Effects of urban development on breeding bird diversity: the role of diet and migration

Elise Anne Larsen

Seabrook, MD

Bachelor of Science, Michigan State University, 2001

A Thesis presented to the Graduate Faculty
of the College of William and Mary in Candidacy for the Degree of
Master of Science

Department of Biology

The College of William and Mary
January, 2008

APPROVAL PAGE

This Thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

Elise A. Larsen

Approved by the Committee, September, 2007

Committee Chair
Research Professor Bryan D. Watts, Biology
The College of William and Mary

Associate Professor George W. Gilchrist, Biology
The College of William and Mary

Associate Professor John P. Swaddle, Biology
The College of William and Mary

Professor Stewart A. Ware, Biology
The College of William and Mary

ABSTRACT PAGE

Many migratory bird species are declining in abundance. Habitat loss and fragmentation due to urban development is considered a main cause of these declines, and diversity of bird species generally declines with urban development. However, not all bird species respond similarly. Our research explores how bird species respond differently to urban development, according to shared life history traits. We studied the relationship between bird diversity and urban sprawl using spatial analyses of the U.S. Geological Survey's Breeding Bird Survey (BBS) and National Land Cover Data (NLCD) datasets and U.S. Census population data for the Mid-Atlantic Coastal Plain. Environmental parameters representing landscape composition, landscape structure, and human population density were measured for sites at 300 meter and 1000 meter areas around BBS sub-route study sites. Landscape data was spatially related to breeding bird diversity, as measured by species richness, species evenness and bird abundance). Bird diversity was measure for bird groups identified according to migratory, dietary and habitat groups. Analyses using mixed linear models indicate that breeding bird diversity responds differently to urbanization parameters according to these life history traits. Among dietary groups, insect-eating birds demonstrated the most negative response to urban development, while birds with generalized diets demonstrated the most positive response. These results suggest that food resources are changing with urbanization, with naturally occurring food resources becoming limiting resources for some bird populations, and anthropogenic food resources augmenting others. Among migratory groups, diversity of neotropical migrants declines most dramatically with urban development. In order to understand how continued urban development will affect bird populations and related conservation efforts, future research must examine urbanization impacts in terms of life history traits and community interactions.

TABLE OF CONTENTS

List of tables and diagrams	ii
Dedication	iii
Acknowledgments	iv
Introduction	1
Methods	4
Results	12
Discussion	22
References	32
Appendix 1	39
Appendix 2	44
Appendix 3	45
Vita	48

LIST OF TABLES AND DIAGRAMS

Diagram A: Map of Study Area 5

Table 1: Principal Components Analysis 15

Table 2: Model Comparisons 17

Diagram A: Diversity trends for dietary groups 19

Diagram B: Diversity trends for migratory groups 21

Diagram C: Diversity trends for habitat groups 23

Appendix 1: Summary of species data 39

Appendix 2: Summary data of birds by life history traits 44

Appendix 3: Parameter estimates of best models 45

DEDICATION

I dedicate this work to my parents who support me in everything I do.

ACKNOWLEDGMENTS

I would like to thank Bryan Watts for his never ending patience and guidance during my time at the College of William and Mary and the Center for Conservation Biology. I am indebted to Bryan and the CCB staff for their wisdom and technical guidance including Barton Paxton's GIS expertise. I would also like to thank my committee members for their support. I thank George Gilchrist for sharing his tremendous statistical know-how, John Swaddle for encouraging further analytical depth within my work, and Stewart Ware for his emphasis on broader applications and practical use.

INTRODUCTION

Conservation of biological diversity is currently of great interest to the scientific community in light of increasing human impacts on ecosystems. Loss of biodiversity is often attributed to habitat loss and fragmentation, which typically follow human population growth and land use change (Emlen 1974, Mills et al. 1989, Brooks et al. 2002). Development restricts natural areas such as grassland and forest to smaller patches of land within a matrix of agricultural, residential, and commercial land use. Development is not easily reversible; recovery of natural lands after development is rare due to ongoing human population growth, and often takes many years or decades to return to pre-development conditions. Therefore, conservation efforts must take into account current land use and development.

For birds, urban development has been linked to a decline in species richness and an increase in the abundance of urban-associated species (Cam et al. 2000, Crooks et al. 2004). Remaining habitat patches in a developed area typically support fewer species. Development also facilitates the spread of urban-associated species along corridors of urban land use, potentially leading to a homogenization of bird communities within and among regions (Blair 2004, McKinney and Lockwood 2001). Given the current rate of land development, understanding the factors affecting bird diversity is critical to developing and implementing appropriate conservation strategies.

Land use changes over time and space impact the composition of wildlife habitat in a region. This leads to changes in the wildlife community, through variation in the availability of different habitat classes, as well as specific nesting

requirements for various species (Mills et al. 1989, Blewett and Marzluff 2005). Fragmentation of natural areas decreases core habitats and increases habitat edges. In recent years, both grassland and forest interior species groups have been identified as a high conservation concern (Aldrich and Coffin 1980). This suggests that urban development may affect bird communities according to their habitat requirements, by changing the quantity or quality of the habitats.

Urban development may also affect bird communities according to their foraging guild. The availability of food resources is important in determining community structure, including species richness and relative abundances (Tilman 1982). Birds may feed on plants, fruit, seeds, insects, other invertebrates, or vertebrates, according to their dietary guild (Hamel et al. 1982). Any change in these food resources is likely to impact the avian community. Studies of urbanization in the tropics have found that avian dietary guilds respond differently to development; in these studies, low density residential areas favor omnivorous (often including fruit in the diet) and frugivorous (feeding predominantly on fruits) birds, while all urban development negatively affects insectivorous and carnivorous birds (Canaday 1996, Lim and Sodhi 2004). Food resources seem to play a role in the impacts of urbanization on avian diversity, but have not been studied in temperate regions. Examining temperate bird communities according to foraging guild, as has been done in the tropics, could provide important information on the effects of urbanization.

Urban development may also affect bird communities according to their migratory status. Neotropical migrants are generally of higher conservation concern than short-distance migrant and resident birds, and have received more

attention in regards to urbanization (Blewett and Marzluff 2005, Allen and O'Connor 2000, Donovan et al. 1995). Bird migration strategies may be associated with birds' habitat perception on the landscape scale or timing of habitat choice. Previous studies have found that birds of different migratory status respond differently to development; in these studies, migrants appear to respond more to changes in landscape composition and structure associated with urbanization, generally declining while resident species increase (Aldrich and Coffin 1980, Mayer and Cameron 2003). No consistent pattern has been established in this research; these relationships need to be further explored.

Historically the Mid-Atlantic Coastal Plain has been dominated by forest. Agricultural practices and urban development over the last 400 years have changed and continue to change the landscape. The Mid-Atlantic Coastal Plain is experiencing significant population growth and urbanization. Between 1990 and 2000, the human population in the Mid-Atlantic Coastal Plain increased 9.5%, from 15.5 million to almost 17 million (U.S. Census Bureau 2007). The growing human population has dramatic effects on the regional landscape through agricultural, residential, and commercial land use change. Between 1992 and 2001, forested lands declined by 4.8%, agricultural lands declined by 0.5%, and urban lands increased by 3.1% (U.S. Geological Survey 1992 and 2001). Land use changes are ongoing and cumulative, reducing opportunities for lands to be used for conservation purposes.

This study evaluates bird diversity and abundance to explore the role of different traits affecting breeding bird responses to urbanization in the Mid-Atlantic Coastal Plain. Our objective was to determine the relative power of dietary,

migratory, and habitat groupings to describe patterns in avian responses to development. Each of these traits is potentially important in determining bird habitat selection. We examined land cover and U.S. Census data at two spatial scales to assess the ability of landscape characteristics combined with species traits to explain the bird diversity across the Mid-Atlantic Coastal Plain, as measured by species richness, species evenness, and bird abundance. From these relationships, we evaluated the relative importance of species' traits related to foraging, migration, and habitat in avian responses to urbanization.

METHODS

1. Study Area

The Mid-Atlantic Coastal Plain (MACP) was our study area (diagram A). We define this area as extending west from the Atlantic Ocean to the fall line (separating coastal plain from piedmont), bounded on the south by the Virginia-North Carolina border, and on the north by the New Jersey-New York border. This area corresponds largely to the U.S. Bureau of Land Management Physiographic Area 44. This is a suitable study area because the area includes substantial areas of both rural lands and intense ongoing urbanization.

2. Data collection

2.1 Bird diversity data

Bird count data were collected from the North American Breeding Bird Survey (BBS). The BBS is organized by the US Geological Survey (USGS) and is

Diagram A: Map of Mid-Atlantic Coastal Plain with BBS study sites marked.

available from the Patuxent Wildlife Research Center website (http://www.pwrc.usgs.gov/BBS).

