LONG-TERM AVIAN COMMUNITY CHANGES IN A FRAGMENTED DECIDUOUS FOREST LANDSCAPE

By

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LONG-TERM AVIAN COMMUNITY CHANGES IN A FRAGMENTED DECIDUOUS FOREST LANDSCAPE

INTRODUCTION

A large body of comparative conservation biology research describes how avian communities have changed in response to habitat changes associated with human land use in North America. The negative impact of forest loss and fragmentation on forest-breeding birds, for instance, is well known. We have focused less intently, however, on the subsequent long-term dynamics of avian communities when humans maintain altered habitats in a relatively stable state. While incremental habitat changes such as forest succession and human activity will continue to have influence, longitudinal studies can provide evidence for or against several additional ecological processes that may cause avian community change: source-sink dynamics, geographic range shifts, mortality in non-breeding habitats, disease, and extinction debt. We utilized historical data to compare avian communities, vegetation, and land cover composition in the early 1950s and the early 2000s at 38 fragmented deciduous forest sites across the largely agricultural and urbanizing landscape of southern Wisconsin.

In chapter 1, we compared avian communities in 2006 to those in the early 1950s. Our findings largely corroborate the findings of other avian community studies in fragmented forest habitats. We observed declines in the richness and abundance of neotropical forest specialists, but increases in species associated with early successional and urban habitats, and species that migrate within the temperate region or do not migrate. Overall avian abundances remained stable over this interval. Site-level avian communities became more similar to each other between the 1950s and 2006. This pattern of biotic homogenization was driven by increasingly ubiquitous native species, not exotic species. We also documented a surprisingly strong increase in avian species richness. Increased species richness is associated with moderate-intensity human development, but the magnitude of the increase we observed exceeds what we expected based on previous research. In some ways, our findings indicate that the status of avian communities may be more hopeful than was previously believed.

In chapter 2, we examined evidence for mechanisms of avian community change. Sites experienced only modest changes in forest stand vegetation and landscape composition between the early 1950s and the early 2000s. Within stands, canopy tree assemblages trended toward later succession. Mean forest cover, the forest edge / area ratio, and the number of houses within 1 km of study sites all increased. Avian ecological guilds defined by habitat associations and migratory habits responded to these landscape and vegetation changes, but only to a limited extent. Increases in species richness were not related to measured habitat changes, but species whose ranges are expanding into the study area contributed significantly. We found little evidence for other hypothesized mechanisms of long-term avian community change.

We suggest evolutionary adaptation to fragmented forest habitat may contribute to some of the increases we observed. If so, habitat stability is likely an important condition for adaptation. Since much of the world is and will be altered by humans, future research should focus on conservation strategies in these habitats and the specific conditions that allow species to persist and adapt.

CHAPTER 1: CHANGES IN AVIAN COMMUNITIES, 1950S TO 2006

Introduction

A large and growing proportion of land area in North America is affected by human land use (Foley et al. 2005). Changes in biodiversity caused by humans have tremendous ecological and societal consequences (Chapin et al. 2000), so monitoring and conservation of biodiversity is important. Human land use alters breeding bird community structures and biodiversity. We have a limited amount of knowledge, however, about trends in avian biodiversity and community dynamics over long time periods in altered habitats.

Long-term studies have indicated that especially woodland neotropical migrant bird species are declining (e.g., Robbins 1989), some precipitously. Cerulean Warblers have declined by 4.0% per year since 1966 in eastern North America, and Wood Thrushes by 1.6 % (Sauer et al. 2007). From 1980 to 2006 in eastern North America, 50 % of woodland neotropical species declined significantly, while only 24 % increased significantly (Sauer et al. 2007). Habitat loss and degradation in tropical wintering areas and along migration routes likely contribute to observed declines among neotropical migrant species (e.g., Rappole & McDonald 1994).

A large body of research indicates that breeding habitat changes in North America also influence avian communities. Forest fragmentation reduces the amount of available habitat, the size of habitat patches, and increases isolation among patches, all of which negatively impact birds (Andrén 1994). Forest fragmentation reduces insect prey availability (Burke & Nol 1998) and increase risks of nest predation (Gates & Gysel 1978) and parasitism by Brown-headed Cowbirds (Brittingham & Temple 1983). Smaller forest fragments are associated with decreased abundance of woodland neotropical migrant species and increased abundance of species associated with early succession or forest edge habitats (e.g., Whitcomb et al. 1981; Ambuel & Temple 1983; Lynch & Whigham 1984; Freemark & Merriam 1986).

Housing development is a cause of forest fragmentation and a widespread driver of landscape change. Since 1950, low-density rural development has become the fastest-growing land use in the United States, and now covers almost 25% of the area of the 48 coterminous states (Brown et al. 2005). In addition to causing forest loss and fragmentation, housing influences avian communities through structural habitat changes (Odell et al. 2003), higher populations of mesopredators such as cats (Crooks & Soule 1999), and homeowner activities such as landscaping and feeding (Lepczyk et al. 2004), even at very low housing densities (Kluza et al. 2000, Odell & Knight 2001). Housing density is influential on woodland bird native species richness (Pidgeon et al. 2007), and bird species richness in the Midwest reaches a maximum at intermediate housing densities (Lepczyk et al. 2008).

Human land use alters vegetation composition even in forest habitats not directly transformed by changing disturbance regimes (Lorimer 2001) and introducing exotic species (Asner & Vitousek 2005). Changes in relative abundance of tree species resulting largely from fire suppression (Abrams 2005) may reduce insectivorous bird species by supporting lower insect prey densities (Rodewald & Abrams 2002). Exotic plants alter habitat structure, food availability, and nest success (Borgmann & Rodewald 2004).

Biotic homogenization, the increase in similarity among communities (beta diversity) occurs across many taxa in the context of human development (McKinney & Lockwood 1999). In avian communities, generalists and permanent residents tend to become more dominant with increasingly urbanized habitats, while foraging specialists and migrants decline (Chace & Walsh 2006, McKinney 2006). Species richness and abundance may peak at intermediate levels of natural habitat alteration, perhaps because of increased habitat heterogeneity (Blair 1996), but effects on avian communities are evident even at low-density exurban development (Hansen et al. 2005).

Results from the studies cited above support concerns regarding effects of forest fragmentation and development on avian communities, but they are limited by lack of long-term data and reliance on "space-for-time" substitutions, i.e. they compared an altered with a non-altered site, inferring changes detected in the altered site are similar to changes that occur over time (Flather & Sauer 1996). Because such studies are susceptible to confounding sources of variation among study sites and because many land use effects occur gradually over time (Hansen et al. 2005), long-term longitudinal studies are particularly important when possible. Longitudinal studies are rarely feasible, however, especially over long time periods.

The existence of historical avian community data (Bond 1957, Ambuel & Temple 1982) gives us a unique opportunity to compare avian communities directly over a long time interval, and thus transcend the limitations of space-for-time substitution. Our objective was to determine whether the avian community changes that would be predicted from other studies occurred in fragmented forests of southern Wisconsin between the early 1950s and 2006. We predicted: 1) declines in abundance and richness among woodland neotropical migrants, based on previous local and regional observations and effects of forest fragmentation and forest succession; 2) increases in abundance and richness of species associated with early succession and urban habitats, because of forest fragmentation and housing development; 3) biotic homogenization occurring a result of housing development; and 4) increased species richness, with reduced richness of woodland neotropical migrants offset by increases in other guilds because of housing development.

Methods

Study Area

Bond (1957) studied birds in 52 forest sites throughout southern Wisconsin. In 2006 we resurveyed bird communities at 38 of these sites (Figure 1). Approximately two thirds of the sites are privately owned, and the rest are managed as parks or natural areas by local, county, or state agencies. Curtis (1959) and Rogers et al. (in press) have described plant communities at these sites near the times the bird surveys were conducted. Modern forests are predominantly small, second-growth, forest islands in an agricultural and urbanizing landscape. Oak savanna, oak-hickory forest, and maple-basswood forest predominated in southern Wisconsin prior to European settlement. Settlers converted most savanna to agriculture, and due to fire exclusion, oak forest associations replaced any remaining savanna (Peet & Loucks 1977).

Bird surveys

During the 1952-1954 breeding seasons, Richard Bond (1957) conducted point and transect counts of avian populations at 64 wooded upland sites (> 6 ha, without recent grazing, logging, or fire) in southern Wisconsin. Each site was visited in only one of the three study years. In 2006, two field observers (A. Olson and J. Nadolski), working individually, resurveyed 38 of these sites. Prior to beginning surveys, we calibrated our observations by conducting simultaneous test surveys to ensure comparability. The theory and practice of avian sampling methods has advanced considerably since the 1950s, including estimates of detectability functions using distance measurements (Bibby et al. 2000). For purposes of comparison with 1950s observations, however, we replicated Bond's field protocol. Within each site interior (45m from edge), we recorded all birds seen or heard (except those only flying over) in five sample units: pairs of alternating point and transect counts (infinite radius), each count lasting for five minutes, with transect length averaging 150-175 m. During the season we visited each site twice on days without rain or strong wind: once May 20 – June 14, and once June 8 - July 4. To minimize time-of-day effects, one of the two visits to each site was at dawn and the other later in the morning.

Analyses

All analyses except Non-metric multidimensional scaling (NMDS) ordination were conducted using R statistical software (R Development Core Team 2006) and appropriate contributed packages. We first verified that the mean number of birds (of all species) detected per sample unit did not differ between observers over all surveys using a paired permutation test with 10,000 runs ($p > 0.4$; Good 2005). We then compared avian communities in the 1950s to those in 2006 at each site. As per Bond (1957), we used the higher of the two counts of each species on each site as the estimate of abundance from which community composition metrics were calculated.

Presence/absence

We compared patterns of presence/absence in the 1950s to those in 2006 for each species to assess changes in frequencies of occurrence and in occurrence distributions. To assess change in frequency of occurrence we constructed 2 x 2 presence/absence contingency tables for each species in which we categorized each site according to species presence in 1950s and 2006 surveys. We then tested for changes in frequency of occurrence using McNemar's test with exact p-values (Agresti 2002). We assessed the degree of agreement among prior and current species occurrence distributions by calculating Cohen's Kappa (0: no agreement to 1: perfect agreement; Cohen 1960) of the same 2x2 contingency tables used to analyze species frequency of occurrence. We performed a z-test using the kappa2 function in the 'irr' package contributed to R (R Development Core Team 2006).

Ambuel &Temple (1982) surveyed southern Wisconsin forest bird communities at 14 sites, different from ours, in 1979. We compared frequency of occurrence for 31 species observed in both studies. We applied Fisher's exact test (Agresti 2002) to assess changes in the frequency of occurrence from the early 1950s - 1979 and from 1979 - 2006.

Relative abundance

We calculated the relative abundance of each species at each site (no. individuals of species at site / total no. individuals at site) in the early 1950s and in 2006, and compared relative abundances across time periods using two-sample paired permutation tests with 10,000 runs (Good 2005). We assigned species to an ecological guild based on published information about habitat use (woodland, early succession / scrub, and urban) and migration habit (permanent resident, short-distance migrant, neotropical migrant) (Peterjohn & Sauer 1993, Appendix 1). We assessed changes in relative abundance for each guild and for intersected habitat-migration guilds, again using two-sample paired permutation tests with 10,000 runs.

Absolute Abundance

A limitation in our study is that we have incomplete knowledge of sampling effort from the 1950s survey. Bond conducted a full 5 sample-unit survey at most sites, but when a full survey was not possible because of small forest size or inaccessible areas, it is not clear how many transects he completed (R. Bond, pers. comm.). Therefore, we conducted a sensitivity analysis to test the importance of potential differences in sampling effort in the two time periods. We calculated changes in abundance between the two periods under three alternative assumptions of sampling effort in Bond’s study relative to ours: Bond sampled 1) half as much, 2) the same amount, or 3) 125% as much as we did. Alternative 1 represents a larger proportional difference, than the change in surveyed forest patch areas we estimated (mean 1950s patch area = 65% mean 2006 patch area) in a landscape change analysis (ch.2). Alternative 3 corresponds to the difference between sampling 4 and 5 units. Since in 2006 we averaged 4.1 sample units per site, 125% is the maximum by which Bond’s sample effort could have exceeded ours. We scaled Bond’s (1957) observed abundances to correct for the assumed differences in sampling effort (multiplied by 2 for assumption 1, and by 0.8 for assumption 3). We then assessed changes in abundance for each species, each ecological guild, and the entire avian community using paired permutation tests (10,000 runs), with sites serving as replicates.

Species Richness

To compare avian species richness between time periods within ecological guilds and in the entire community, we constructed individual-based rarefaction curves (Mao Tau) with 95% confidence intervals for each time period using EstimateS software (Gotelli & Colwell 2001, Colwell 2006). This allowed us to visually compare the expected species richness between time periods across a range of sample sizes. We also calculated the species richness within ecological guilds and in the entire community at each site for each time period and compared site-level species richness between time periods. We tested for differences in species richness using paired paired permutation tests (10,000 runs), with sites serving as replicates.

Biotic Homogenization

We examined the similarity among site-level avian communities within each time period to determine whether biotic homogenization or differentiation has occurred among avian communities. Using relative abundance community matrices, we calculated the Bray-Curtis distance between all pairs of sites (Olden & Rooney 2006). We tested for a difference among time periods in the mean distance between each site and all other sites using a paired t-test. We conducted this test first including all species, and second among only those species present in both time periods, in order to examine the effect of new species on site-level similarity.

