	PC4	PC5
IA1800	-0.669	-0.305	-0.354	-0.074	0.084
IA2000	-0.619	-0.251	-0.279	-0.031	-0.001
IA2200	-0.664	-0.345	-0.305	-0.034	-0.040
IA2400	-0.627	-0.373	-0.306	-0.024	-0.088
IA2600	-0.595	-0.400	-0.304	-0.006	-0.131
IA2800	-0.565	-0.422	-0.312	0.021	-0.155
IA3000	-0.562	-0.433	-0.308	0.045	-0.165
IA3200	-0.575	-0.435	-0.286	0.068	-0.185
IA3400	-0.584	-0.431	-0.277	0.089	-0.194
IA3600	-0.591	-0.417	-0.278	0.108	-0.195
IA3800	-0.589	-0.402	-0.285	0.128	-0.196
IA4000	-0.585	-0.394	-0.289	0.143	-0.198
IA4200	-0.576	-0.389	-0.289	0.160	-0.201
IA4400	-0.564	-0.386	-0.286	0.172	-0.206
IA4600	-0.546	-0.393	-0.281	0.178	-0.219
IA4800	-0.531	-0.407	-0.270	0.184	-0.226
IA5000	-0.522	-0.415	-0.259	0.195	-0.227
LA200	0.606	-0.064	-0.441	-0.173	0.165
LA400	0.916	-0.262	-0.322	-0.142	-0.173
LA600	0.972	-0.175	-0.352	-0.063	-0.218
LA800	0.975	-0.212	-0.231	0.060	-0.231
LA1000	0.993	-0.139	-0.235	0.060	-0.183
LA1200	0.990	-0.118	-0.217	-0.002	-0.112
LA1400	0.971	-0.165	-0.161	-0.035	-0.049
LA1600	0.932	-0.159	-0.128	-0.051	0.017
LA1800	0.965	-0.194	-0.111	-0.091	0.044
LA2000	0.994	-0.256	-0.096	-0.120	0.030
LA2200	0.996	-0.288	-0.085	-0.095	0.023
LA2400	0.975	-0.277	-0.051	-0.067	0.051
LA2600	0.929	-0.258	-0.022	-0.037	0.106
LA2800	0.881	-0.245	0.003	-0.020	0.168
LA3000	0.817	-0.227	0.040	-0.016	0.248
LA3200	0.761	-0.224	0.045	-0.012	0.331
LA3400	0.712	-0.222	0.080	-0.020	0.379
LA3600	0.654	-0.244	0.112	-0.008	0.419
LA3800	0.576	-0.243	0.133	-0.006	0.471
LA4000	0.494	-0.241	0.130	0.026	0.528
LA4200	0.423	-0.232	0.118	0.057	0.582
LA4400	0.372	-0.233	0.105	0.087	0.613
LA4600	0.330	-0.232	0.081	0.088	0.650
LA4800	0.309	-0.233	0.063	0.077	0.677
LA5000	0.299	-0.253	0.082	0.057	0.674
U200	-0.144	0.373	0.315	-0.382	-0.498
U400	-0.109	0.394	0.224	-0.366	-0.563

Appendix 2. con't

Variable	PC1	PC2	PC3	PC4	PC5
U600	-0.118	0.450	0.194	-0.343	-0.578
U800	-0.192	0.188	0.454	-0.362	-0.646
U1000	-0.139	0.481	0.214	-0.319	-0.558
U1200	-0.156	0.534	0.233	-0.267	-0.503
U1400	-0.159	0.620	0.228	-0.200	-0.437
U1600	-0.159	0.724	0.176	-0.150	-0.347
U1800	-0.138	0.821	0.087	-0.095	-0.284
U2000	-0.119	0.901	-0.004	-0.040	-0.218
U2200	-0.104	0.948	-0.074	0.001	-0.164
U2400	-0.092	0.978	-0.123	0.038	-0.117
U2600	-0.079	0.997	-0.162	0.066	-0.077
U2800	-0.070	1.008	-0.191	0.086	-0.046
U3000	-0.064	1.012	-0.208	0.094	-0.030
U3200	-0.055	1.011	-0.217	0.095	-0.029
U3400	-0.050	1.009	-0.222	0.093	-0.029
U3600	-0.043	1.004	-0.229	0.090	-0.032
U3800	-0.036	0.999	-0.236	0.088	-0.033
U4000	-0.026	0.994	-0.244	0.087	-0.031
U4200	-0.017	0.991	-0.248	0.086	-0.027
U4400	-0.012	0.989	-0.245	0.084	-0.021
U4600	-0.009	0.986	-0.244	0.080	-0.014
U4800	-0.001	0.984	-0.254	0.081	-0.004
U5000	0.008	0.982	-0.268	0.082	0.005

Appendix 3. Artificial nest predator groups as identified by tooth, bill and claw marks on wax eggs. The percent of sites (n=23) in which each predator group was identified and the mean number of eggs depredated by each group is shown.

Predator group	Common names	Scientific names	% of sites	mean #/site
mouse	Mice species	<i>Peromyscus</i>	86.9	2.3
	Vole species	<i>Clethrionomys</i>		
	Shrew species	<i>Sorex</i> and <i>Blarina</i>		
squirrel	Squirrel species	<i>Sciurus</i> , <i>Tamiasciurus</i> , and <i>Glaucomys</i>	34.8	1.4
	Eastern Chipmunk	<i>Tamias striatus</i>		
weasel	Weasel speices	<i>Mustela</i>	17.4	1.2
raccoon	Northern Raccoon	<i>Procyon lotor</i>	65.3	2.6
	Striped Skunk	<i>Mephitis mephitis</i>		
bird	Blue Jay	Corvid species	43.5	1.2
	American Crow			
missing	unknown		78.3	4.3