The BBS has been collecting data on breeding birds in North America annually since 1966. For this study, samples from the years 2000 and 2001 were used, which aligned temporally with the landscape data available. The data are collected annually in May and June by competent field observers. The survey relies on volunteers, and therefore data are not available for every route in every year. The BBS is an extraordinary data set that provides scientists with much

valuable data on breeding birds. However, the survey does suffer from data quality issues that must be addressed in any analysis. First, the USGS categorizes all BBS data according to internal standards for use in analysis. Any BBS data that did not fit these criteria were omitted from the analysis. Data from first-time observers were also omitted, as first-time observers report statistically fewer birds (Flather and Sauer 1996). The BBS data are biased due to the roadside locations of point counts, which limit the habitats accessed by BBS and the breadth of BBS coverage in non-developed areas (Bart et al. 1995). However, as development increases, roadside habitats become more representative of the landscape of the regions. The BBS also avoids heavily developed areas, limiting our ability to explore urban bird communities. Variations in the detectability of birds in various habitats also bias BBS data, which we acknowledge but do not correct for (Flather and Sauer 1996). Using these criteria, 65 BBS routes contained valid data for this study.

BBS data are collected along routes consisting of 50 individual three-minute point counts of the avian species detected along a roadside route approximately 40 km long. The scale of a BBS route is not an appropriate scale to observe the variation in land use in the MACP, as a single route may easily traverse a large range within the gradient of urban development. Therefore, each BBS route was subdivided into five sub-route samples for this analysis. Each samples consisted of ten point counts of birds, spaced over a route approximately 8 km long. A recent study found that using this structure of sub-samples from BBS provides data at an appropriate scale to examine bird community data (O'Connell et al. 2007).

In order to focus on the study question, bird diversity and abundance estimates were determined using only terrestrial species. The species detected by BBS were identified according to migratory status, foraging guild and habitat preference. These classifications were assigned using information from species accounts given in Hamel et al. (1982), unless otherwise noted.

Species migratory status was given as resident, short-distance, or neotropical. Resident species are commonly found to remain at or near their breeding grounds year round within the MACP. Short-distance migrants include species with short-distance migration patterns within or from the MACP, including species with variation in individual migration distances. Neotropical migrants include species which migrate south to the tropics during the non-breeding season, returning to the MACP at the start of the next breeding season.

Species were identified by foraging guild using information on food habits in narrative species accounts which identify the breeding season dietary guilds according to the known food items of each species (Hamel et al. 1982, Gough et al. 1998). Four dietary guilds were identified: insectivore, carnivore, herbivore and omnivore. Insectivores eat invertebrate prey, while carnivores each primarily vertebrate prey. Herbivores eat plant material, primarily grain or seed. Omnivores eat both plant and animal material. Hamel et al. (1982) did not provide information for all species. Gough et al. (1998) served as a second source of dietary information when needed.

Habitat preference was identified using information on bird-habitat relationships during the breeding season. Bird species were grouped as

generalists, or as preferring forested or open land. Species found commonly in both habitats and species requiring both forested and open land were classified as generalists, species commonly found in or requiring mature trees were classified as forest species, and species commonly found in grassland and scrubland were classified as open species.

Within each guild, we calculated the species richness and total bird abundance detected by the BBS for each site. Bird species richness was determined by the number of species within each guild detected at a study site. Total abundance was the total number of birds within each guild detected for a given site.

2.2 Landscape data

We analyzed landscape data from within spatial buffers of 300 meters and 1000 meters around each study site. The 300 meter buffer represents the local habitat in which the birds were detected. Bart et al. (1995) found that 300 meters corresponds to the area in which birds could generally be detected by BBS point counts. The 1000 meter buffer reflects a landscape scale to include breeding territory habitat and surrounding lands. This scale is commonly considered in landscape ecology research involving birds and often found to provide explanatory information (Cam et al. 2000, Fearer et al. 2007).

The BBS data were spatially aligned with landscape data as geographically referenced grids using Environmental Systems Research Institute (ESRI) software Arcview 3.2 and ArcGIS. The BBS study site grids were created from a USGS

shapefile, in which features represent BBS routes. The shapefile is geo-referenced using an adjusted Albers-Equal Area Conical projection, as defined in the shapefile metadata (USGS Patuxent Wildlife Research Center 2007). Each BBS route with applicable data was split into five separate line features, representing the five segments, or study sites, for that BBS route. For almost all routes, the segments were delineated using the actual BBS maps of survey locations. The electronic file was compared to individual route maps to determine the locations of point counts. These point locations were used to divide each route into five sub-route sites. Many routes have portions of highway or large road where no point counts occur; these sections were removed from the site's line feature for this analysis. In a few cases, the map of actual survey locations was not available. In this case, point counts were assumed to be exactly 0.80 km apart, and the route feature was split to create five segments of equal length. The resulting 325 individual line features represented our study sites.

2.2.1 Land cover data

Landscape variables were collected from the 2001 USGS National Land Cover Data (NLCD), which is available from the Multi-Resolution Land Characterization Consortium website (http://www.mrlc.gov/mrlc2k_nlcd_map.asp). The NLCD are available as grids with a resolution of 30 meter cells, each of which is coded with the dominant land cover within that cell. Land cover categories describe agricultural (pasture, row crops, orchards), anthropogenic development (low, medium, and high density residential, commercial/industrial), and natural

areas such as grassland, scrubland, and forest (deciduous, evergreen or mixed). Because of variation in the shape of BBS routes, the study sites did not all have equal areas. Therefore landscape composition was represented by the total proportion of agriculture (cultivated crop and pasture/hay) and forest (deciduous, evergreen and mixed). Landscape structure was parameterized using Fragstats software to represent forest fragmentation. Degree of forest fragmentation was estimated by patch density of forest land, calculated as the number of forest patches per hectare at each site.

2.2.2 Urban development data

Two parameters of urban development were used in this study: impervious surface and human population density. The 2001 NLCD characterizes developed areas based on a within-cell percent impervious surface metric. Therefore, we used the mean impervious surface at each site to represent urban development, which was then log-transformed. Impervious surface indicates the presence of roads, buildings, and other man-made structures, which correspond to the loss and fragmentation of bird habitat. This represents a specific change to the landscape caused by development.

Urban development was also estimated by the human population density at each site. Population data were collected from the 2000 U.S. Census. The U.S. Census data is collected in geo-referenced census blocks, which are available as TIGER/Line shapefiles. The census blocks were converted to a grid with a 30 meter cell size, to correspond to the study sites and NLCD data. Human

population density was calculated from the proportion of each census block at the site, and the population density of each census block.

2.3 Analysis

Data from the BBS were used to examine the importance of species traits related to migration, diet and habitat preference in determining bird diversity across a gradient of land use. The BBS count data fit an overdispersed Poisson distribution and contained excessive zero-count cells. Therefore, the data were analyzed using generalized linear modeling that examined avian species richness and abundance at each study site as Quasi-poisson distributed dependent variables. The model included effects of year, location, landscape variables and bird classifications. Because the same observer collected the data for the five study sites within each route on the same day and in the same geographic region, we expect the data within each BBS route to be correlated with each other. Similarly, geographic patterns in bird distributions suggest that nearby BBS routes will also correlate with each other (Thogmartin et al. 2004). The effects of location were addressed by incorporating latitude and longitude into the model as covariates, and BBS route and segment numbers as factors.

Landscape variables were expected *a priori* to be correlated, so a principal components analysis was performed on the correlation matrix of all five landscape variables. In order to normalize the data, NLCD forest composition and structure parameters were square-root transformed and urban development parameters were log transformed prior to the principal components analysis. The principal

component variables (PCs) were applied to the generalized linear model to examine bird diversity and abundance against these landscape gradients and the species classification factors (migratory and foraging). Habitat preference was not included in the initial analysis, to prevent any confounding with landscape variables. Model selection removed non-explanatory variables in a stepwise manner to identify the simplest model with the highest explanatory power for species richness and abundance, according to adjusted R^2 values. Adjusted R^2 values for over-dispersed Poisson distributed data were calculated according to methods developed by Heinzl and Mittlböck (2003) using model deviance. Analysis of variance was also run on each set of models to verify the simplest model that retained explanatory power.

RESULTS

3.1 Sites analyzed

This study examined 250 sites along 50 BBS routes in 2000, and 255 sites along 55 BBS routes in 2001. Though BBS, like many ecological surveys, does not collect data across the complete gradient of urbanization, data are available for undeveloped, agricultural and suburban areas. In 2001, the land within 1000 meters of these sites contained on average 38 ± 19 % forest, 40 ± 21 % agriculture (23 ± 17% cultivated crops and 17 ± 12 % pasture and hay), 13 ± 16 % developed, 10 ± 11% wetland, 0.4 ± 0.2 % barren, and 0 % each grassland and scrubland. Compared to the overall landscape of the MACP, the study sites may over-represent agriculture and under-represent forest lands, but otherwise match the regional landscape closely. This bias is likely due to the prevalence of secondary

roads through agricultural areas compared to forested areas. According to the NLCD data, the entire MACP in 2001 comprised 40% forest, 31% agriculture (18% cultivated crops and 13% pasture and hay), 13% developed, 13% wetland, 2% barren, and <1 % each grassland and scrubland. With the exception of the relatively rare barren land class, these regional values all fall within one standard deviation of the site averages. Land within 300 meters of these sites is further biased towards agriculture, with an average 33 ± 19 % forest, 45 ± 24 % agriculture (26 ± 18 % cultivated crops and 19 ± 14 % pasture and hay), 12 ± 18 % developed, 8 ± 9 % wetland, 2 ± 2 % barren, and 0 % each grassland and scrubland.