NMDS ordination

To explore patterns of avian composition, we performed Nonmetric Multidimensional Scaling (NMDS) ordination with varimax rotation on all sites from both years together, using PC-ORD software v.5.0 (Kruskal 1964, Mather 1976, Clarke 1993, McCune & Mefford 1999). We first removed data from the species in which fewer than five individuals were detected in all surveys, and standardized the community matrix by the total number of birds detected at each site, so that the value for each entry represented the relative abundance of a given species at a given site. This standardization was necessary for a fair comparison of the two datasets because we have limited information about the sampling efforts for the earlier survey. We used the Bray-Curtis distance measure for the original dissimilarity matrix. Our algorithm included 250 runs of real data with random starting configurations, 250 Monte Carlo runs of randomized data, and 120 iterations for the final solution. We examined the

NMDS scree plot to determine the final number of axes to accept. To test whether early 1950s bird communities differed from 2006 communities, we performed a two-way crossed Analysis of Similarity (ANOSIM; site nested within time period, 999 random permutations; Clarke 1993) using PRIMER software (Clarke & Gorley 2006).

Results

Presence/absence

We observed 61 species in 2006, compared to 41 at the same 38 sites in the early 1950s (Appendix 1; Appendix 2 provides 2006 raw survey data). Twenty-two species occurred in 2006 but not in the early 1950s, while only two species occurred in the early 1950s but not in 2006. Fifteen species increased and 5 species decreased in frequency of occurrence among the 38 study sites ($p < 0.05$). American Robin frequency increased most dramatically, from no sites in the 1950s to 37 (of 38) in 2006 ($p < 0.0001$). Frequency of Northern Cardinals, House Wrens, and American Goldfinches also increased very strongly (15 to 38 sites, 2 to 25 sites, and 2 to 23 sites, respectively, all $p < 0.0001$). Least Flycatchers declined most dramatically in frequency, occurring at 14 sites in the 1950s and none in 2006 ($p = 0.0001$). Cerulean Warblers and Ovenbirds also decreased strongly in frequency (18 to 5 sites, $p = 0.0024$ and 34 to 22 sites, $p = 0.0005$ respectively, Table 1A).

Six species increased significantly in frequency of occurrence from the early 1950s to 2006 and were analyzed by Ambuel & Temple (1982) in 1979 at 19 sites separate from Bond's study sites but in the same southern WI forest landscape. Of these, frequency of occurrence increased monotonically over the three surveys in three species: Cedar Waxwing, Black-capped Chickadee, and American Robin. Of the five species that decreased from the early 1950s to 2006, all except Ovenbirds decreased monotonically over the three surveys (Table 1B).

Analysis of occurrence distributions revealed little agreement between species-level distributions in the 1950s and 2006. Based on Cohen's Kappa, five species showed evidence of fidelity to sites between the 1950s and 2006: Acadian Flycatcher (Cohen's Kappa (C.K.) = 0.2785, $z = 1.7686$, p-value = 0.0770), Blue-gray Gnatcatcher (C.K. = 0.4124, $z = 2.5922$, p-value = 0.0095), Ovenbird (C.K. = 0.2785, $z = 2.4793$, p-value = 0.0132), Tufted Titmouse (C.K. = 0.3342, $z = 2.4937$, p-value =0.0132). The American Goldfinch showed evidence of negative agreement between its 1950s and 2006 distributions (C.K. = -0.1080, $z = -2.0149$, p-value = 0.0439, Table 2).

Relative Abundance

We observed significant increases in the relative abundance of 15 species and decreases in 10 species ($p < 0.05$). Changes were very similar to changes in frequency of occurrence. Fourteen of the fifteen species increasing in frequency of occurrence also increased in relative abundance. All of the species decreasing in frequency of occurrence also decreased in relative abundance. The remaining five species declining in relative abundance did not decline in frequency of occurrence. The latter included the most abundant species in both study periods, Red-eyed Vireos (0.17 to 0.10, $p < 0.0001$) and Eastern Wood-Pewees (0.12 to 0.07, $p < 0.0001$; Table 3).

Among migratory habit guilds, neotropical migrants declined in relative abundance from 0.74 to 0.51 ($p < 0.0001$), while relative abundance of short-distance migrants and residents increased from 0.14 to 0.23 ($p < 0.0001$) and from 0.12 to 0.26 ($p < 0.0001$) respectively. Among habitat use guilds, woodland species decreased in relative abundance from 0.81 to 0.62 ($p < 0.0001$), while early succession and urban species increased from 0.04 to 0.18 ($p < 0.0001$) and 0.04 to 0.10 ($p < 0.0001$) respectively. Among intersected habitat-migratory habit guilds, neotropical migrant species that breed in woodlands declined in relative abundance, while other guilds were stable or increased (Figure 2).

Absolute Abundance

We accepted species' absolute abundance changes as biologically significant only if test results were statistically significant under the most conservative assumption (i.e. comparing 125% of Bond's recorded abundance with 2006 abundance for species that decreased, and 50% of Bond's recorded abundance for species that increased). Test results agree closely with results for relative abundance and for frequency of occurrence. Ten species increased, while six species decreased (Table 4).

We used the same assumptions and criteria for assessing significance of abundance changes in ecological guilds and of the entire community as were used for assessing species abundance changes. We found evidence for an increase in abundance of early succession species ($p < 0.0001$), urban species ($p = 0.0223$), and resident species ($p = 0.0086$) from the early 1950s to 2006. We did not detect declines in abundance among habitat use guilds or among migratory habit guilds. Among intersected habitat-migration guilds, we found weak evidence that the abundance of woodland breeding neotropical migrant species has declined ($p = 0.0505$), while other intersected guilds remained stable or increased (Figure 3 and Table 5). Although we detected more birds in 2006 than Bond (1957) had in the 1950s (mean 57.6 birds per site vs. 38.7), we found no evidence for significant changes in entire community abundance under conservative assumptions about Bond's sampling effort (Table 5).

Species Richness

Overall species richness increased between the early 1950s and 2006. Among all surveys, 41 species were detected in the early 1950s, while 61 species were detected in 2006 (Appendix 1). Figure 4a, a sample-based rarefaction curve scaled by the number of individuals, indicates clear differences in species richness after ~ 250 individuals. Among habitat use guilds, urban species richness increased from the early 1950s to 2006 (Figure 4d). Among migratory habit guilds, neotropical migrant species increased in richness (Figure 4e).

Site-level avian species richness increased by 6.24 species per site, from a mean value of 17.97 species in the early 1950s to 24.21 species in 2006 ($p < 0.0001$). Among habitat use guilds, species richness of early successional species increased from 1.32 to 3.84 species per site ($p < 0.0001$), richness of urban species increased from 0.82 to 2.45 species per site ($p < 0.0001$), and richness of woodland species increased from 13.39 to 14.53 species per site ($p = 0.0693$). Among guilds based on migratory habit, richness of short-distance migrants and residents increased (from 3.00 to 6.39 species/site and 3.74 to 6.47 species/site respectively; both $p < 0.0001$). Richness of neotropical migrant species did not change significantly (11.21 to 11.18 species/site). Among intersected habitat-migration guilds, we found evidence for decline in richness only among neotropical migrant species that use woodland habitat. This group declined from 9.87 to 8.84 species per site ($p = 0.0244$). All other guilds were stable or increased in richness (Figure 5).

Biotic Homogenization

Avian communities underwent site-level taxonomic homogenization between the early 1950s and 2006. Mean similarity of each site to all other sites increased from 0.57 to

0.69 (paired permutation test, 10,000 runs, p-value < 0.0001). Among only species that appeared in both time periods, mean similarity remained unchanged at 0.57.

NMDS ordination

Avian communities in the early 1950s were significantly different from those in 2006 (2-way crossed ANOSIM: Global R = 0.626, p-value < 0.001). The NMDS final solution contained 3 dimensions with final stress = 14.2 (p-value < 0.001), and final instability < 0.0001. Axes 1, 2, and 3 represented 52.9%, 13.7% and 18.3% of the original variance, respectively. NMDS plots (Figure 6) reveal clear separation of sites by time period along axes 1 and 3, while trajectory arrows indicate consistency of species changes across sites. NMDS Axis 1 was correlated most positively with species that increased in relative abundance (e.g., American Robin, Black-capped Chickadee, Northern Cardinal), and most negatively with species that decreased in relative abundance (e.g., Eastern Wood-Pewee, Ovenbird, Red-eyed Vireo; Table 6).

Discussion

We observed significant changes in avian communities between the 1950s and 2006, and most of these changes supported our initial predictions. Our observations were consistent with our first prediction: declines among woodland neotropical migrants. We found that for six of eighteen woodland neotropical migrant species, abundances have declined since the 1950s in southern Wisconsin forests. Among all guilds, the neotropical migrant woodland guild was the only one for which we observed declines in site-level abundance and species richness. Many studies have demonstrated reduced densities and species richness of forest interior birds and neotropical migrants in forest habitats isolated by agriculture and urbanization (e.g., Whitcomb et al. 1981; Ambuel & Temple 1983; Lynch & Whigham 1984; Freemark & Merriam 1986). We documented declines in some of the same species that previous studies have found to be sensitive to fragmentation and development: Eastern wood-pewees, Least Flycatchers, Ovenbirds, Baltimore Orioles, and Cerulean Warblers (Beissinger & Osborne 1982, Friesen et al. 1985, Kluza et al. 2000). Results also corroborate previous findings in southern Wisconsin and eastern North America about long-term declines in woodland neotropical migrant species (Ambuel & Temple 1982, Sauer et al. 2007, Holmes & Sherry 2001).

We also observed predicted increases in other guilds. Among habitat guilds, species associated with early successional habitats and urban habitats both increased in relative and absolute abundance. Among migratory habit guilds, permanent residents increased in relative and absolute abundance. Among ten species that increased in abundance in our study, nine were members of at least one of these migratory or habitat guilds. These results are consistent with effects of forest fragmentation and housing development (Chace & Walsh 2006, McKinney 2006).

We found evidence for our third prediction, that biotic homogenization of avian communities has occurred. The mean similarity of site-level avian communities increased by 21% between the early 1950s and 2006. This pattern is also consistent with effects of housing development (McKinney 2006). Since we found no change in the similarity among only species that appeared in both time periods, addition of new species into communities, rather than extirpations was responsible for this pattern. Species such as American Robins that appeared ubiquitously in 2006 increased community similarity among sites. This mechanism for biotic homogenization has been proposed and observed in other taxa (Olden & Poff

2004). Our results are unique, however, in that the new species driving homogenization are not introduced non-natives as is typical, but are native species whose ubiquity has increased within the range of our study.

Observed increases in species richness support our fourth prediction, but we were surprised at the magnitude of increase. Despite decreased site-level species richness among woodland neotropical migrant species, we documented increases greater than 30% in site-level and overall species richness. These patterns were driven by strong increases in the species richness of short-distance migrant, resident, early succession, and urban species. Avian species richness in southern Wisconsin forests in 1979 were not different from those in 1954 (Ambuel & Temple 1982), indicating that the entire increase occurred after this time. A potentially relevant methodological difference is that both Bond (1957) and Ambuel & Temple (1982) excluded sites with building structures within the woodlot, while we did not. Only three sites contained homes within forest patches, so this likely cannot explain the observed richness differences.

Previous studies have predicted maxima in avian species richness at intermediate locations along rural to urban gradients (McDonnell & Pickett 1990) based on the hypothesis that intermediate disturbances offer the greatest habitat and resource diversity (Connell 1978). This hypothesis would predict increases in species richness with housing growth in rural areas where housing density is initially low. Rural housing density increased by 146% in the Midwest between the 1940s and 2000, and was particularly strong in and around forests (Radeloff 2005). Models developed by Lepczyk et al. (2008) predict a maximum avian species richness increase of ~ 15% with this level of housing growth, half the amount we observed. The magnitude of increase is also larger than that documented in other long-term studies, even where housing growth was stronger (Aldrich & Coffin 1979).

In order to interpret these results as being biologically significant, we must distinguish long-term avian trends from other potential sources of variation: 1) bias originating from observer or methodological differences; 2) local, stochastic population changes; and 3) regional fluctuations around stable mean levels (Ambuel & Temple 1982). We cannot verify the equivalence of our avian detection skills with Bond's, but we have no reason to suspect significant differences. Our study design replicated Bond's in order to maximize comparability between the studies, but we lack complete knowledge of his sampling effort. We therefore assessed changes in absolute abundance conservatively using a sensitivity analysis and also considered evidence from frequency of occurrence and relative abundance measures.

We cannot definitively distinguish the influences of stochastic local and regional departures from long-term trends directly from our data because our study relies on abundance data from just two points in time. We believe, however, that the magnitude of the changes observed and our conservative assumptions about observer effort strongly suggest that this study uncovers evidence for long-term change rather than stochastic temporal variability in avian populations. Evidence from other studies also corroborates our results. Results from Ambuel & Temple (1982) provide additional evidence for long-term trends in some species. Among eleven species whose frequencies of occurrence changed significantly between the 1950s and 2006 and were also analyzed in 1979, the observed frequencies of occurrence for seven species changed monotonically over the three points in time, suggesting long-term trends.

Other long-term studies of avian change place our results into a broader context. Most long-term studies of bird communities in highly fragmented forest habitats corroborate the guild changes we observed (e.g., Lynch & Whitcomb 1978, Ambuel & Temple 1982, Leck et al. 1988), documenting declines among forest-dwelling neotropical migrant bird species, and simultaneous increases in species utilizing forest edges and that migrate shorter distances or do not migrate (Askins et al 1990). Isolated woodlots in Illinois did not experience declines in woodland neotropical migrants between 1927 and 1976, apparently because they had already disappeared prior to the study (Kendeigh 1982). In studies from more extensively forested regions, declines among woodland neotropical migrants described above have been less dramatic than in fragmented habitats (Holmes & Sherry 2001, Hall 1984), or not evident (Wilcove 1988). Avian responses to suburban growth over time in deciduous forest habitats have been similar in terms of habitat and migratory guild changes, but observed changes were less consistent. Species richness increased by 26% with suburban growth in a Virginia deciduous forest between 1942 and 1979 (Aldrich & Coffin 1979), but decreased by 65% with similar habitat changes in Massachusetts between 1860 and 1964 (Walcott 1974).