Human population density and percent impervious surface were also compared between the study sites and the general study area. Human population density at the study sites averaged 2.07 ± 5.07 people per hectare. These values are representative of the average population density of the MACP (2.18 people per hectare). The population density found at study sites ranged from 0 people per hectare to approximately 77 people per hectare, which accounts for the variation found within the MACP landscape. Impervious surface in the MACP averages 4.5 % of the landscape. The study sites, despite following roadside routes, have a mean impervious surface of 3.8 ± 7.5 % within the 300 meter buffer, and 2.9 ± 5.4 % within the 1000 meter buffer. The maximum within 300 meters of a study site was 68.9%; within 1000 meters the maximum was 33.5 % impervious surface. Human population density and impervious surface at the study sites also represent the Mid-Atlantic Coastal Plain fairly well.

3.2 Principal components analysis

Human population density and impervious surface were correlated within the range of our data. (slope = 0.723, $p < 2x10^{-16}$, $R^2 = 0.549$), and both agriculture and forest had a weak negative relationship to impervious surface. To address the relatedness of the landscape variables, a principal components analysis was performed for each buffer size. The resulting principal components (PCs) were similar for the 300 meter and the 1000 meter areas. PC1 roughly corresponds to the gradient from agriculture and forest to urban development and forest fragmentation, representing 44% of the variation in the landscape. PC2 roughly corresponds to the gradient from forest to agriculture, representing an additional 28-30% of the variation in the landscape. PC3 represents the gradient of forest fragmentation by agriculture, explaining an additional 15.4% of the variation in the landscape (Table 1). Because principal components 1, 2 and 3 described the major gradients in the landscape and explained over 85% of the variance in the landscape parameters, only these PCs were applied to the analysis of breeding bird diversity.

3.3 Breeding bird diversity

I examined bird count data for 115 species belonging to 35 families (Appendix 1). These species were distributed across four dietary groups (66 insectivores, 32 omnivores, 14 carnivores, and 3 herbivores), three migration strategies (56 neotropical migrants, 39 short-distance migrants and 20 year-round residents) and three habitat preferences (56 forest species, 49 open species and

Table 1. Results of principal components analysis of landscape variables given as the loading of each landscape variable on each principal component. Loadings are given for landscape variables at each of two spatial scales (300 meters and 1000 meters). The percent variance explained by each principal component is also given. Principal components 1-3 were used in the analysis of breeding bird diversity, as cumulatively they explained >85% of the variance in the landscape parameters.

Scale	Landscape parameter	PC1	PC2	PC3	PC4	PC5
300	% Impervious surface	0.615	0.159	-0.240	-0.208	0.704
300	Human pop. density	0.572	0.215	-0.081	0.695	-0.370
300	% Forest	-0.104	-0.751	-0.068	0.518	0.391
300	% Agriculture	-0.381	0.558	0.376	0.432	0.463
300	Forest patch density	0.372	-0.231	0.889	-0.136	-0.010
	Variance Explained	**43.8%**	**30%**	**15.4%**	**7.8%**	**2.9%**
1000	% Impervious surface	0.624	-0.054	-0.304	-0.120	0.708
1000	Human pop. density	0.586	0.061	-0.267	0.544	-0.534
1000	% Forest	-0.271	-0.668	-0.025	0.632	0.284
1000	% Agriculture	-0.189	0.731	0.115	0.534	0.362
1000	Forest patch density	0.398	-0.111	0.907	0.070	0.041
	Variance Explained	**43.6%**	**28%**	**15.4%**	**10.3%**	**2.7%**

10 generalist species). Seven species were detected only once at our study sites. On average, 183.8 ± 88.4 individual birds were detected at each sub-route site in a given year, belonging to 34.8 ± 8.4 species (Appendix 2).

3.4 Generalized linear models

My analysis found that bird communities to vary in their responses to urbanization according to migratory status, diet or habitat (Table 2). The best fit models were those using that examined bird diversity according to these traits. Bird diversity was best explained by models using bird species diets (adjusted R^2 ranged from .735 to .950.) Subdividing the bird community by more than one trait

led to greater heteroscedasticity in the data and poorer model fit. Specific bird diversity patterns across the gradient of development varied according to trait categories and often varied from the overall trends in the bird community. Species richness and evenness were most closely correlated to the landscape within 1000 meters of the study route, while bird abundance was better described by the local landscape within 300 meters of the route. Observed trends related to forest fragmentation (PC3) were controlled largely by very few relatively unfragmented sites; therefore the specific results presented focus on PC1 and PC2.

3.4.1 Models using diet

Models using diet to group bird species explained the most variation in species richness (R_D^2 = .950; Table 2). Species richness of insectivores was highest in forested landscapes, carnivores and omnivores in agricultural landscapes, and herbivores in developed areas (Diagram A). However, very few species belonged to the herbivore category, and their trends are explained by urban rock pigeons. Species richness of carnivores correlated positively with agriculture and forest fragmentation and negatively with urban development (impervious surface and human population density). Lower species richness of insectivores corresponded most strongly to impervious surface and population density (PC1), though also to agriculture (PC2) and forest fragmentation (PC3). Omnivore species richness correlated positively to agriculture and forest fragmentation, and negatively to both forest and urban development, though to a lesser extent than other groups (Appendix 3). Year, latitude and longitude were not significant factors in species richness models ($p>0.05$), and were excluded

Table 2. Summary model comparison of bird diversity (species richness, species evenness, or abundance) modeled by bird species trait, location, and landscape. Landscape scale (300 meter or 1000 meter) is given for each model in parentheses. Adjusted R^2 is given as for goodness of fit. R_D^2 indicates an adjusted R^2 that is based on model deviance for over-dispersed Poisson distributed data (Heinzl and Mittlböck, 2003). The asterisk (*) indicates that individual variables and interactions were part of the model ["(PC1 + PC2)*diet" indicates that PC1, PC2, diet, PC1:diet interactions, and PC2:diet interactions were significant].

Response Variable	Model Summary (landscape scale)	R^2
Species Richness		R_D^2
	route + segment + (PC1+PC2 + PC3)*diet (1000)	.950
	route + segment + (PC1+PC2 + PC3)*habitat (1000)	.809
	route + segment + (PC1+PC2 + PC3)*migration (1000)	.743
Species Evenness		R^2
	route + segment + (PC1+PC2 + PC3)*diet (1000)	.735
	route + (PC1+PC2 + PC3)*habitat (1000)	.574
	route + segment + (PC1+PC2 + PC3)*migration (1000)	.313
Abundance		R_D^2
	route + segment + (PC1+PC2 + PC3)*diet (1000)	.840
	route + segment + (PC1+PC2 + PC3)*migration (300)	.792
	route + segment + (PC1+PC2 + PC3)*habitat (300)	.698

from the best fit model. Route and segment had significant effects on species richness, unrelated to landscape composition and structure. These effects were therefore included in the best fit models. The effect of BBS route segment indicated consistently higher species richness and abundance detected at mid-route sites. This may be related to the diurnal activity patterns of many bird species, and possibly to observer error, such as lower detection rates at the start of a route. After accounting for route and segment effects, diet was a significant predictor of species richness across the urban gradient, with insectivores responding most negatively to development.

Species evenness was also best explained in models that grouped birds according to diet (R^2 = .735; Diagram A). For the generally diverse insectivore and omnivore groups, species evenness declined with urban development (PC1) and agriculture (PC2). However, omnivores maintained more species evenness in agricultural areas than insectivores. Species evenness for herbivores and omnivores was very low, confounded by to the limited species pools. Omnivores and insectivores both showed relatively high species evenness across the landscape.

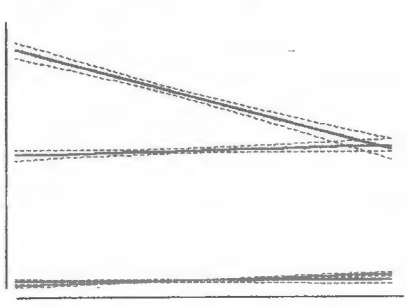
Abundance patterns for dietary groups paralleled species richness patterns across the gradient of development (PC1), with more omnivores and herbivores, and fewer insectivores and carnivores in urbanized areas. The low numbers of abundances for herbivores and carnivores provide little useful interpretation, so the trends presented focus on insectivores and omnivores (Diagram A). Across the agricultural land use gradient, abundance of both omnivores and insectivores increased, though the trend was more pronounced in insectivores. Overall, distinct patterns of bird abundance across different land use were also linked to dietary groups (R_D^2 = .840).

3.4.2 Models using migration

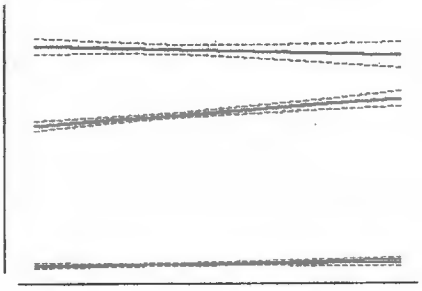
Models using migratory status to group bird species also explained significant variation in species richness (R_D^2 = .743; Table 2). Species richness of neotropical migrant species richness responded most dramatically to the landscape parameters, corresponding strongly to greater proportion of forest lands, and lower levels of impervious surface and human population density (PC1; see

Diagram A. Trends and confidence intervals for species diversity (richness, evenness, and bird abundance) according to diet groups along PC gradients. (Insectivore: Blue, Omnivore: Red, Carnivore: Purple, Herbivore: Orange)

a. Species Richness

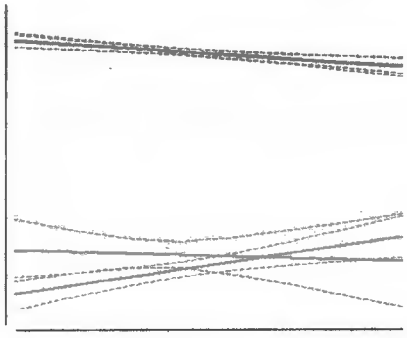


PC1 (Development)

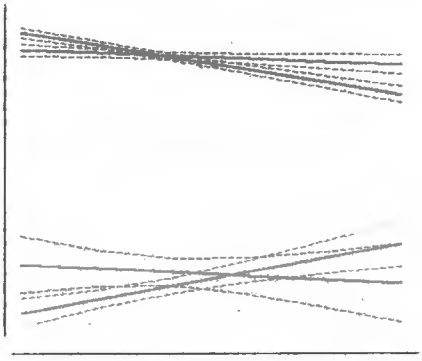


PC2 (Agriculture)

b. Species Evenness

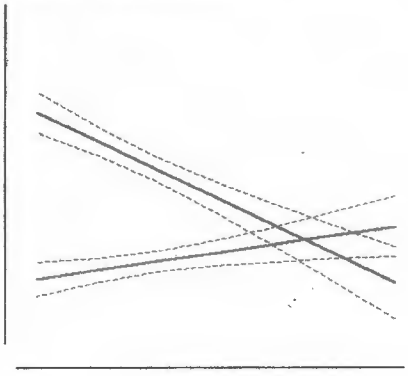


PC1 (Development)

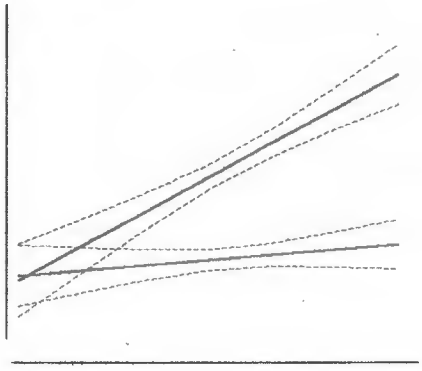


PC2 (Agriculture)

c. Bird Abundance



PC1 (Development)



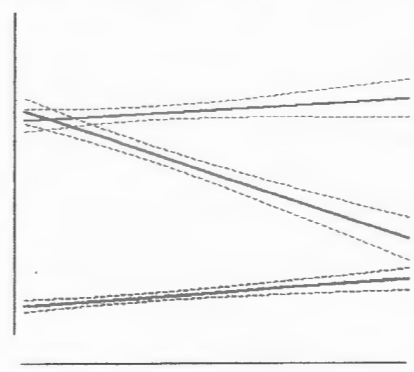
PC2 (Agriculture)

Diagram B). Short-distance migrants responded to landscape changes less dramatically, with greatest species richness corresponding to agricultural land (PC2). Resident species richness had a much weaker relationship with the landscape, increasing very slightly with impervious surface and human population density (PC1). Overall, neotropical migrant diversity was typically associated with forest habitat and declined more dramatically than other migratory groups in urbanized areas. Short-distance migrants and resident birds had greatest species richness in fragmented agricultural landscapes, but short-distance migrants also declined with urban development.

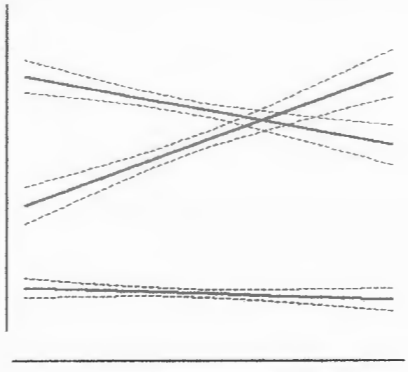
Migratory status was not strongly related to species evenness (R^2 = .313; Diagram B), but was linked to species richness (R_D^2 = .743) bird abundance (R_D^2 = .792). Species richness of neotropical migrants was lower at sites with increased impervious surface and human population density (PC1), but higher at agricultural sites (PC2; Diagram B). Short-distance migrants showed slight patterns of higher species richness at more urban sites and lower species richness at agricultural sites. Species richness of residents demonstrated patterns similar to short-distance migrants, but even less pronounced. Abundance of neotropical migrants declined in relation to both development and agriculture. Both short distance migrants and residents were slightly more abundant at sites with more urban or agricultural development. Short-distance migrant abundance increased particularly at agricultural sites. Urban development and land use gradients were related to distinct patterns of species richness and abundance within the different migratory groups of birds.

Diagram B. Trends and confidence intervals for species diversity (richness, evenness, and bird abundance) according to migratory groups along PC gradients. (Neotropical: Red, Resident: Blue, Short-distance: Purple)

a. Species Richness

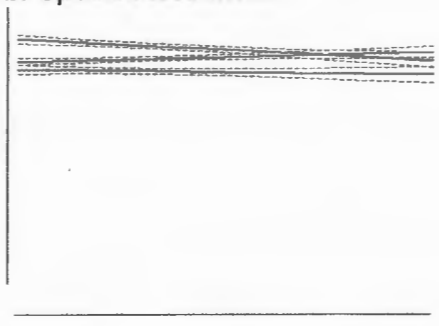


PC1 (Development)

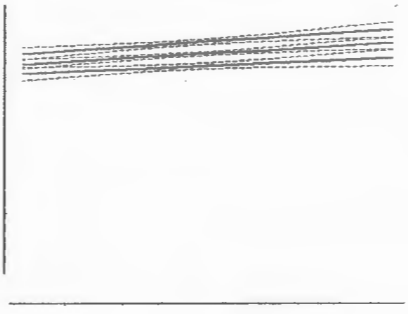


PC2 (Agriculture)

b. Species Evenness

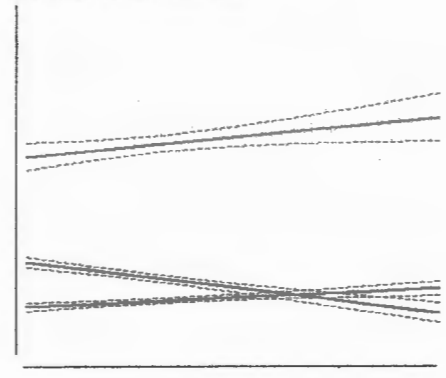


PC1 (Development)

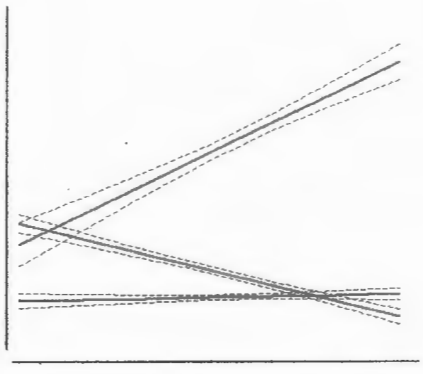


PC2 (Agriculture)

c. Bird Abundance



PC1 (Development)



PC2 (Agriculture)

3.4.3 Models using habitat

Models that grouped birds by habitat preference also explained species richness (R_D^2 = .809; Table 2), species evenness (R^2 = .574) and bird abundance (R_D^2 = .698) across the study sites. Species richness and species evenness of all habitat groups declined at sites with greater urban development (PC1; Diagram C). However, species richness and species evenness of forest birds and generalists was higher at agricultural sites, while that of birds preferring open habitat was lower. This could be explained in that detection probabilities are generally greater in simplified landscapes like agricultural areas, particularly for birds that typically perch off the ground. Birds preferring open habitat were more abundant at sites with greater urban or agricultural development; this group's trends match those of the overall bird community, with greater abundance and fewer species associated with development. Forest birds were less abundant at sites with urban or agricultural development. Habitat generalists were also less abundant at more urbanized sites, but more abundant at agricultural sites.