In many ways our study is consistent with trends observed in previous studies in fragmented forest habitats. It therefore supports conservation concerns, particularly regarding woodland neotropical migrant species. Declines in this guild have been modest, however, in comparison with previous studies in southern Wisconsin. Site-level species richness of woodland neotropical migrant species decreased by 30% between the early 1950s and 1979, while we observed only an 11% decline between the early 1950s and 2006. Increases among other guilds of native birds compensated for declines among woodland neotropical migrants, and overall abundance of birds appears to have remained stable over the period. The exceptionally strong increases in species richness we observed thus represent a departure from previous findings, and this pattern warrants further investigation. Given that biotic homogenization has also occurred, however, conservation biologists should still be concerned about the biodiversity trends we observed. We conclude that fragmented forest habitats remain important habitat for supporting avian biodiversity. Land use planners should consider the conservation opportunities of these habitats and limit development in surrounding areas. We suggest that future conservation biology research continue to investigate long-term dynamics in human-altered habitats.

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Tables

Table 1. Tests of differences in avian species presence/absence in 38 southern Wisconsin woodlots over a 50 year period. (A) Frequency of occurrence by species in 1950s and 2006, and results of McNemar's test of significant difference between the two time periods. (B) Frequency of occurrence of species in 1979 (Ambuel & Temple 1982) and Fisher's exact test results for significant difference between the 1950s and 1979, and between 1979 and 2006.

	A.			**B.**		
Species	**sites 1950s**	**sites 2006**	**p-val 50s-06**	**sites 1979**	**p-val 50s-79**	**p-val 79-06**
Increasing						
Wild Turkey	0 / 38	10 / 38	**0.0020**			
Mourning Dove	0 / 38	12 / 38	**0.0005**			
Downy Woodpecker	21 / 38	32 / 38	**0.0074**			
Pileated Woodpecker	0 / 38	7 / 38	**0.0156**			
Red-bellied Woodpecker	16 / 38	34 / 38	**0.0001**			
Northern Flicker	7 / 38	18 / 38	**0.0127**			
American Crow	12 / 38	31 / 38	**< 0.0001**			
American Goldfinch	2 / 38	25 / 38	**< 0.0001**			
Chipping Sparrow	0 / 38	6 / 38	**0.0313**			
Northern Cardinal	15 / 38	38 / 38	**< 0.0001**	4 / 14	0.5335	**< 0.0001**
Cedar Waxwing	0 / 38	16 / 38	**< 0.0001**	3 / 14	**0.0165**	0.2090
House Wren	2 / 38	23 / 38	**< 0.0001**	9 / 14	**< 0.0001**	1.0000
Tufted Titmouse	9 / 38	20 / 38	**0.0034**	3 / 14	1.0000	0.0615
Black-capped Chickadee	19 / 38	35 / 38	**0.0001**	9 / 14	0.5319	**0.0254**
American Robin	0 / 38	37 / 38	**< 0.0001**	8 / 14	**< 0.0001**	**0.0009**
Decreasing						
Least Flycatcher	14 / 38	0 / 38	**0.0001**	3 / 14	0.3414	**0.0165**
Brown-headed Cowbird	38 / 38	32 / 38	**0.0313**	10 / 14	**0.0037**	0.4283
Baltimore Oriole	19 / 38	9 / 38	**0.0309**	5 / 14	0.5319	0.4849
Cerulean Warbler	18 / 38	5 / 38	**0.0024**	2 / 14	0.0518	1.0000
Ovenbird	34 / 38	22 / 38	**0.0005**	4 / 14	**< 0.0001**	0.1164
Undetermined						
Northern Bobwhite	0 / 38	1 / 38	1.0000			
Ruffed Grouse	1 / 38	0 / 38	1.0000			
Ring-necked Pheasant	0 / 38	1 / 38	1.0000			
Cooper's Hawk	5 / 38	5 / 38	1.2734			
Red-tailed Hawk	6 / 38	8 / 38	0.7905			
Red-shouldered Hawk	3 / 38	1 / 38	0.6250			
Broad-winged Hawk	0 / 38	3 / 38	0.2500			
Barred Owl	1 / 38	6 / 38	0.1250			
Great Horned Owl	2 / 38	2 / 38	1.3750			

Yellow-billed Cuckoo	18 / 38	22 / 38	0.5235			
Black-billed Cuckoo	6 / 38	1 / 38	0.1250			
Hairy Woodpecker	24 / 38	29 / 38	0.3018			
Red-headed Woodpecker	9 / 38	7 / 38	0.7744			
Ruby-throated Hummingbird	12 / 38	8 / 38	0.4545			
Great Crested Flycatcher	33 / 38	27 / 38	0.1796	12 / 14	1.0000	0.4721
Eastern Phoebe	0 / 38	4 / 38	0.1250			
Eastern Wood-Pewee	38 / 38	38 / 38	1.0000	14 / 14	1.0000	1.0000
Acadian Flycatcher	10 / 38	14 / 38	0.3877	2 / 14	0.4753	0.1788
Alder Flycatcher	0 / 38	1 / 38	1.0000			
Blue Jay	31 / 38	37 / 38	0.0703	14 / 14	0.1689	1.0000
Red-winged Blackbird	0 / 38	1 / 38	1.0000	5 / 14	**0.0008**	**0.0039**
House Finch	0 / 38	1 / 38	1.0000			
Field Sparrow	0 / 38	2 / 38	0.5000			
Song Sparrow	0 / 38	1 / 38	1.0000			
Eastern Towhee	1 / 38	5 / 38	0.2188			
Rose-breasted Grosbeak	21 / 38	26 / 38	0.3593	10 / 14	0.3533	1.0000
Indigo Bunting	22 / 38	28 / 38	0.2379	11 / 14	0.2090	1.0000
Scarlet Tanager	34 / 38	30 / 38	0.3438	9 / 14	**0.0477**	0.2996
Red-eyed Vireo	38 / 38	37 / 38	1.0000	12 / 14	0.0686	0.1729
Yellow-throated Vireo	25 / 38	20 / 38	0.3018	3 / 14	**0.0058**	0.0615
Blue-headed Vireo	0 / 38	1 / 38	1.0000			
Blue-winged Warbler	0 / 38	2 / 38	0.5000			
Chestnut-sided Warbler	0 / 38	5 / 38	0.0625	1 / 14	0.2692	1.0000
Black-throated Green Warbler	0 / 38	5 / 38	0.0625			
Mourning Warbler	0 / 38	2 / 38	0.5000	1 / 14	0.2692	1.0000
Common Yellowthroat	0 / 38	2 / 38	0.5000			
Hooded Warbler	0 / 38	5 / 38	0.0625			
American Redstart	22 / 38	14 / 38	0.0768	2 / 14	**0.0105**	0.1788
Gray Catbird	8 / 38	11 / 38	0.5811	7 / 14	0.0809	0.1966
White-breasted Nuthatch	35 / 38	37 / 38	0.6250	14 / 14	0.5547	1.0000
Blue-gray Gnatcatcher	29 / 38	26 / 38	0.5078	7 / 14	0.0939	0.3307
Wood Thrush	19 / 38	28 / 38	0.0636	2 / 14	**0.0266**	**0.0002**
Veery	4 / 38	4 / 38	1.2734	2 / 14	0.6548	0.6548

Table 2: Test of agreement in species distributions among sites in 38 southern Wisconsin woodlots over a 50 year period. We used Cohen's Kappa as a measure of agreement and assessed significance using a z-test.

Species	Cohen's kappa	z-score	p-val
Positive agreement			
Ovenbird	0.2785	2.4793	0.0132
Blue-gray Gnatcatcher	0.4124	2.5922	0.0095
Negative agreement			
American Goldfinch	-0.108	-2.0149	0.0439
Undetermined			
Northern Bobwhite	0	0	1
Ruffed Grouse	0	0	1
Ring-necked Pheasant	0	0	1
Wild Turkey	0	0	1
Mourning Dove	0	0	1
Cooper's Hawk	0.0788	0.4857	0.6272
Red-tailed Hawk	-0.2202	-1.3784	0.1681
Red-shouldered Hawk	-0.0411	-0.2967	0.7667
Broad-winged Hawk	0	0	1
Barred Owl	-0.0472	-0.4388	0.6608
Great Horned Owl	-0.0556	-0.3425	0.732
Yellow-billed Cuckoo	-0.1484	-0.9351	0.3497
Black-billed Cuckoo	-0.0472	-0.4388	0.6608
Hairy Woodpecker	0.0836	0.5412	0.5884
Downy Woodpecker	0.1493	1.1773	0.2391
Pileated Woodpecker	0	0	1
Red-headed Woodpecker	0.0539	0.3367	0.7363
Red-bellied Woodpecker	-0.0296	-0.3381	0.7353
Northern Flicker	0.0745	0.5734	0.5664
Ruby-throated Hummingbird	-0.0704	-0.4505	0.6523
Great Crested Flycatcher	-0.0683	-0.4734	0.6359
Eastern Phoebe	0	0	1
Eastern Wood-Pewee	N/A	N/A	N/A
Acadian Flycatcher	0.2785	1.7686	0.077
Alder Flycatcher	0	0	1
Least Flycatcher	0	0	1
Blue Jay	-0.0483	-0.4816	0.6301
American Crow	0.1034	1.0898	0.2758

Brown-headed Cowbird	0	0	1
Red-winged Blackbird	0	0	1
Baltimore Oriole	0.0526	0.3816	0.7028
House Finch	0	0	1
Chipping Sparrow	0	0	1
Field Sparrow	0	0	1
Song Sparrow	0	0	1
Eastern Towhee	-0.0459	-0.3945	0.6932
Northern Cardinal	0	0	1
Rose-breasted Grosbeak	-0.0403	-0.2586	0.796
Indigo Bunting	-0.024	-0.1571	0.8752
Scarlet Tanager	0.0306	0.2047	0.8378
Cedar Waxwing	0	0	1
Red-eyed Vireo	0	0	1
Yellow-throated Vireo	0.1972	1.2615	0.2071
Blue-headed Vireo	0	0	1
Blue-winged Warbler	0	0	1
Cerulean Warbler	0.0692	0.607	0.5438
Chestnut-sided Warbler	0	0	1
Black-throated Green Warbler	0	0	1
Mourning Warbler	0	0	1
Common Yellowthroat	0	0	1
Hooded Warbler	0	0	1
American Redstart	0.1915	1.2906	0.1969
Gray Catbird	0.0952	0.6003	0.5483
House Wren	-0.0186	-0.3129	0.7544
White-breasted Nuthatch	-0.0411	-0.2967	0.7667
Tufted Titmouse	0.3342	2.4937	0.0126
Black-capped Chickadee	0.0526	0.6016	0.5475
Wood Thrush	0	0	1
Veery	-0.1176	-0.7252	0.4683
American Robin	0	0	1

Table 3: Relative abundance of avian species averaged over 38 sites sampled in the 1950s and 2006, and significance test for difference (paired permutation test, 10,000 runs) results.

species	mean rel. abund. 1950s	mean rel. abund. 2006	2-s. p-val
Increasing			
Wild Turkey	0.0000	0.0084	0.0020
Mourning Dove	0.0000	0.0086	0.0005
Hairy Woodpecker	0.0134	0.0205	0.0333
Pileated Woodpecker	0.0000	0.0030	0.0156
Red-bellied Woodpecker	0.0124	0.0321	0.0003
Northern Flicker	0.0045	0.0117	0.0149
American Crow	0.0141	0.0301	0.0010
American Goldfinch	0.0009	0.0284	0.0000
Chipping Sparrow	0.0000	0.0052	0.0313
Northern Cardinal	0.0096	0.0576	0.0000
Cedar Waxwing	0.0000	0.0135	0.0000
House Wren	0.0014	0.0385	0.0000
Tufted Titmouse	0.0064	0.0132	0.0470
Black-capped Chickadee	0.0144	0.0492	0.0000
American Robin	0.0000	0.0400	0.0000
Decreasing			
Great Crested Flycatcher	0.0474	0.0286	0.0076
Eastern Wood-Pewee	0.1181	0.0700	0.0000
Least Flycatcher	0.0162	0.0000	0.0001
Brown-headed Cowbird	0.0614	0.0322	0.0000
Baltimore Oriole	0.0139	0.0041	0.0040
Scarlet Tanager	0.0443	0.0301	0.0423
Red-eyed Vireo	0.1740	0.0986	0.0000
Cerulean Warbler	0.0262	0.0028	0.0001
Ovenbird	0.1070	0.0323	0.0000
American Redstart	0.0411	0.0123	0.0007
Undetermined			
Northern Bobwhite	0.0000	0.0009	1.0000
Ruffed Grouse	0.0010	0.0000	1.0000
Ring-necked Pheasant	0.0000	0.0004	1.0000
Cooper's Hawk	0.0029	0.0020	0.5820
Red-tailed Hawk	0.0040	0.0042	0.9579
Red-shouldered Hawk	0.0018	0.0011	0.7500

Broad-winged Hawk	0.0000	0.0015	0.2500
Barred Owl	0.0004	0.0026	0.0781
Great Horned Owl	0.0010	0.0007	0.7500
Yellow-billed Cuckoo	0.0122	0.0152	0.4151
Black-billed Cuckoo	0.0042	0.0007	0.0938
Downy Woodpecker	0.0188	0.0262	0.0761
Red-headed Woodpecker	0.0067	0.0043	0.4043
Ruby-throated Hummingbird	0.0091	0.0043	0.1268
Eastern Phoebe	0.0000	0.0025	0.1250
Acadian Flycatcher	0.0092	0.0113	0.5077
Alder Flycatcher	0.0000	0.0004	1.0000
Blue Jay	0.0412	0.0426	0.8467
Red-winged Blackbird	0.0000	0.0004	1.0000
House Finch	0.0000	0.0003	1.0000
Field Sparrow	0.0000	0.0007	0.5000
Song Sparrow	0.0000	0.0004	1.0000
Eastern Towhee	0.0005	0.0021	0.1875
Rose-breasted Grosbeak	0.0198	0.0263	0.1471
Indigo Bunting	0.0239	0.0342	0.1036
Yellow-throated Vireo	0.0205	0.0132	0.0619
Blue-headed Vireo	0.0000	0.0004	1.0000
Blue-winged Warbler	0.0000	0.0013	0.5000
Chestnut-sided Warbler	0.0000	0.0023	0.0625
Black-throated Green Warbler	0.0000	0.0037	0.0625
Mourning Warbler	0.0000	0.0010	0.5000
Common Yellowthroat	0.0000	0.0010	0.5000
Hooded Warbler	0.0000	0.0053	0.0625
Gray Catbird	0.0050	0.0085	0.2167
White-breasted Nuthatch	0.0410	0.0489	0.1320
Blue-gray Gnatcatcher	0.0271	0.0289	0.6716
Wood Thrush	0.0203	0.0267	0.2682
Veery	0.0027	0.0025	0.9141

Table 4: Mean site-level absolute abundance by species in 2006, 1950s abundance under 3 sampling effort assumptions, and significance test for difference (paired permutation test, 10,000 runs) results. The 100% scenario compares Bond's (1957) observed abundances to those in 2006. For the 125% and 50% scenarios, we multiplied Bond's (1957) abundances by 80% and 200% respectively, which represent estimates of the abundances that Bond would have observed had his sampling effort been equal to our 2006 sampling effort. The 125% scenario is a conservative assumption for assessing a significant decrease in abundance, while the 50% scenario is a conservative assumption for assessing significant increases (significant conservative results are in bold).