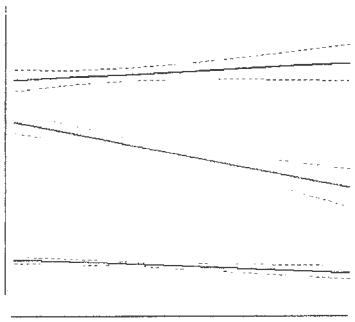
DISCUSSION

4.1 Analytical methods for BBS data

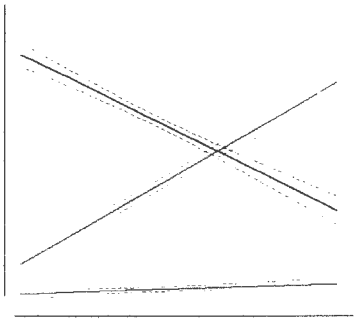
Studies examining bird diversity according to shared species traits are a cost-effective and efficient means to observing broad community responses to environmental change. The BBS provides a valuable tool for observing spatial and temporal trends in bird diversity and abundance, and the availability of data at the sub-route level allows for comprehensive and scale-appropriate landscape

Diagram C. Trends and confidence intervals for species diversity (richness, evenness, and bird abundance) according to habitat groups along PC gradients. (Forest: Red, Open: Blue, Generalist: Purple)

a. Species Richness

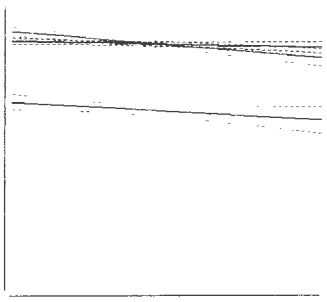


PC1 (Development)

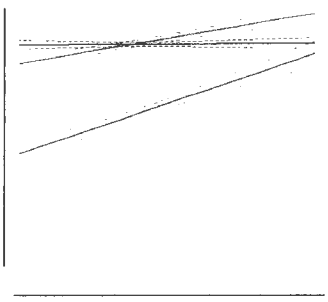


PC2 (Agriculture)

b. Species Evenness

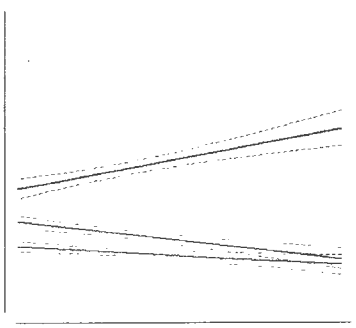


PC1 (Development)

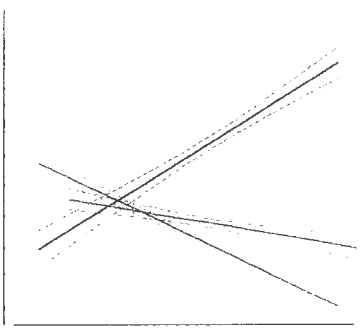


PC2 (Agriculture)

c. Bird Abundance



PC1 (Development)



PC2 (Agriculture)

analysis of this dataset. The use of sub-route sites for analysis of BBS data was found to be an effective means of exploring community-wide effects of landscape on breeding bird diversity. The BBS sites were found to be representative of the overall landscape of the Mid-Atlantic Coastal Plain. BBS sites have also been found to be consistent with the surrounding landscape in other areas nearby, with the actual landscape composition within one standard deviation of the average BBS site. Roadside point count data, while biased, are becoming more representative of regional landscapes due to the degree of urban development in the eastern U.S. (O'Connell et al. 2007). The landscape within a local (300 meter) buffer and a landscape (1000 meter) buffer was found to be significantly related to the local breeding bird diversity, as seen in other studies (Drapeau et al. 2000, Cam et al. 2000, Fearer et al. 2007).

4.2 Urban development parameters

Human population density and percent impervious surface were highly correlated, which indicates that they provide similar estimates of the urban development and associated human disturbance of a landscape. These variables were the main components of principal component 1, against which bird species richness, evenness and abundance responded significantly, suggesting that both may serve as effective indices for future studies of bird populations in developing areas. Human population density has potential to allow for extrapolation into both the past and future, for example using the decennial census figures from the U.S.

Census. Future studies should examine the appropriateness of impervious surface or human population density according to the specific study.

4.3 Bird diversity

This study examined trends in bird diversity across a range of site embedded in a gradient of human development. For the overall bird community, species richness declines with urban development, but bird abundance increases due to greater bird densities in urban areas (Crooks et al. 2004, Allen and O'Connor 2000). However, I found that species richness and abundance relate in similar ways to urban development for subsets of the bird community grouped by life history traits. Species life history traits are important links between the dynamics of individual species / populations and the dynamics of the bird community as a whole. These traits identify the "winners" and "losers" of urban development as a large-scale landscape change. While this study looked at sites distributed across a gradient of urbanization at a given time, previous research has shown that trends seen across a range of land uses at a given time correspond to trends seen over time with changes in land use in a given location, suggesting there is great potential for changes over time in a local bird community with development (Aldrich and Coffin 1980). Also, while detection probability varies among species, changes in detection probability across landscapes are not likely to artificially decrease overall bird counts at sites with greater urban or agricultural land cover.

The abundance and species richness of neotropical migrants declined most dramatically with urban development (Diagram B). Resident bird species richness and abundance was less sensitive to changes in land use gradients, and development led to greater species richness and abundances in areas disturbed by development. Declines in species evenness for neotropical migrants and residents at more urbanized sites indicate that a minority of these species are successful in developed areas. Existing hypotheses propose that the decline of neotropical migrant abundance and species richness may be due to differences in susceptibility of migrants and residents to habitat fragmentation, which is commonly caused by development, or by differences in susceptibility to severe weather or ecological tolerances among migratory groups (Flather and Sauer 1996). In addition, resident species that are willing to breed in developed areas will be more likely to adapt to changes in environmental conditions due to development, allowing increases to continue over time. Migratory groups appear to be differentially susceptible to environmental stressors associated with urban development, which indicates a pattern of shared life history strategies and traits within migratory groups.

Similarly, abundance and species richness of insectivores and carnivores was lower in areas of urban development, while that of omnivores was maintained or slightly higher with development. These responses of bird diversity in the temperate region are consistent with the patterns recorded in the tropics, where diet has been an important predictor of bird abundances in tropical areas of urbanization (Sigel et al. 2006, Lim and Sodhi 2004). Patterns in tropical bird

abundance find granivore/herbivore abundance most associated with development and relatively stable or increased omnivore abundances. However, temperate insectivore patterns did vary from the patterns in the tropics in that insectivore abundance in the coastal plain stayed fairly constant in relation to urban development, contrary to patterns in the tropics where insectivore abundance declines with development (Canaday 1996). Omnivores and herbivores were proportionally more abundant in developed areas, which has been seen in temperate lakeshore assemblages (Allen and O'Connor 2000). The abundance patterns in the coastal plain are consistent with the hypothesis that resource limitation is an important factor in determining bird abundances across a range of habitats. These urban declines in insectivore and carnivore species richness may be related to resource limitation directly (food limitation caused by changes or declines in the prey base) or through competition (from disturbance adapted omnivores) and increased habitat sensitivity in insectivores due to their high degree of ecological specialization (Canaday 1996). In general these groupings had lower species evenness at both urban and agricultural sites, indicating that even within these groups, there are winners and losers. Overall, insectivores were most susceptible to stressors associated with development.

While open-habitat birds mirrored the overall pattern of lower species richness and greater abundance at developed sites, forest birds were less specious and less abundant at developed sites. Forest bird species richness increased at agricultural sites, but abundance decreased; this anomaly may be due to greater detection probabilities for some forest bird species. Both species

richness and abundance of habitat generalists also decreased in species richness and abundance with urban development, but increased at agricultural sites.

These stressors associated with urban development may include competition for limiting resources, predation and other factors (Blair 2004). Food and nest sites have been identified as potential determinants in urban bird assemblages as limiting resources (Lim and Sodhi 2004, Blewett and Marzluff 2005). Stressors in developed areas may also differentially affect species according to the strategies used to find and collect food. Further research is needed to better understand what mechanisms contribute to the different patterns of species richness in developed areas according to migratory groups.

4.5 Resource limitation

One mechanism that may influence bird diversity of migratory or dietary groups in urbanized landscapes is resource limitation. By definition, urban development limits the quantity of available land that can be used for bird habitat. The remaining habitat areas may also be of lower quality than habitat in undeveloped areas, which could render it unusable for species with specific habitat or resource requirements. Specific nesting sites are an example of a resource that may be limiting in developed areas. For example, developed areas contain fewer and lower quality snags, which provide nest sites for cavity nesting species, than undisturbed forest (Blewett and Marzluff 2005). Food resources may also change with development. Anthropogenic food sources may replace or augment natural food resources for some generalist species. Limitation of food resources is also

cited as a potential factor in bird diversity changes with urban development with regards to changing prey base or foraging sites for insectivores (Blewett and Marzluff 2005, Lim and Sodhi 2004). The decrease in stream insect diversity with impervious surface provides some support for this hypothesis of resource limitation in association with development (Morse et al. 2003). Changes in the prey base may exclude specialized insectivores or lead to increased competition for food resources, while omnivores and granivores may exploit anthropogenic food sources unavailable to insectivores.

4.6 Invasive species

Human development of the landscape is as a form of disturbance, which often increases the chances of invasion by exotic or introduced species (Hobbs and Huenneke 1996). Species able to successfully invade following introductions often occur commonly in areas of disturbance. Human disturbance through urban development can promote the spread of introduced species across the landscape, confounding the problem of disturbance and habitat loss for native species. Invading species for North American birds include both avian competitors and novel predators. Several species of bird have been successfully introduced into North America and are now found commonly in many regions. These birds compete with native species for limited resources, and often benefit from a longer evolutionary history of close contact with human disturbance and urban development. Predation may vary with urban development due to exotic predators such as domestic cats and changes in the natural predator community. However,

the overall difference in predation risk associated with development remains unclear (Blair 2004). Many studies find an overall decrease in predation (Anderies et al. 2007), but a different predator community in developed areas may relate to a shift in how predation affects different groups within the bird community. Habitat fragmentation may also cause increased brood-parasitism by edge-associated species such as the brown-headed cowbird (Lloyd et al. 2005).

4.7 Implications for regional bird communities

Homogenization of bird communities on the regional and national scale is increasingly becoming a reality due to urban development. Blair (2004) and Crooks et al. (2004) found that the similarity of bird community composition between sites in California and Ohio was significantly correlated to the degree of urbanization at each site. Species associated with urban sites in California and Ohio in these studies (American Robin, House Finch, House Sparrow, Mourning Dove, Rock Pigeon, European Starling, Northern Mockingbird) were also found at MACP sites. All species but Rock Pigeon were found at over 60% of the MACP study sites. These species, many of which are introduced in North America, demonstrate that bird community homogenization is occurring in developed landscapes on a national scale.

4.8 Implications for future conservation and research

Neotropical migrants and insectivores appear most sensitive to urban development in ecologically diverse regions. It is critical that conservation efforts

and land management account for these sensitive species and species with life histories specialized to a given environment and set of resources. The high conservation priority given to many species of insectivorous neotropical migrants highlights the importance of addressing these landscape level effects of urban development on bird diversity. Avian declines caused by urban development are exacerbated by lower nesting success of migratory birds associated with forest fragmentation (Robinson et al. 1995). Conservation plans which address these species groups must prioritize the protection of large reserves of undisturbed land. Similarly, regional conservation efforts must be planned and carried out in context of the regional land use and an understanding of the limitations of the land as bird habitat. By understanding the land available and its utility for various species, conservation biologists may better manage undeveloped lands to protect the species most at-risk.

Future research is needed to better understand the mechanisms driving bird – landscape interactions. Conservation efforts will benefit greatly from studies which elucidate the mechanisms that drive habitat selection in birds. Examining the mechanisms driving habitat selection and the changes in urban bird diversity will provide insight into mitigation strategies and potentially provide greater opportunity for conservation within developed landscapes. Community and guild-based analyses and species-specific studies will complement each other to improve our understanding of the relationships between birds and their habitats.

REFERENCES

Aldrich, J.W. and R.W. Coffin. 1980. Breeding bird populations from forest to suburbia after thirty-seven years. American Birds 34: 3-7.

Allen, A.P. and R.J. O'Connor. 2000. Interactive effects of land use and other factors on regional distributions. Journal of Biogeography 27: 889-900.

Anderies, J.M., M. Katti, and E. Shochat. 2007. Living in the city: resource availability, predation, and bird population dynamics in urban areas. Journal of Theoretical Biology 247: 36-49.

Askins, R.A., J.F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Current Ornithology 7: 1-57.

Bart, J., M. Hofschen, and B.G. Peterjohn. 1995. Reliability of the Breeding Bird Survey: effects of restricting surveys to roads. The Auk 112: 758-761.

Blair, R. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society 9:* 2. Retrieved September 7, 2007, from http://www.ecologyandsociety.org/vol9/iss5/art2.

Blewett, C.M., and J.M. Marzluff. 2005. Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. The Condor 107: 678-693.

Brooks, T.M., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, A.B. Rylands, W.R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16: 909-923.

Cam, E., J.D. Nichols, J.R. Sauer, J.E. Hines, and C.H. Flather. 2000. Relative species richness and community completeness: birds and urbanization in the Mid-Atlantic States. Ecological Applications 10: 1196-1210.

Canaday, C. 1996. Loss of insectivorous birds along a gradient of human impact in Amazonia. Biological Conservation 77: 63-77.

Crooks, K.R., A.V. Suarez, and D.T. Bolger. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biological Conservation 115: 451-461.

Devictor, V., R. Julliard, D. Couvet, A. Lee, and F. Jiguet. 2007. Functional homogenization effect of urbanization on bird communities. Conservation Biology 21: 741-751.

Donovan, T.M., R.H. Lamberson, A. Kimber, F.R. Thompson, and J. Faaborg. 1995. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. Conservation Biology 9: 1396-1407.

Drapeau, P., A. Leduc, J. Giroux, J.L. Savard, y. Bergeron, and W.L. Vickery. 2000. Landscape scale disturbances and changes in bird communities of boreal mixed-woods forests. Ecological Monographs 70: 423-444.

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

Fearer, T.M., S.P. Prisley, D.F. Stauffer, and P.D. Keyser. 2007. A method for integrating the Breeding Bird Survey and Forest Inventory and Analysis databases to evaluate forest bird-habitat relationships at multiple spatial scales. Forest Ecology and Management 243: 128-143.

Flanders, A.A., W.P. Kuvlesky, D.C. Ruthven, R.E. Zaiglin, R.L. Bingham, T.E. Fulbright, F. Hernandez, and L.A. Brennan. 2006. Effects of invasive exotic grasses on South Texas rangeland breeding birds. Auk 123: 171-182.

Flather, C.H. and J.R. Sauer. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77: 28-35.

Gough, G.A., J.R. Sauer, and M. Iliff. 1998. *Patuxent Bird Identification Infocenter.* Version 97.1. Patuxent Wildlife Research Center, Laurel, MD. Gough, G.A., J.R. Sauer, and M. Iliff [online]. 1998. *Patuxent Bird Identification Infocenter.* Version 97.1. Patuxent Wildlife Research Center, Laurel, MD. Retrieved November 10, 2006, from http://www.mbr-pwrc.usgs.gov/id/framlst/infocenter.html.

Hamel, P.B., H.E. LeGrand Jr., M.R. Lennartz, and S.A. Gauthreaux [eds.]. 1982. Bird-habitat relationships on Southeastern forest lands. USDA Forest Service, General Technical Report SE-22, 417 pp. Southeastern Forest Experiment Station, Asheville, NC.

Heinzl, H. and M. Mittlböck. 2003. Pseudo *R*-squared measures for Poisson regression models with over- or underdispersion. Computational Statistics & Data Analysis 44: 253-271.

Hobbs, R.J. and L.F. Huenneke. 1996. Disturbance, Diversity and Invasion: Implications for Conservation. In Samson, F.B. and F.L. Knopf [eds]. Ecosystem Management: Selected Readings. Springer, New York, NY, USA. Pp. 164-182.

Lim, H.C. and N.S. Sodhi. 2004. Responses of avian guilds to urbanisation in a tropical city. Landscape and Urban Planning 66: 199-215.

Link, W.A., E. Cam, J.D. Nichols, and E.G. Cooch. 2002. Of bugs and birds: markov chain monte carlo for hierarchical modeling in wildlife research. Journal of Wildlife Management 66: 277-291.

Lloyd, P., T.E. Martin, R.L. Redmond, U. Langner, and M.M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15: 1504-1514.

Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell, Malden, MA. 256 pp.

Mayer, A.L. and G.N. Cameron. 2003. Landscape characteristics, spatial extent, and breeding bird diversity in Ohio, USA. Diversity and Distributions 9: 297-311.

McKinney, M.L. and J.L. Lockwood. 2001. Biotic homogenization: a sequential and selective process. In: Lockwood, J.L. and M.L. McKinney (eds). Biotic homogenization. Kluwer Academic/Plenum, New York, NY, USA. Pp 1-17.

Mills, G.S., J.B. Dunning Jr., and J.M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. The Condor 91: 416-428.

Morse, C.C., A.D. Huryn, and C. Cronan. 2003. Impervious surface area as a predictor of the effects of urbanization on stream insect communities in Maine, U.S.A. Environmental Monitoring and Assessment 89: 95-127.

O'Connell, T.J., J.A. Bishop, and R.P. Brooks. 2007. Sub-sampling data from the North American Breeding Bird Survey for application to the Bird Community Index, an indicator of ecological condition. Ecological Indicators 7: 679-691.

Robinson, S.K., F.R. Thompson, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987-1990.

Sigel, B.J., T.W. Sherry, and B.E. Young. 2006. Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. Conservation Biology 20: 111-121.

Söderström, B., B. Svensson, K. Vessby, and A. Glimskär. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodiversity and Conservation 10: 1839-1963.

Thogmartin, W.E., J.R. Sauer, and M.G. Knutson. 2004. A hierarchical spatial model of avian abundance with application to cerulean warblers. Ecological Applications 14: 1766–1779.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

U.S. Census Bureau [online]. 2007. Virginia QuickFacts: generated by Elise Larsen using State and County QuickFacts. Retrieved January 22, 2007, from http://quickfacts.census.gov/qfd/states/51000.html.

USGS Patuxent Wildlife Research Center. 2007. North American Breeding Bird Survey ftp data set, version 2007.0 Retrieved June 30, 2006, from ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/datafiles/.

U.S. Geological Survey [online]. 1992. National Land Cover Dataset. Retrieved January 22, 2007, from http://www.mrlc.gov.

U.S. Geological Survey [online]. 2001. National Land Cover Database Zone 60 Land Cover Layer. Retrieved January 22, 2007, from http://www.mrlc.gov.