Bond's (1957) assumed effort (percent of 2006 sampling):		125% (conservative for assessing decrease)			100%			50% (conservative for assessing increase)		
Species	mean abund 2006	80% abund 1950s	dir	2-sided p-value	mean abund 1950s	dir	2-s. p-val	200% abund 1950s	dir	2-sided p-value
Increasing										
Wild Turkey	0.47	0	inc	0.0020	0	inc	0.0020	**0**	**inc**	**0.0020**
Mourning Dove	0.45	0	inc	0.0005	0	inc	0.0005	**0**	**inc**	**0.0005**
Pileated Woodpecker	0.18	0	inc	0.0156	0	inc	0.0156	**0**	**inc**	**0.0156**
American Goldfinch	1.58	0.04	inc	<0.0001	0.05	inc	<0.0001	**0.11**	**inc**	**<0.0001**
Chipping Sparrow	0.32	0	inc	0.0313	0	inc	0.0313	**0**	**inc**	**0.0313**
Northern Cardinal	3.11	0.38	inc	<0.0001	0.47	inc	<0.0001	**0.95**	**inc**	**<0.0001**
Cedar Waxwing	0.74	0	inc	<0.0001	0	inc	<0.0001	**0**	**inc**	**<0.0001**
House Wren	1.92	0.04	inc	<0.0001	0.05	inc	<0.0001	**0.11**	**inc**	**<0.0001**
Black-cap. Chickadee	2.95	0.55	inc	<0.0001	0.68	inc	<0.0001	**1.37**	**inc**	**0.0012**
American Robin	2.18	0	inc	<0.0001	0	inc	<0.0001	**0**	**inc**	**<0.0001**
Decreasing										
Eastern Wood-Pewee	3.95	**4.48**	**dec**	**0.0121**	5.61	dec	<0.0001	11.21	dec	<0.0001
Least Flycatcher	0	**0.67**	**dec**	**0.0001**	0.84	dec	0.0001	1.68	dec	0.0001
Baltimore Oriole	0.24	**0.55**	**dec**	**0.0229**	0.68	dec	0.0085	1.37	dec	0.0001
Cerulean Warbler	0.21	**1.16**	**dec**	**0.0004**	1.45	dec	0.0003	2.89	dec	<0.0001
Ovenbird	1.89	**4.19**	**dec**	**<0.0001**	5.24	dec	<0.0001	10.47	dec	<0.0001
American Redstart	0.82	**1.89**	**dec**	**0.0279**	2.37	dec	0.0073	4.74	dec	0.0001
Undetermined										
Northern Bobwhite	0.05	0	inc	1	0	inc	1	0	inc	1.0000
Ruffed Grouse	0	0.04	dec	1	0.05	dec	1	0.11	dec	1.0000
Ring-neck. Pheasant	0.03	0	inc	1	0	inc	1	0	inc	1.0000
Cooper's Hawk	0.13	0.11	inc	0.7305	0.13	nc	1.2734	0.26	dec	0.3945
Red-tailed Hawk	0.26	0.15	inc	0.4108	0.18	inc	0.7032	0.37	dec	0.6895
Red-shoulder. Hawk	0.05	0.06	dec	1	0.08	dec	1	0.16	dec	0.6250
Broad-winged Hawk	0.11	0	inc	0.25	0	inc	0.25	0	inc	0.2500
Barred Owl	0.18	0.02	inc	0.0313	0.03	inc	0.1094	0.05	inc	0.2813
Great Horned Owl	0.05	0.04	inc	0.75	0.05	nc	1.375	0.11	dec	0.7500

Yellow-bill. Cuckoo	0.76	0.44	inc	0.0503	0.55	inc	0.2851	1.11	dec	0.2157
Black-billed Cuckoo	0.05	0.13	dec	0.3594	0.16	dec	0.3594	0.32	dec	0.1250
Hairy Woodpecker	1.21	0.51	inc	0.0001	0.63	inc	0.0023	1.26	dec	0.8983
Downy Woodpecker	1.58	0.69	inc	0.0002	0.87	inc	0.0055	1.74	dec	0.7108
Red-hd. Woodpecker	0.26	0.25	inc	0.9801	0.32	dec	0.8606	0.63	dec	0.1343
Red-bel. Woodpecker	1.84	0.48	inc	<0.0001	0.61	inc	0.0001	1.21	inc	0.1114
Northern Flicker	0.58	0.17	inc	0.0018	0.21	inc	0.0112	0.42	inc	0.4683
Ruby-thr. Hmngbrd.	0.26	0.34	dec	0.5942	0.42	dec	0.3667	0.84	dec	0.0269
Great Crst. Flycatcher	1.61	1.77	dec	0.5967	2.21	dec	0.0846	4.42	dec	<0.0001
Eastern Phoebe	0.13	0	inc	0.125	0	inc	0.125	0	inc	0.1250
Acadian Flycatcher	0.71	0.4	inc	0.0816	0.5	inc	0.3313	1	dec	0.4129
Alder Flycatcher	0.03	0	inc	1	0	inc	1	0	inc	1.0000
Blue Jay	2.39	1.54	inc	0.0081	1.92	inc	0.2041	3.84	dec	0.0205
American Crow	1.66	0.53	inc	0.0001	0.66	inc	0.0013	1.32	inc	0.4745
Brown-hd. Cowbird	1.95	2.25	dec	0.3123	2.82	dec	0.0116	5.63	dec	<0.0001
Red-wing. Blackbird	0.03	0	inc	1	0	inc	1	0	inc	1.0000
House Finch	0.03	0	inc	1	0	inc	1	0	inc	1.0000
Field Sparrow	0.05	0	inc	0.5	0	inc	0.5	0	inc	0.5000
Song Sparrow	0.03	0	inc	1	0	inc	1	0	inc	1.0000
Eastern Towhee	0.16	0.02	inc	0.0625	0.03	inc	0.1875	0.05	inc	0.4063
Rose-brstd. Grosbeak	1.55	0.78	inc	0.0028	0.97	inc	0.035	1.95	dec	0.3050
Indigo Bunting	1.87	0.88	inc	0.004	1.11	inc	0.0405	2.21	dec	0.5114
Scarlet Tanager	1.84	1.75	inc	0.7704	2.18	dec	0.3487	4.37	dec	<0.0001
Red-eyed Vireo	5.63	6.29	dec	0.2638	7.87	dec	0.0018	15.74	dec	<0.0001
Yellow-throat. Vireo	0.82	0.86	dec	0.8367	1.08	dec	0.2869	2.16	dec	0.0004
Blue-headed Vireo	0.03	0	inc	1	0	inc	1	0	inc	1.0000
Blue-winged Warbler	0.11	0	inc	0.5	0	inc	0.5	0	inc	0.5000
Chestnut-sid. Warbler	0.16	0	inc	0.0625	0	inc	0.0625	0	inc	0.0625
Blk.-th. Grn. Warbler	0.26	0	inc	0.0625	0	inc	0.0625	0	inc	0.0625
Mourning Warbler	0.05	0	inc	0.5	0	inc	0.5	0	inc	0.5000
Common Yellowthrt.	0.08	0	inc	0.5	0	inc	0.5	0	inc	0.5000
Hooded Warbler	0.32	0	inc	0.0625	0	inc	0.0625	0	inc	0.0625
Gray Catbird	0.53	0.21	inc	0.0377	0.26	inc	0.1235	0.53	nc	1.1062
White-br. Nuthatch	2.87	1.58	inc	0.0002	1.97	inc	0.011	3.95	dec	0.0208
Tufted Titmouse	0.76	0.29	inc	0.0023	0.37	inc	0.0257	0.74	inc	1.0000
Blu.-gry. Gnatcatcher	1.82	1.14	inc	0.0124	1.42	inc	0.1706	2.84	dec	0.0122
Wood Thrush	1.55	0.86	inc	0.0268	1.08	inc	0.177	2.16	dec	0.2448
Veery	0.16	0.13	inc	0.8359	0.16	nc	1.1563	0.32	dec	0.5859

Table 5: Mean site-level absolute abundance by ecological guild and entire community in 2006, 1950s abundance under 3 sampling effort assumptions, and significance test for difference (paired permutation test, 10,000 runs) results. The 100% scenario compares Bond's (1957) observed abundances to those in 2006. For the 125% and 50% scenarios, we multiplied Bond's (1957) abundances by 80% and 200% respectively, which represent estimates of the abundances that Bond would have observed had his sampling effort been equal to our 2006 sampling effort. The 125% scenario is a conservative assumption for assessing a significant decrease in abundance, while the 50% scenario is a conservative assumption for assessing a significant increase.

Bond's (1957) assumed effort (percent of 2006):		125% (conservative for assessing decrease)			100%			50% (conservative for assessing increase)		
Ecological Guild	mean abund 2006	80% abund 1950s	dir	2-sided p-value	mean abund 1950s	dir	2-sided p-value	200% abund 1950s	dir	2-sided p-value
Habitat use										
Woodland (W)	36.58	31.62	inc	0.0197	39.53	dec	0.1840	79.05	dec	<0.0001
Early succ./scrub (ES)	9.71	1.58	inc	<0.0001	1.97	inc	<0.0001	**3.95**	**inc**	**<0.0001**
Urban (U)	5.37	1.54	inc	<0.0001	1.92	inc	<0.0001	**3.84**	**inc**	**0.0223**
Migratory habit										
Neotropical (NT)	29.63	28.97	inc	0.6846	36.21	dec	0.0005	72.42	dec	<0.0001
Short-distance (SD)	12.66	5.12	inc	<0.0001	6.39	inc	<0.0001	12.79	dec	0.9277
Resident (R)	15.11	4.57	inc	<0.0001	5.71	inc	<0.0001	**11.42**	**inc**	**0.0086**
Intersected										
W & NT	24.34	**27.28**	**dec**	**0.0505**	34.11	dec	<0.0001	68.21	dec	<0.0001
W & SD *	0.18	0.17	inc	0.9277	0.21	dec	1.0000	0.42	dec	0.1934
W & R	11.87	4.15	inc	<0.0001	5.18	inc	<0.0001	10.37	inc	0.2219
ES & NT	4.74	1.14	inc	<0.0001	1.42	inc	<0.0001	**2.84**	**inc**	**0.0141**
ES & SD	1.82	0.06	inc	<0.0001	0.08	inc	<0.0001	**0.16**	**inc**	**<0.0001**
ES & R	3.16	0.38	inc	<0.0001	0.47	inc	<0.0001	**0.95**	**inc**	**<0.0001**
U & NT **	0.32	0.00	inc	0.0313	0.00	inc	0.0313	**0.00**	**inc**	**0.0313**
U & SD	5.05	1.54	inc	<0.0001	1.92	inc	<0.0001	3.84	inc	0.0740
U & R	No species in this guild									
Entire community										
All species	57.58	38.67	inc	0.0021	48.34	inc	0.0000	96.68	dec	<0.0001

* only 2 species in guild: Cooper's Hawk and Red-shouldered Hawk

** only 1 species in guild: Chipping Sparrow

Table 6: Pearson and Kendall correlations between species and NMDS ordination axes, n = 76. Species in bold are those whose relative abundance changed significantly from the early 1950s to 2006 at 38 forest sites in southern WI.