Appendix 1. Species detected at study sites in 2000 or 2001, listed by family. Common species names according to AOU listings are identified by their dietary group (C – Carnivore, H – herbivore, I - insectivore, O – omnivore), migratory status (NTM – Neotropical migrant, SDM – short-distance migrant, R – resident) and habitat preference (forest, open, or Generalist). For each species, the number of samples where the species was detected is given, where each sample represents a single study site in a single year. The mean number of birds detected per sample ± one standard deviation is given. Standard deviation is not given when species was detected only once.

Family	Common Species Name	Dietary Group	Migratory Status	Habitat Preference	Number of samples where detected	Average number of birds/sample, when detected
Accipitridae	Broad-winged Hawk	C	NTM	Forest	4	1 ± 0
Accipitridae	Bald Eagle	C	SDM	Forest	16	1.75 ± 1.24
Accipitridae	Cooper's Hawk	C	SDM	Forest	7	1 ± 0
Accipitridae	Red-shouldered Hawk	C	SDM	Forest	36	1.17 ± 0.45
Accipitridae	Red-tailed Hawk	C	SDM	Forest	86	1.35 ± 0.72
Accipitridae	Sharp-shinned Hawk	C	SDM	Forest	1	1
Accipitridae	Northern Harrier	C	SDM	Open	6	1 ± 0
Alaudidae	Horned Lark	I	SDM	Open	142	3.58 ± 3.12
Alcedinidae	Belted Kingfisher	C	SDM	Open	18	1.17 ± 0.38
Anatidae	Canada Goose	H	SDM	Open	129	12.42 ± 20.09
Anatidae	Wood Duck	O	SDM	Forest	23	2.17 ± 2.01
Apodidae	Chimney Swift	I	NTM	Open	242	3.37 ± 2.59
Bombycillidae	Cedar Waxwing	O	SDM	Forest	185	2.63 ± 1.71
Caprimulgidae	Chuck-will's-widow	I	NTM	Forest	19	2.21 ± 1.78
Caprimulgidae	Whip-poor-will	I	NTM	Forest	14	2.43 ± 2.24
Caprimulgidae	Common Nighthawk	I	NTM	Open	1	1
Cardinalidae	Rose-breasted Grosbeak	O	NTM	Forest	1	1

Appendix 1 (continued). Species detected at study sites in 2000 or 2001, listed by family.

Cardinalidae	Indigo Bunting	O	NTM	Generalist	409	5.99	±	4.18
Cardinalidae	Blue Grosbeak	O	NTM	Open	278	3.17	±	2.42
Cardinalidae	Dickcissel	O	NTM	Open	3	2.33	±	1.15
Cardinalidae	Northern Cardinal	O	R	Forest	467	5.95	±	3.84
Cathartidae	Black Vulture	C	R	Forest	47	3.68	±	5.15
Cathartidae	Turkey Vulture	C	SDM	Forest	191	6.59	±	7.4
Charadriidae	Killdeer	I	SDM	Open	210	2.27	±	3.2
Columbidae	Rock Pigeon	H	R	Open	122	8.31	±	13.02
Columbidae	Mourning Dove	H	SDM	Open	479	7.25	±	5.88
Corvidae	Blue Jay	O	SDM	Forest	361	3.03	±	2.08
Corvidae	American Crow	O	SDM	Generalist	484	9.91	±	7.47
Corvidae	Fish Crow	O	SDM	Generalist	173	4.75	±	17.56
Cuculidae	Black-billed Cuckoo	I	NTM	Forest	9	1.11	±	0.33
Cuculidae	Yellow-billed Cuckoo	I	NTM	Forest	132	1.95	±	1.79
Emberizidae	Grasshopper Sparrow	I	NTM	Open	105	2.68	±	2.25
Emberizidae	Chipping Sparrow	O	NTM	Generalist	434	4.44	±	3.34
Emberizidae	Eastern Towhee	O	SDM	Generalist	238	3.32	±	4.42
Emberizidae	Field Sparrow	O	SDM	Open	228	2.27	±	1.73
Emberizidae	Seaside Sparrow	O	SDM	Open	19	5.58	±	3.42
Emberizidae	Song Sparrow	O	SDM	Open	295	3.76	±	2.86
Emberizidae	Swamp Sparrow	O	SDM	Open	11	3.55	±	2.58
Emberizidae	Vesper Sparrow	O	SDM	Open	13	1.85	±	1.21
Falconidae	American Kestrel	C	SDM	Open	19	1.11	±	0.32
Fringillidae	American Goldfinch	O	SDM	Generalist	306	3.17	±	2.53
Fringillidae	House Finch	O	SDM	Open	314	4.28	±	3.76
Hirundinidae	Bank Swallow	I	NTM	Open	10	3.8	±	3.55
Hirundinidae	Barn Swallow	I	NTM	Open	335	5.2	±	5.54

Appendix 1 (continued). Species detected at study sites in 2000 or 2001, listed by family.

Hirundinidae	Cliff Swallow	I	NTM	Open	1	2		
Hirundinidae	Northern Rough-winged Swallow	I	NTM	Open	28	2.21	±	1.42
Hirundinidae	Purple Martin	I	NTM	Open	214	6.57	±	6.89
Hirundinidae	Tree Swallow	I	SDM	Open	91	3.12	±	3.66
Icteridae	Baltimore Oriole	I	NTM	Open	106	1.5	±	0.95
Icteridae	Orchard Oriole	I	NTM	Open	227	2.18	±	1.61
Icteridae	Common Grackle	I	SDM	Generalist	485	28.45	±	32.31
Icteridae	Eastern Meadowlark	I	SDM	Open	136	2.28	±	1.75
Icteridae	Red-winged Blackbird	I	SDM	Open	388	12.74	±	16.51
Icteridae	Brown-headed Cowbird	O	SDM	Generalist	304	2.58	±	2.07
Mimidae	Gray Catbird	I	NTM	Open	315	3.46	±	3.12
Mimidae	Northern Mockingbird	I	R	Open	465	5.46	±	3.55
Mimidae	Brown Thrasher	I	SDM	Open	177	1.68	±	1.17
Odontophoridae	Northern Bobwhite	O	R	Generalist	240	3.55	±	2.99
Paridae	Carolina Chickadee	O	R	Forest	316	2.75	±	2.06
Paridae	Tufted Titmouse	O	R	Forest	415	4.09	±	2.78
Parulidae	American Redstart	I	NTM	Forest	12	1.92	±	1.56
Parulidae	Black-and-white Warbler	I	NTM	Forest	45	1.6	±	1.01
Parulidae	Black-throated Green Warbler	I	NTM	Forest	1	1		
Parulidae	Hooded Warbler	I	NTM	Forest	41	1.44	±	0.74
Parulidae	Kentucky Warbler	I	NTM	Forest	48	1.04	±	0.2
Parulidae	Louisiana Waterthrush	I	NTM	Forest	26	1.12	±	0.33
Parulidae	Northern Parula	I	NTM	Forest	79	2.86	±	2.93
Parulidae	Ovenbird	I	NTM	Forest	273	2.89	±	2.5
Parulidae	Prothonotary Warbler	I	NTM	Forest	44	1.52	±	0.88
Parulidae	Swainson's Warbler	I	NTM	Forest	1	1		
Parulidae	Worm-eating Warbler	I	NTM	Forest	36	1.28	±	0.61

Appendix 1 (continued). Species detected at study sites in 2000 or 2001, listed by family.

Parulidae	Yellow-throated Warbler	I	NTM	Forest	10	1.5	±	0.71
Parulidae	Blue-winged Warbler	I	NTM	Open	1	1		
Parulidae	Chestnut-sided Warbler	I	NTM	open	3	1	±	0
Parulidae	Common Yellowthroat	I	NTM	Open	358	3.49	±	3.63
Parulidae	Prairie Warbler	I	NTM	Open	101	2.3	±	2.17
Parulidae	Yellow Warbler	I	NTM	Open	67	1.55	±	1.22
Parulidae	Yellow-breasted Chat	I	NTM	Open	158	1.93	±	1.35
Parulidae	Pine Warbler	I	SDM	Forest	195	3.58	±	3.9
Passeridae	House Sparrow	O	R	Open	349	8.42	±	8.82
Phasianidae	Wild Turkey	O	R	Forest	30	2.37	±	2.3
Phasianidae	Ring-necked Pheasant	O	R	Open	6	1	±	0
Picidae	Downy Woodpecker	I	R	Forest	189	1.59	±	0.92
Picidae	Hairy Woodpecker	I	R	Forest	41	1.15	±	0.36
Picidae	Pileated Woodpecker	I	R	Forest	59	1.37	±	0.72
Picidae	Yellow-shafted Flicker	I	SDM	Forest	193	1.55	±	0.88
Picidae	Red-bellied Woodpecker	O	R	Forest	349	2.55	±	1.72
Picidae	Red-headed Woodpecker	O	SDM	Forest	10	1.4	±	0.7
Sittidae	White-breasted Nuthatch	I	R	Forest	76	1.71	±	1.31
Sittidae	Brown-headed Nuthatch	O	R	Forest	15	2.33	±	1.45
Strigidae	Barred Owl	C	R	Forest	6	1.5	±	0.84
Strigidae	Eastern Screech-Owl	C	R	Forest	5	1.2	±	0.45
Strigidae	Great Horned Owl	C	R	Forest	16	1.44	±	0.81
Sturnidae	European Starling	O	SDM	Open	454	18.85	±	21.26
Sylviidae	Blue-gray Gnatcatcher	I	NTM	Forest	141	2.51	±	2.54
Thraupidae	Scarlet Tanager	I	NTM	Forest	174	1.54	±	0.89
Thraupidae	Summer Tanager	I	NTM	Forest	74	1.32	±	0.76
Trochilidae	Ruby-throated Hummingbird	O	NTM	Generalist	39	1.08	±	0.27

Appendix 1 (continued). Species detected at study sites in 2000 or 2001, listed by family.

Troglodytidae	House Wren	I	NTM	Open	177	2.18	±	1.62
Troglodytidae	Carolina Wren	I	R	Forest	411	3.79	±	2.88
Turdidae	Veery	I	NTM	Forest	1	1		
Turdidae	Wood Thrush	I	NTM	Forest	357	3.65	±	2.81
Turdidae	American Robin	I	SDM	Open	485	12.4	±	11.34
Turdidae	Eastern Bluebird	I	SDM	Open	220	2.24	±	1.74
Tyrannidae	Acadian Flycatcher	I	NTM	Forest	171	2.36	±	1.65
Tyrannidae	Eastern Wood-Pewee	I	NTM	Forest	280	2.12	±	1.52
Tyrannidae	Great Crested Flycatcher	I	NTM	Forest	274	2.11	±	1.86
Tyrannidae	Eastern Kingbird	I	NTM	Open	178	1.64	±	1.04
Tyrannidae	Willow Flycatcher	I	NTM	Open	21	1.38	±	0.8
Tyrannidae	Eastern Phoebe	I	SDM	Open	108	1.21	±	0.47
Vireonidae	Red-eyed Vireo	I	NTM	Forest	330	3.8	±	3.44
Vireonidae	Yellow-throated Vireo	I	NTM	Forest	39	1.28	±	0.6
Vireonidae	Warbling Vireo	I	NTM	Open	14	1.5	±	0.85
Vireonidae	White-eyed Vireo	I	NTM	Open	196	1.82	±	1.33
Vireonidae	Blue-headed Vireo	O	NTM	Forest	5	1.2	±	0.45

Appendix 2. Average species richness and abundance of bird communities according to migratory status, diet and habitat preference. (Values ± 1 standard deviation.)

Migratory Status	Average Species Richness			Average Abundance		
Neotropical	13.337	±	4.813	42.524	±	22.439
Resident	7.250	±	2.001	31.895	±	18.121
Short-distance	14.218	±	3.591	109.429	±	69.686

Diet	Average Species Richness			Average Abundance		
Carnivore	1.547	±	0.793	5.823	±	7.338
Herbivore	1.476	±	0.638	12.124	±	15.294
Insectivore	19.054	±	5.749	95.332	±	54.170
Omnivore	13.404	±	3.211	73.359	±	36.178

Habitat	Average Species Richness			Average Abundance		
Forest	12.904	±	5.009	39.352	±	21.809
Generalist	6.213	±	1.647	54.301	±	37.820
Open	15.712	±	4.365	90.267	±	58.660

Appendix 3. Parameter estimates and standard errors for the magnitude of the effects of landscape principal components on species richness (SR), species evenness (SE), and bird abundance (AB) for each dietary (C – carnivore, H – herbivore, I – insectivore, O – omnivore), habitat (F – forest, G – generalist, O – open), and migratory (NTM – neotropical migrant, SDM – short-distance migrant, R – resident) groupings of bird species.

3-A: Parameter estimates for models using dietary groups.
C = carnivore, H = herbivore, I = insectivore, O = omnivore.

	Diet	PC1				PC2				PC3		
SR (1000m)	C	-0.0252	+/-	0.0259		-0.0099	+/-	0.0280		-0.1714	+/-	0.0384
SR (1000m)	H	0.0739	+/-	0.0302		-0.0695	+/-	0.0346		-0.0430	+/-	0.0476
SR (1000m)	I	-0.0906	+/-	0.0258		0.0502	+/-	0.0279		-0.0299	+/-	0.0384
SR (1000m)	O	-0.0073	+/-	0.0260		-0.0025	+/-	0.0281		-0.0325	+/-	0.0388
SE (1000m)	C	-0.0439	+/-	0.0426		-0.0630	+/-	0.0469		0.2735	+/-	0.0633
SE (1000m)	H	0.1581	+/-	0.0522		0.2535	+/-	0.0622		0.0997	+/-	0.0825
SE (1000m)	I	-0.0153	+/-	0.0449		-0.0427	+/-	0.0501		-0.0022	+/-	0.0680
SE (1000m)	O	-0.0154	+/-	0.0705		-0.0112	+/-	0.0501		0.0130	+/-	0.0680
AB (300m)	C	-0.1630	+/-	0.0700		0.0997	+/-	0.0778		0.2896	+/-	0.1152
AB (300m)	H	0.1931	+/-	0.0745		0.2350	+/-	0.0866		0.1064	+/-	0.1268
AB (300m)	I	-0.0212	+/-	0.0703		0.1312	+/-	0.0782		0.0153	+/-	0.1164
AB (300m)	O	0.0624	+/-	0.0705		0.0605	+/-	0.0786		-0.0180	+/-	0.1168

Appendix 3 (continued). Parameter estimates and standard errors for the magnitude of the effects of landscape principal components on species richness (SR), species evenness (SE), and bird abundance (AB).

3-B: Parameter estimates for models using migratory groups.
NTM = neotropical migrant, SDM = short-distance migrant, R = resident.

	Migration	PC1				PC2				PC3		
SR (1000m)	NTM	-0.0935	+/-	0.0084		0.0908	+/-	0.0100		-0.0146	+/-	0.0139
SR (1000m)	SDM	-0.0193	+/-	0.0090		-0.0199	+/-	0.0011		-0.0376	+/-	0.0166
SR (1000m)	R	-0.0063	+/-	0.0108		0.0092	+/-	0.0134		-0.0457	+/-	0.0200
SE (1000m)	NTM	-0.0139	+/-	0.0040		0.0191	+/-	0.0044		-0.0178	+/-	0.0066
SE (1000m)	SDM	0.0063	+/-	0.0044		0.0148	+/-	0.0055		0.0070	+/-	0.0081
SE (1000m)	R	-0.0043	+/-	0.0045		0.0144	+/-	0.0056		-0.0292	+/-	0.0082
AB (300m)	NTM	-0.0895	+/-	0.0175		-0.1351	+/-	0.0205		-0.0358	+/-	0.0298
AB (300m)	SDM	0.0602	+/-	0.0175		0.2230	+/-	0.0209		0.0586	+/-	0.0321
AB (300m)	R	0.0591	+/-	0.0220		0.0605	+/-	0.0268		-0.0195	+/-	0.0408

Appendix 3 (continued). Parameter estimates and standard errors for the magnitude of the effects of landscape principal components on species richness (SR), species evenness (SE), and bird abundance (AB).

3-C: Parameter estimates for models using habitat groups.
F = forest, G = generalist, O = open.

	Habitat	PC1				PC2				PC3		
SR (1000m)	F	-0.0802	+/-	0.0086		0.1665	+/-	0.0103		-0.0212	+/-	0.0142
SR (1000m)	G	-0.0471	+/-	0.0116		0.0320	+/-	0.0144		-0.0473	+/-	0.0215
SR (1000m)	O	-0.0135	+/-	0.0089		-0.0810	+/-	0.0111		-0.0406	+/-	0.0166
SE (1000m)	F	-0.0244	+/-	0.0061		0.0321	+/-	0.0074		-0.0477	+/-	0.0101
SE (1000m)	G	-0.0233	+/-	0.0072		0.0872	+/-	0.0090		-0.0165	+/-	0.0133
SE (1000m)	O	-0.0074	+/-	0.0066		-0.0064	+/-	0.0083		0.0115	+/-	0.0123
AB (300m)	F	-0.0392	+/-	0.0196		-0.2685	+/-	0.0236		-0.0306	+/-	0.0333
AB (300m)	G	-0.0456	+/-	0.0221		0.1456	+/-	0.0267		0.0198	+/-	0.0406
AB (300m)	O	0.1005	+/-	0.0199		0.2545	+/-	0.0248		0.0655	+/-	0.0369

VITA

Elise A. Larsen was born and raised in Seabrook, Maryland. In 2001, she graduated from Michigan State University with a B.S. in Zoology with a concentration in Environmental Biology. From 1999 to 2001, Elise also worked for the USGS at Patuxent Wildlife Research Center, including contributing to the Contaminant Exposure and Effects – Terrestrial Vertebrates (CEE-TV) database. From 2002 to 2005, she coordinated the Avian Incident Monitoring System (AIMS) Program at the American Bird Conservancy. She entered the biology graduate program at the College of William and Mary in the fall of 2005 and defended in 2007. In the fall of 2007, she began a Ph.D. program in Biology at the University of Maryland.