Axis:	1		2		3	
species	r	tau	r	tau	r	tau
Wild Turkey	0.382	0.301	-0.146	-0.130	-0.163	-0.092
Mourning Dove	0.336	0.293	-0.299	-0.218	-0.130	-0.066
Cooper's Hawk	-0.065	-0.004	0.227	0.179	0.238	0.200
Red-tailed Hawk	0.082	0.090	-0.187	-0.175	-0.128	-0.094
Barred Owl	0.140	0.103	-0.105	-0.083	0.196	0.150
Yellow-billed Cuckoo	0.143	0.076	-0.264	-0.137	-0.383	-0.301
Black-billed Cuckoo	-0.252	-0.220	0.233	0.155	-0.215	-0.158
Hairy Woodpecker	0.136	0.037	0.222	0.186	-0.220	-0.155
Downy Woodpecker	0.268	0.200	-0.052	-0.011	-0.055	-0.019
Pileated Woodpecker	0.295	0.230	-0.034	0.004	-0.139	-0.089
Red-headed Woodpecker	0.009	0.008	-0.243	-0.139	0.117	0.118
Red-bellied Woodpecker	0.482	0.356	-0.209	-0.104	-0.134	-0.072
Northern Flicker	0.412	0.299	-0.374	-0.294	-0.302	-0.224
Ruby-throated Hummingbird	-0.247	-0.162	0.176	0.124	0.257	0.211
Great Crested Flycatcher	-0.328	-0.217	0.209	0.159	-0.321	-0.220
Eastern Wood-Pewee	-0.735	-0.534	0.072	0.052	-0.054	-0.030
Acadian Flycatcher	0.002	0.034	0.230	0.178	0.423	0.394
Least Flycatcher	-0.363	-0.339	0.154	0.107	0.369	0.230
Blue Jay	0.071	0.127	-0.546	-0.404	-0.447	-0.295
American Crow	0.352	0.333	0.238	0.151	-0.255	-0.134
Brown-headed Cowbird	-0.579	-0.406	-0.017	-0.059	-0.016	0.004
Baltimore Oriole	-0.161	-0.104	-0.485	-0.429	-0.179	-0.066
American Goldfinch	0.514	0.432	0.309	0.179	0.139	0.116
Chipping Sparrow	0.201	0.216	0.266	0.177	0.267	0.202
Eastern Towhee	0.177	0.132	-0.249	-0.200	0.113	0.110
Northern Cardinal	0.799	0.664	-0.138	-0.119	-0.353	-0.239
Rose-breasted Grosbeak	0.256	0.205	-0.666	-0.528	-0.041	-0.012
Indigo Bunting	0.208	0.185	-0.389	-0.285	-0.523	-0.336
Scarlet Tanager	-0.210	-0.134	-0.361	-0.230	0.139	0.108
Cedar Waxwing	0.392	0.360	0.206	0.135	-0.190	-0.154
Red-eyed Vireo	-0.662	-0.518	0.624	0.472	-0.059	0.051
Yellow-throated Vireo	-0.138	-0.100	-0.124	-0.055	0.467	0.345
Cerulean Warbler	-0.441	-0.343	0.140	0.084	0.403	0.410
Chestnut-sided Warbler	0.144	0.125	0.104	0.121	0.155	0.148
Black-throated Green Warbler	0.186	0.189	0.051	-0.003	0.204	0.136
Ovenbird	-0.698	-0.544	0.267	0.170	0.394	0.316
Hooded Warbler	0.080	0.126	0.271	0.172	0.081	0.158
American Redstart	-0.232	-0.146	-0.139	-0.169	0.635	0.528
Gray Catbird	0.180	0.130	-0.485	-0.373	-0.141	-0.032
House Wren	0.559	0.531	0.014	-0.041	-0.509	-0.365

White-breasted Nuthatch	0.175	0.119	-0.258	-0.187	0.058	0.027
Tufted Titmouse	0.295	0.248	-0.268	-0.222	0.035	0.128
Black-capped Chickadee	0.633	0.492	0.113	0.035	-0.012	-0.016
Blue-gray Gnatcatcher	0.015	-0.057	0.167	0.135	0.331	0.196
Wood Thrush	0.172	0.155	-0.328	-0.258	0.219	0.198
Veery	0.046	0.056	-0.038	-0.052	-0.046	0.028
American Robin	0.734	0.616	0.015	-0.009	-0.131	-0.120

Figures

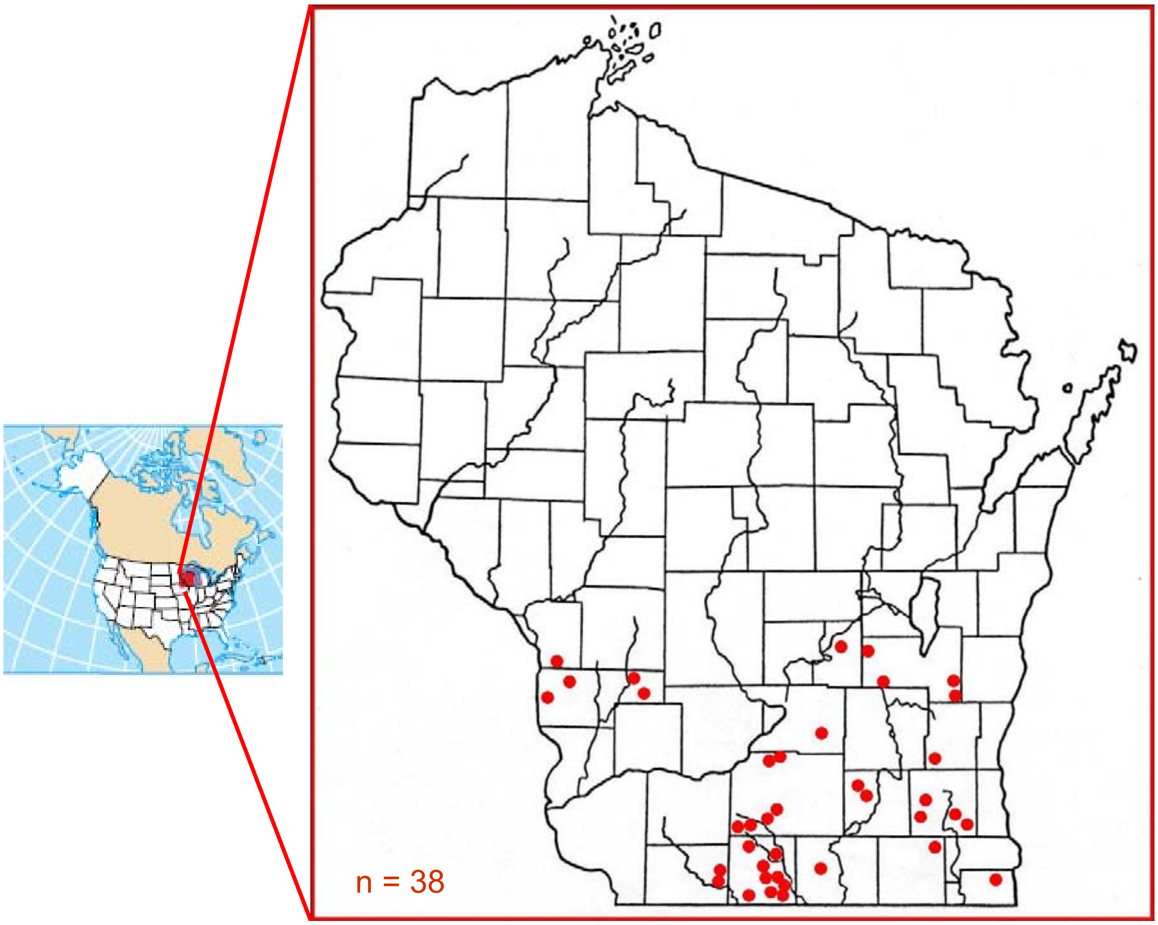
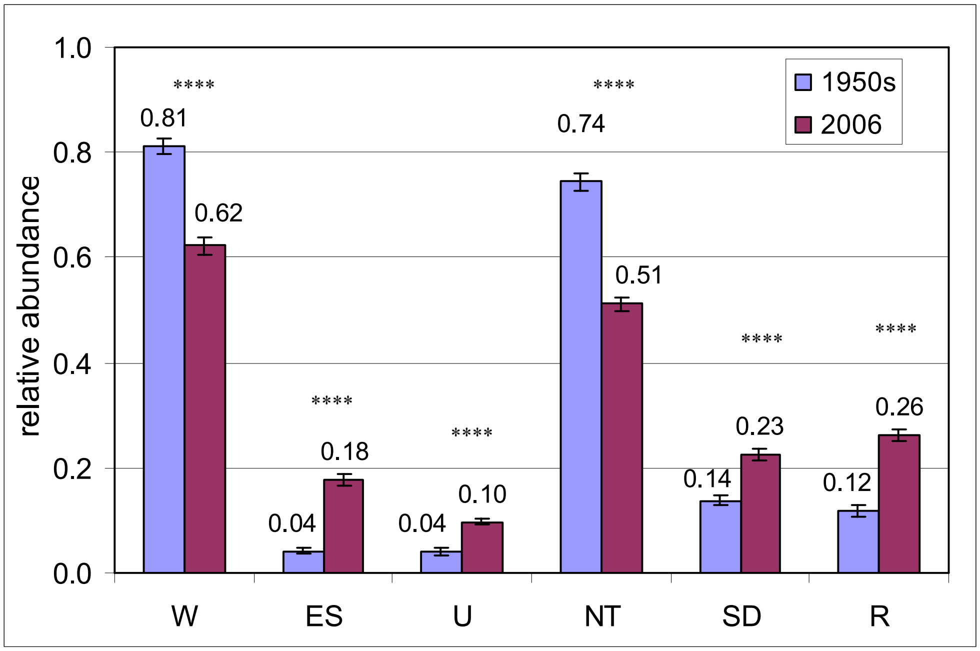
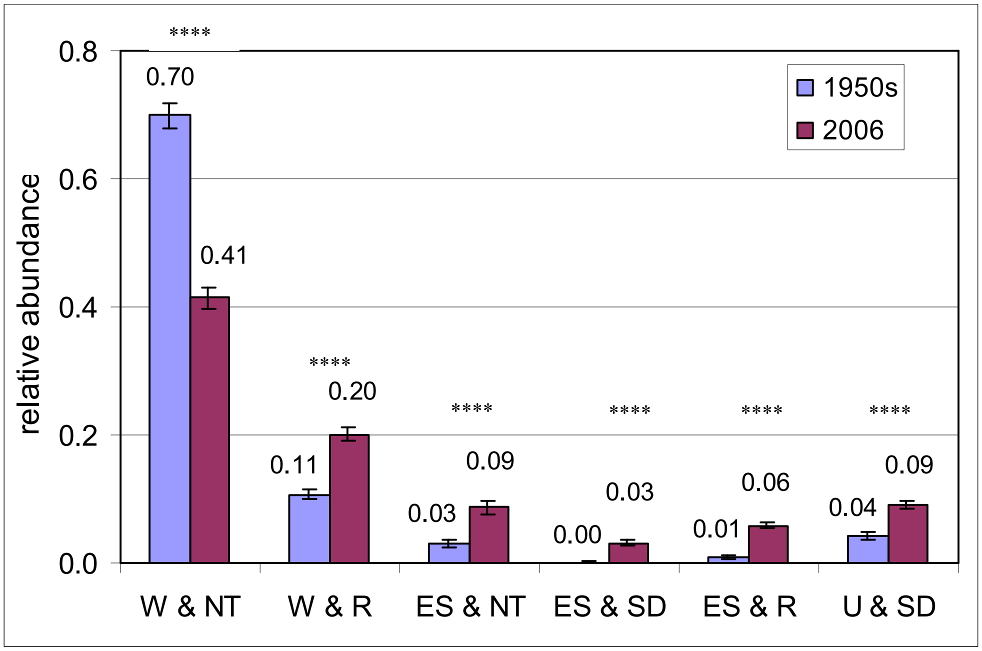


Figure 1. Study site locations. We conducted bird surveys at 38 forest sites across southern Wisconsin, USA, replicating surveys conducted at the same sites from 1952-54 (Bond 1957).

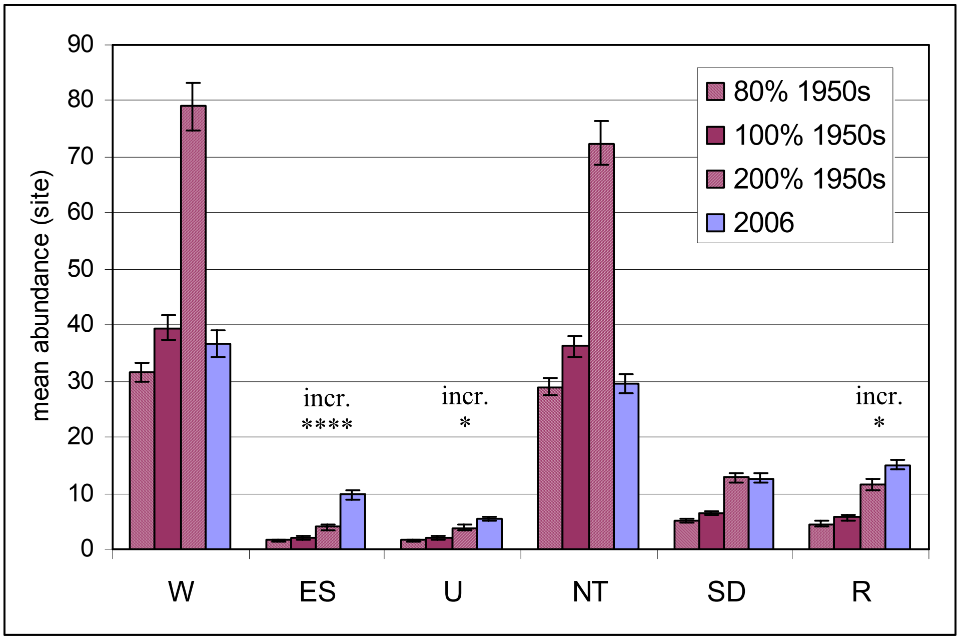


A. Habitat use and migratory habit guilds

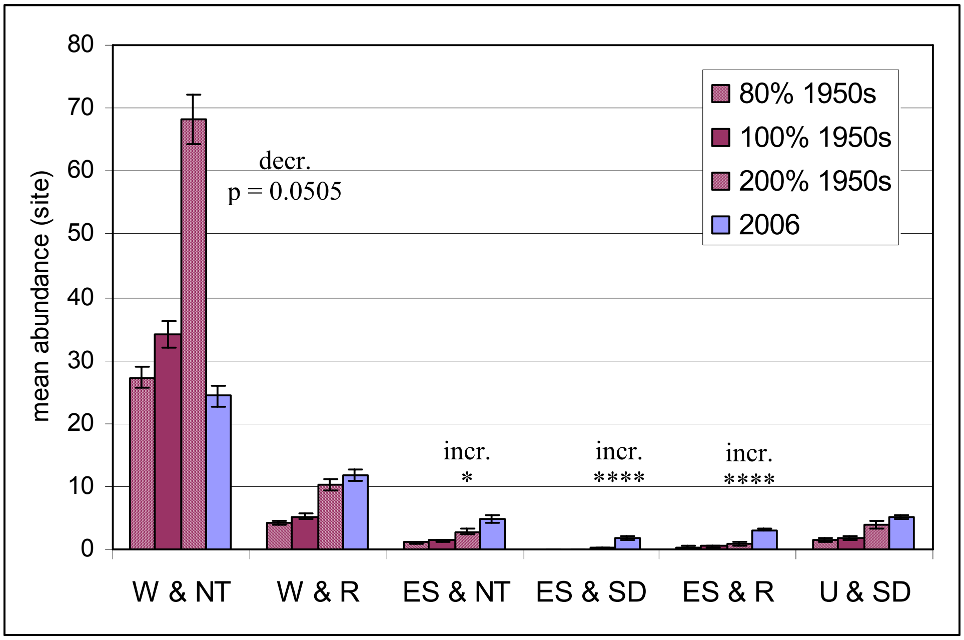


B. Intersected guilds

Figure 2. Relative abundance (+- 1 standard error) of avian ecological guilds averaged over 38 sites sampled in the 1950s and 2006. (A) Habitat use guilds: W: woodland, ES: early succession / scrub, U: urban; Migration form guilds: NT: neotropical migrant, SD: short-distance migrant, R: resident. (B) intersections of habitat use and migratory habit guilds. Paired permutation tests (10,000 runs) of differences between 1950s and 2006 values were highly significant ($p < 0.0001$) for all guilds (A and B).

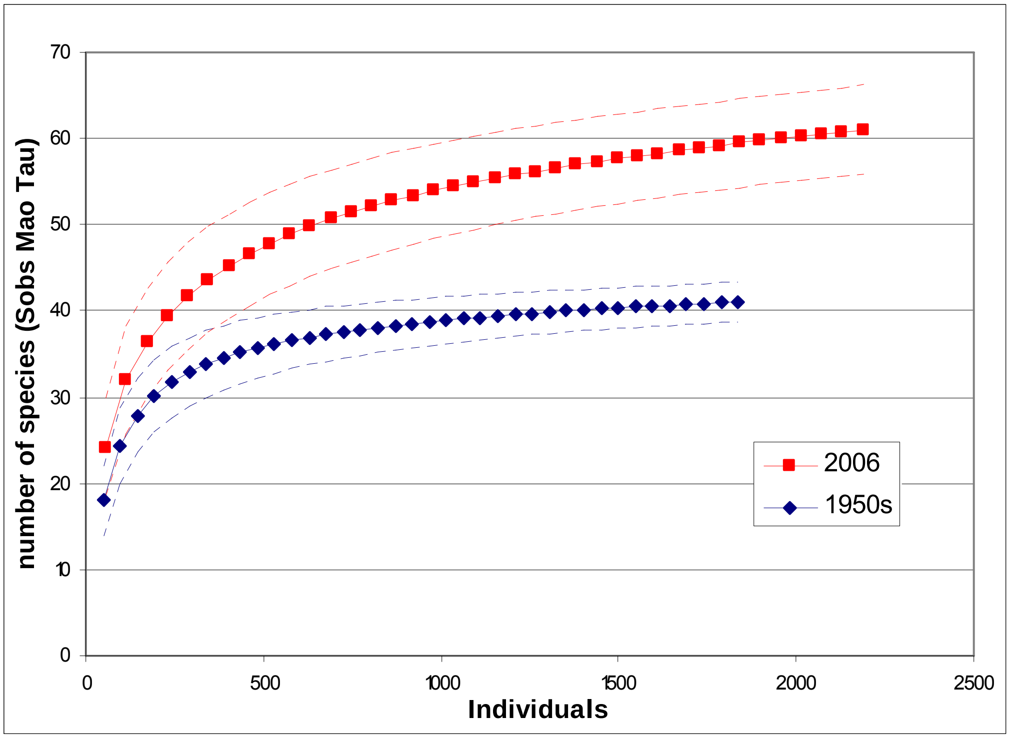


A. Habitat use guilds and migration form guilds

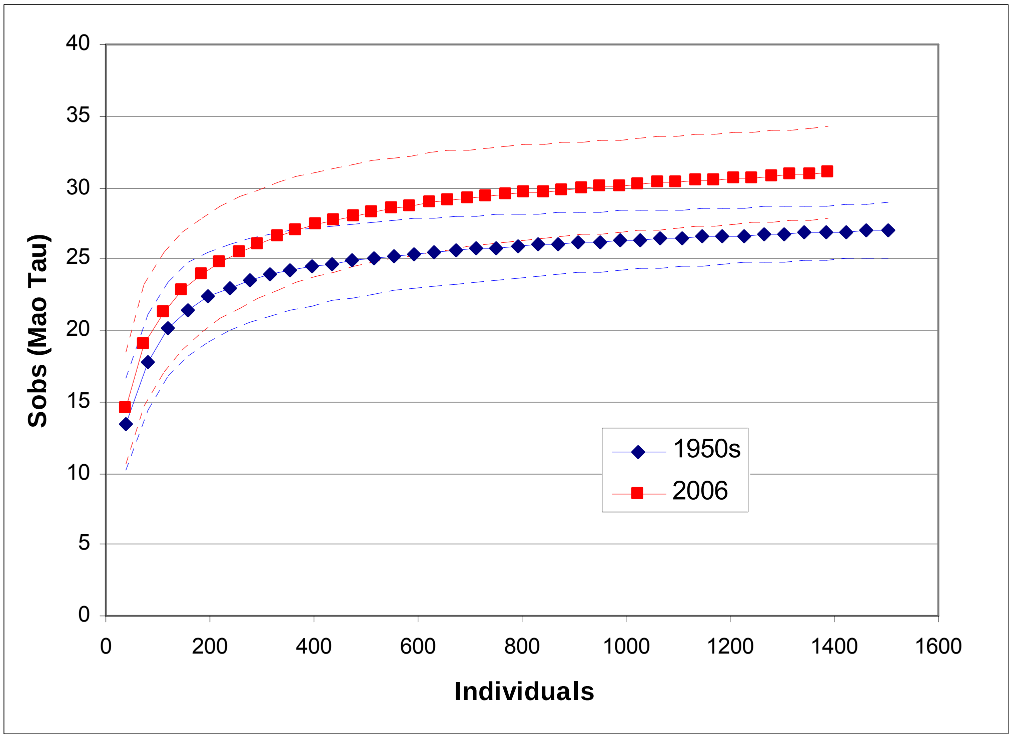


B. Intersected guilds

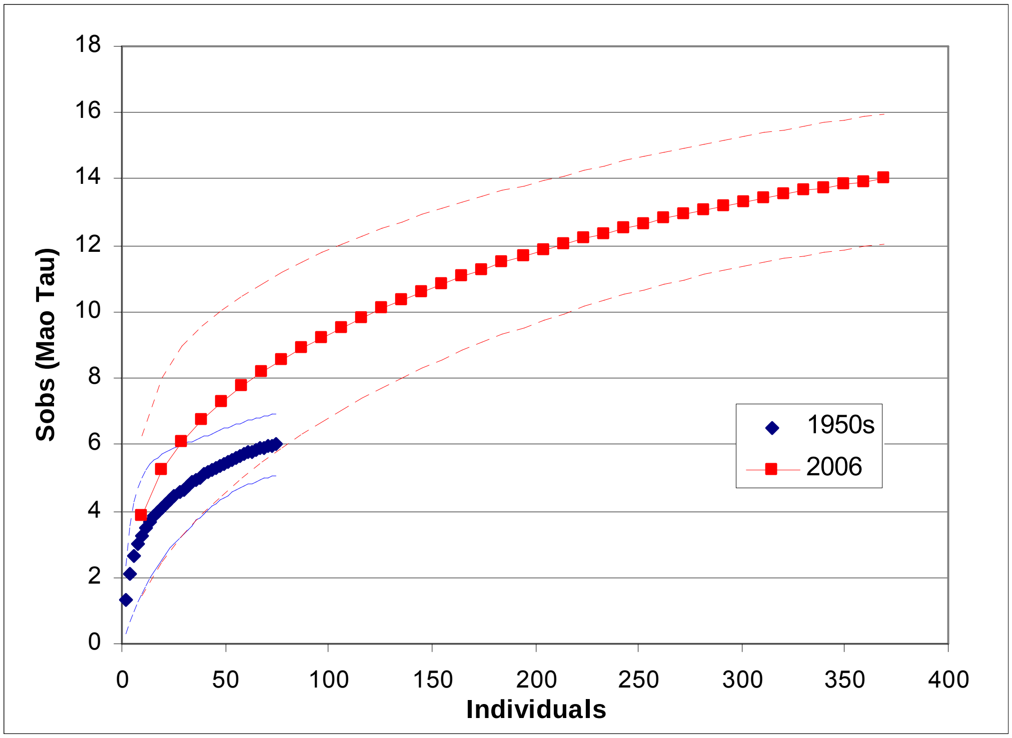
Figure 3. Mean site-level abundance (+- 1 standard error) within avian ecological guilds averaged over 38 sites sampled in the 1950s and 2006. Because 1950s sample effort was uncertain, we scaled Bond's (1957) abundances assuming that it was 25% more than, equal to, and half of 2006 sampling effort. (A) Habitat and migratory habit guilds: W: woodland, ES: early succession / scrub, U: urban; Migration form guilds: NT: neotropical migrant, SD: short-distance migrant, R: resident. (B) Intersected habitat and migratory habit guilds. Table 5 shows paired permutation test results of differences between 1950s and 2006 abundances.



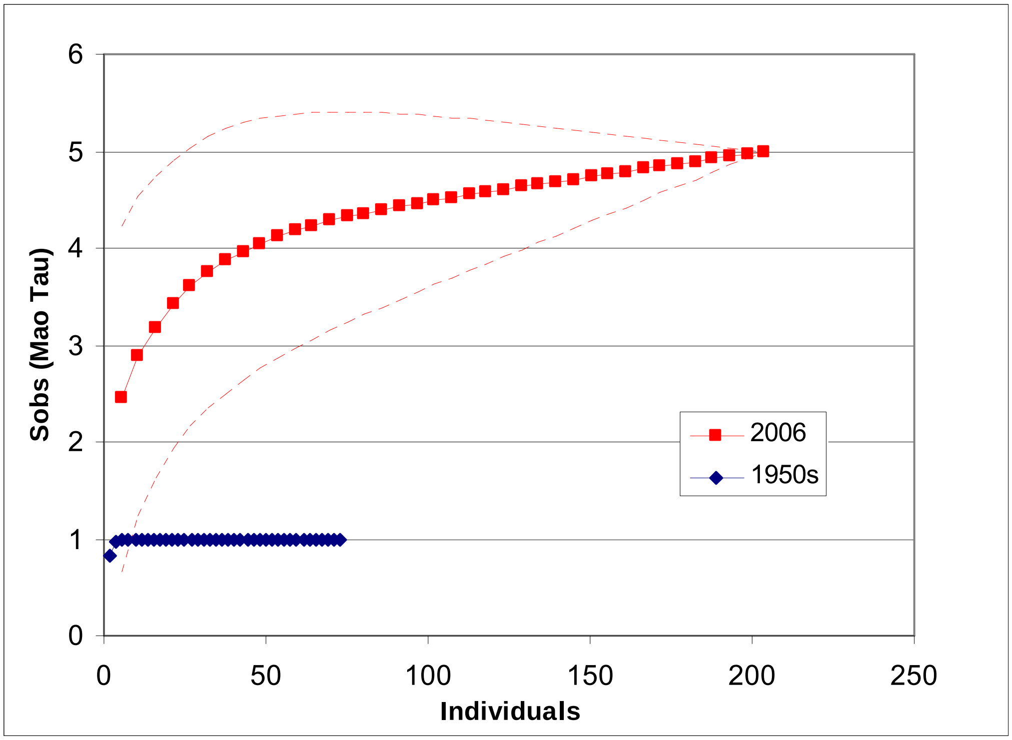
A. Entire Avian Community



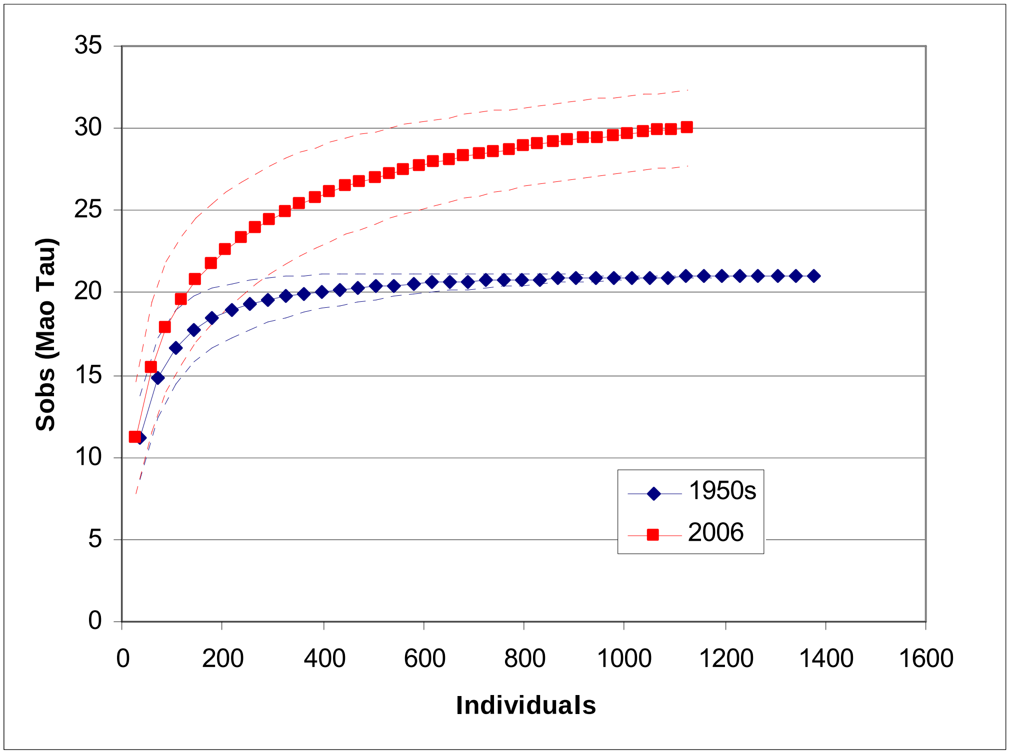
B. Woodland Species



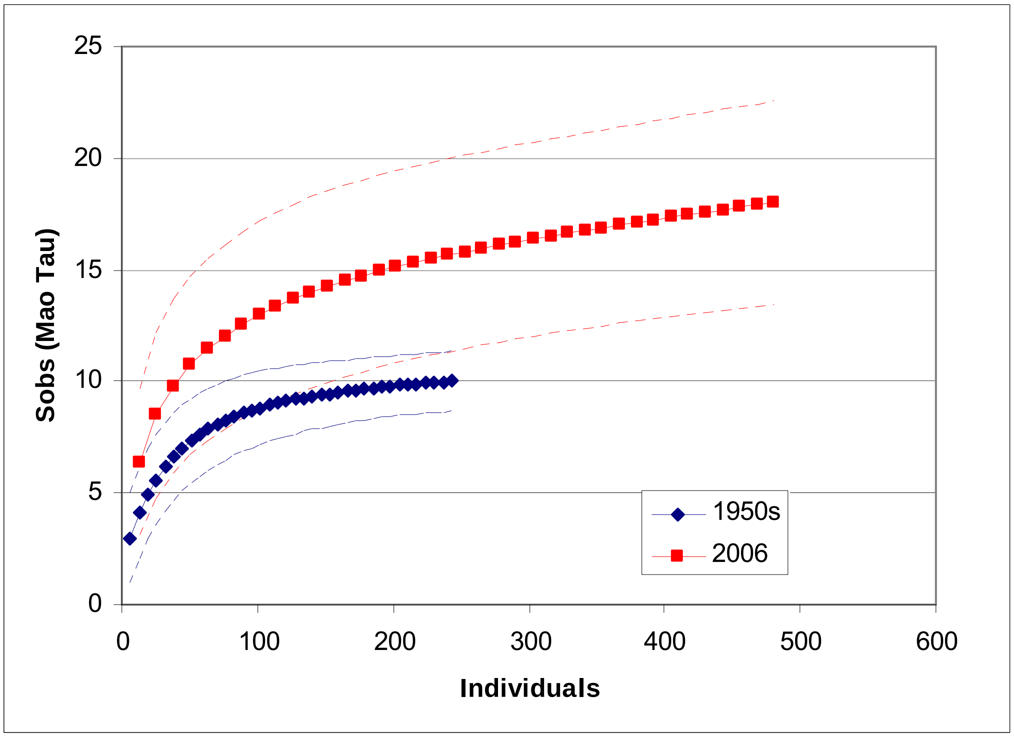
C. Early succession species



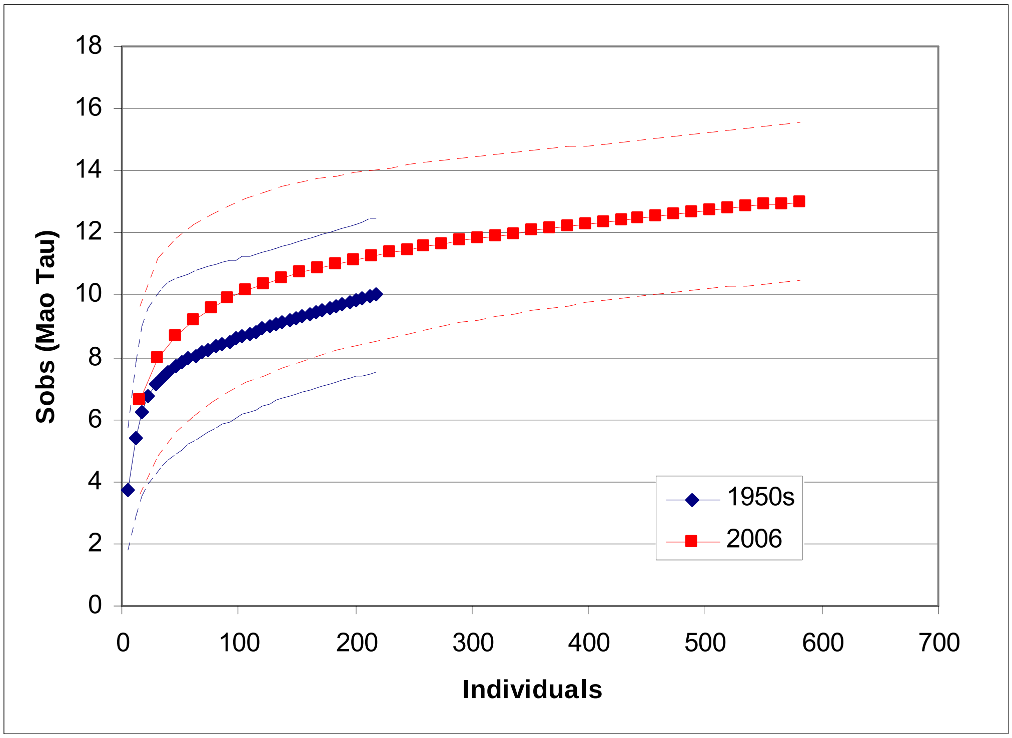
D. Urban species



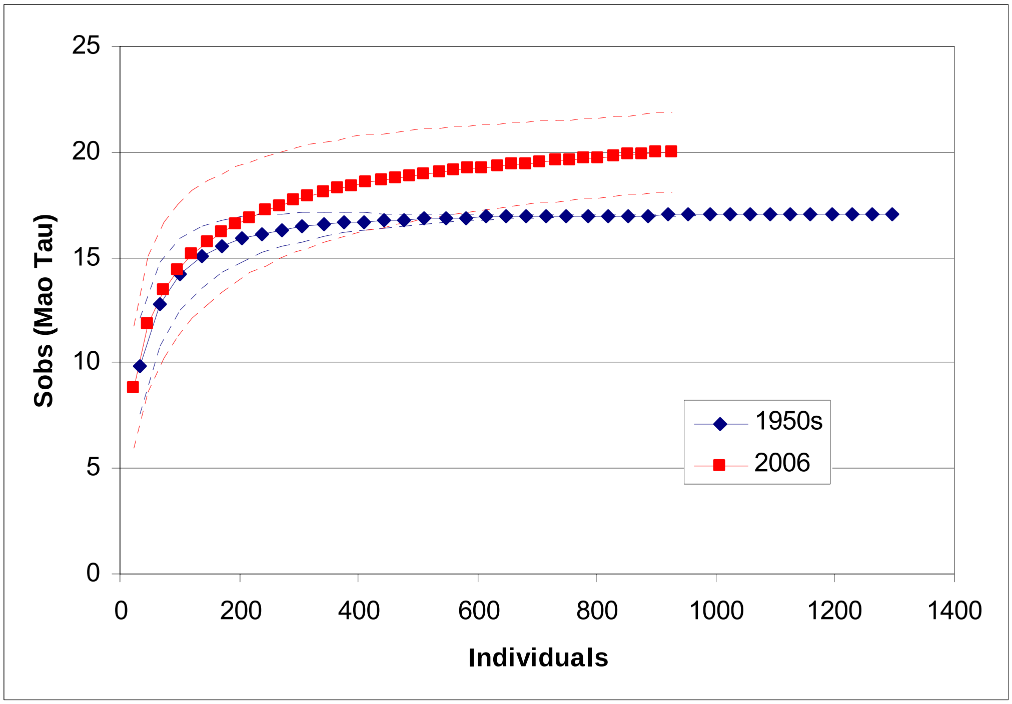
E. Neotropical migrant species



F. Short-distance migrant species

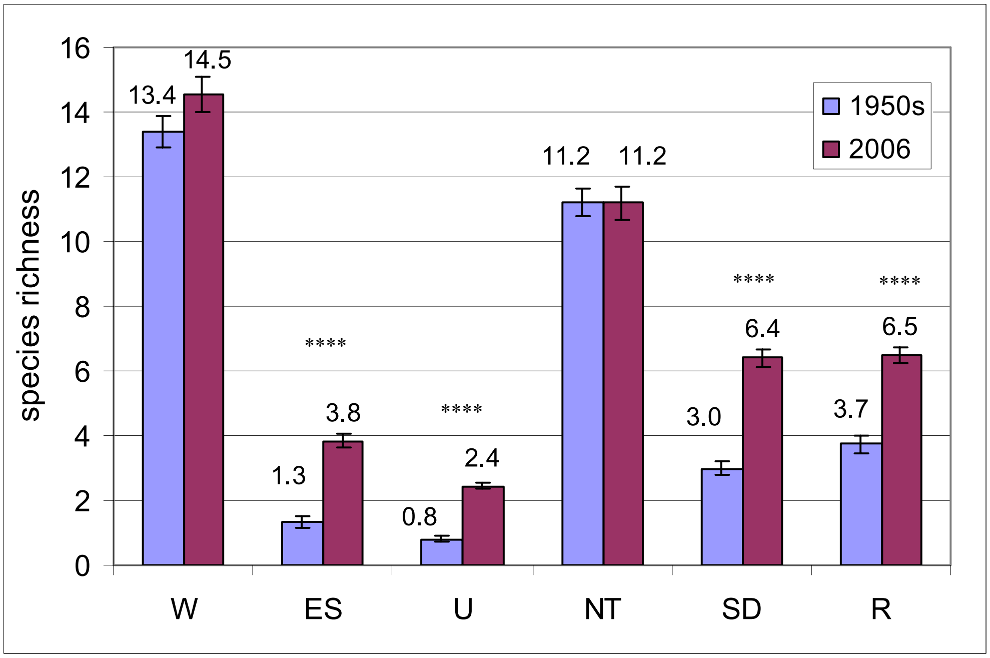


G. Resident species

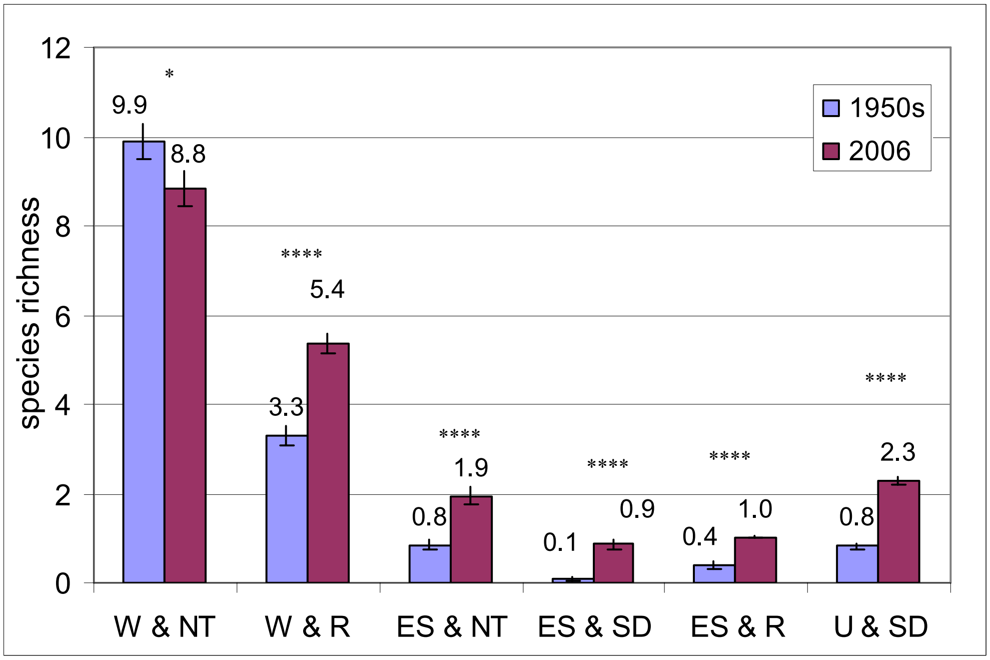


H. Woodland neotropical migrant species

Figure 4: Sample-based rarefaction curves for 1950s and 2006, scaled by number of individuals, for (A) avian community, (B,C,D) habitat preference guilds, (E,F,G) migratory habit guilds, and (H) woodland neotropical migrant species. Dashed lines indicate 95% confidence intervals. Curves created with EstimateS software v.8 (Colwell 2006).



A. Habitat use and migratory habit guilds



B. Intersected guilds

Figure 5. Species richness (+- 1 standard error) within avian ecological guilds averaged over 38 sites sampled in the 1950s and 2006. (A) Habitat use guilds: W: woodland, ES: early succession / scrub, U: urban; Migration form guilds: NT: neotropical migrant, SD: short-distance migrant, R: resident. (B) Intersected habitat use and migratory habit guilds. Paired permutation tests of differences between 1950s and 2006 values were highly significant ($p < 0.0001$) for all guilds except for W ($p = 0.0693$), NT ($p > 0.5$) and W & NT ($p = 0.0244$).

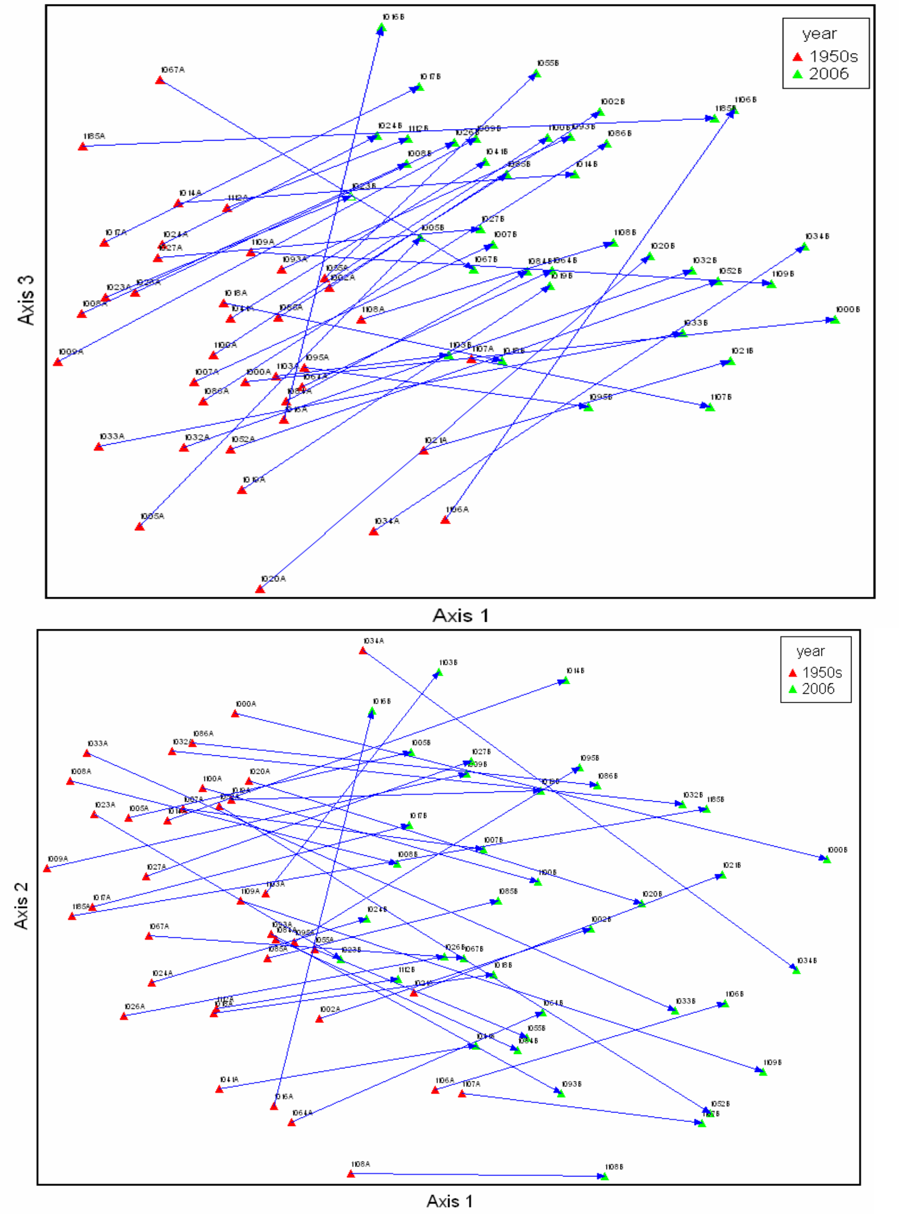


Figure 6: NMDS Ordination Plots for Avian communities at 38 sites in southern WI in the early 1950s and 2006. We first removed data from the species in which fewer than five individuals were detected in all surveys, and standardized the community matrix values by the total number of birds detected at each site, i.e. the proportional abundance of a given species at a given site. Ordination was performed using PC-ORD software v.5.0 (Clarke 1993, McCune & Mefford 1999, method from Mather 1976 and Kruskal 1964) with Sorenson's (Bray-Curtis) distance measure for the original dissimilarity matrix. Algorithm included 250 runs of real data with random starting configurations, 250 Monte Carlo runs of randomized data, and 120 iterations for the final solution. We examined the NMS scree plot to determine the final number (3) of axes to accept. Axes 1, 2, and 3 represented 52.9%, 13.7% and 18.3% of the original variance, respectively. Arrows indicate community change trajectories at each site between 1950s and 2006.

CHAPTER 2: INFLUENCES OF HABITAT CHANGE AND ECOLOGICAL PROCESSES ON AVIAN COMMUNITY DYNAMICS

Introduction

In North America forest habitats are increasingly affected by human development (Brown et al. 2005, Radeloff et al. 2005). The resulting changes to breeding habitats influence avian communities in many ways. Forest loss and fragmentation reduce the amount of forest and the size of forest patches, while increasing isolation among patches. These changes alter habitat availability, connectivity, and suitability (Andrén 1994). Increased forest edge density increases risks of brood parasitism by Brown-headed Cowbirds (Brittingham & Temple 1983, Wilcove 1985, Temple & Cary 1988) and nest predation (Gates & Gysel 1978), and reduces insect prey availability (Burke & Nol 1998).

Widespread housing development influences avian communities through structural habitat changes (Odell 2003), increased mesopredator populations (Crooks & Soule 1999), and homeowner landscaping and feeding activities (Lepczyk et al. 2004). At large spatial scales, housing density influences patterns of avian species richness (Pidgeon et al. 2007). By altering disturbance regimes (Lorimer 2001) and introducing non-native species (Hansen et al. 2005, Maestas et al. 2003), human land use alters vegetation composition even in forest habitats not directly transformed. These changes may alter habitat structure, food availability, and nest success (Rodewald & Abrams 2002, Borgmann & Rodewald 2004). Overall, biotic homogenization accompanies development. Avian generalists and permanent residents become more dominant, while foraging specialists and migrants decline (McKinney 2006).

We know less, however, about how bird communities change in the long-term when there is little new disturbance, but a landscape remains fragmented and settled. Most of the research described above is based on space-for-time substitutions, in which avian communities in disturbed habitats are compared to those in undisturbed habitats, in order to infer the effects of habitat change. Understanding avian dynamics that may result from a variety of long-term temporal phenomena in the absence of dramatic habitat change is challenging, however. It requires either examining many sites with different lengths of time since disturbance, or longitudinal studies that observe changes directly. Full chronosequence studies are very rare, and the number of published long-term avian community records is also limited. The few existing long-term avian studies in fragmented habitats have observed declines in the richness or abundance of forest-dwelling neotropical migrant birds and increases in those that are associated with forest edges and are non-migratory or migrate to temperate winter ranges (e.g., Lynch & Whitcomb 1978, Ambuel & Temple 1982, Leck et al. 1988, Askins 1990). There is a need for more long-term avian studies in fragmented habitats (Andrén 1994).

Ecological theory predicts several potential trends in avian communities of relatively stable fragmented forest habitats, based on alternative hypothesized mechanisms. Five alternative hypotheses potentially apply to avian communities in isolated forest patches in North America include:

1) Source-sink dynamics occur when reproductive success of some species is too low to sustain populations in one habitat (i.e. forest-interior species in small forest fragments), and their continued persistence in these habitats results from ongoing subsidies of individuals from habitats where fecundity is higher (i.e. more forested regions with higher nest success; Temple & Cary 1988, Robinson et al. 1995). Dynamics of these species in source habitats should therefore influence populations in sink habitats. If

source sink dynamics are operating, we would predict that there are relationships between population trends in source and sink areas.

2) Geographic range shifts may influence local abundances of species if their boundaries expand into an area or contract away from an area. Ornithologists have observed changes in the geographic ranges of many North American species (Poole 2005), and several species' geographic ranges appear to have shifted northward, likely as a result of climate change (Hitch & Leberg 2007). If this mechanism is responsible for trends in avian communities, we would predict local increases in species whose observed geographic ranges are expanding into an area and decreases in species whose ranges are moving away.

3) Disease epizootics may cause affected species to decline. West Nile Virus has caused large-scale declines among North American bird populations since its first detection in New York in 1999 (LaDeau et al. 2007). If a disease epizootic influences avian community dynamics we would predict that abundance declines among species that are susceptible to the disease.

4) Migratory species may experience high rates of mortality in non-breeding habitats, particularly woodland neotropical migrant species because of forest destruction and degradation in wintering ranges (e.g., Rappole & McDonald 1994). If non-breeding habitat is the cause of community change, we would predict declines among populations of woodland neotropical migrant species which are not seen in other woodland species or in neotropical species using other habitats, and which are unrelated to breeding habitat factors.

5) The extinction debt hypothesis indicates that previous habitat destruction will cause delayed losses in species richness of remaining habitat patches resulting from metapopulation dynamics and interspecific competition (Tilman et al. 1994). If extinction debt was operating on an avian community we would expect to observe extirpations of species which are unrelated to other factors.

In addition to these five potential causes of avian community change, habitats are not truly static and continue to change over time. Even slow or incremental habitat changes such as forest succession influence bird communities (Holmes & Sherry 2001), so long-term studies should still explicitly consider habitat.

We had a unique opportunity to test these five hypotheses of avian community change using a long-term dataset including birds, vegetation, and landscape conditions of fragmented forests in southern Wisconsin over a 50-year interval. Our objectives were to 1) determine how changes in forest vegetation and landscape configuration influenced long-term avian abundance and species richness in southern Wisconsin fragmented forests, and 2) test the following hypotheses for avian community change by assessing evidence for their corresponding predictions:

1) If a source-sink relationship exists between woodland neotropical migrant populations in the most proximate extensively forested region (northern WI, MN, and MI) and the fragmented forests of our study area, we would expect to find similarities between population trends observed in our study and trends in the northern forests.

2) Geographic range changes should cause increases in species whose observed geographic ranges are expanding into southern Wisconsin and decreases in species whose ranges are moving away from this area.

3) West Nile Virus epizootics should selectively reduce the abundances of susceptible species.

4) If migratory species have experienced high rates of mortality in non-breeding portions of their ranges, we would expect to observe declines among woodland neotropical migrant species that are not shared by other woodland species or neotropical species using other habitats, and that are unrelated to breeding habitat factors in southern Wisconsin forests.

5) Extinction debt should cause reduced species richness in our study sites that is not attributable to other effects.

Methods

Study area

Oak savanna, oak-hickory forest, and maple-basswood forest predominated in southern Wisconsin prior to European settlement. Settlers converted most savanna to agriculture, and due to fire exclusion, oak forest associations replaced any remaining savanna (Peet & Loucks 1977). Agriculture has dominated the landscape since before the 1950s, but housing development is occurring. Study areas were within second-growth forest islands.

Bird surveys

In 2006, we surveyed 38 wooded upland sites (> 6 ha, without recent grazing, extensive logging, or fire) in southern Wisconsin that Bond (1957) surveyed during the early 1950s. Despite subsequent advances in avian sampling theory and practice, we replicated Bond's (1957) field protocol for purposes of comparison. Within each site interior (45m from edge), we recorded all birds seen or heard (except those only flying over) in five sample units: pairs of alternating point and transect counts (infinite radius), each count lasting for five minutes, with transect length averaging 150-175 m. During the breeding season we visited each site twice on days without rain or strong wind: once May 20 – June 14, and once June 8 - July 4. To minimize time-of-day effects, one of the two visits to each site was at dawn and the other later in the morning.

Forest Vegetation Measurements

We collected avian community observations as part of a larger interdisciplinary effort to measure ecological change. Curtis (1959) characterized composition of trees (basal area), shrubs (frequency, 20 quadrats) and under story plants (frequency, twenty 1 m^2 quadrats) from 1951-1954 on the sites where Bond collected avian community data. Rogers et al. (in press) gathered vegetation data comparable to Curtis' on these sites from 2001-2003. They characterized canopy tree composition using succession and moisture-nutrient gradient indices developed by Peet & Loucks (1977). Index values at each site were calculated from species scores (Table 1) along these gradients, weighted by basal areas observed in samples.

Landscape Measurements

We used ArcGIS 9.1 (ESRI, Inc. 2006) to quantify landscape composition in a 1 km radius circular area (3.14 km^2) centered on each study site based on data sources from each time period (Figure 1). We examined a range of radius lengths and found a pattern of decreasing strength of relationship between avian and landscape variables with increasing radius. We selected 1 km because with smaller radii, portions of the survey area were removed from the analysis. For 2006 we obtained forest cover information from the National Land Cover Database 2001 (http://landcover.usgs.gov/uslandcover.php) which is thematic land cover map derived from 2001 Landsat satellite imagery. We used the 'raster to polygon' function included in the ArcGIS 9.1 Spatial Analyst package to create forest patch polygons.

We digitized houses and roads from USGS digital orthophoto quarter quadrangles (USGS 1996) taken between 1992 and 2000. For the 1950s we scanned and orthorectified USGS topographic maps based on aerial photos taken 1951-1963 (USGS 1980). Fortunately, maps with the later dates covered areas that underwent the least landscape change over the study period (personal observation). We digitized forest patch polygons, roads, and houses. Forest cover data from these sources was collected in different ways and may have different resolutions. In order to maximize comparability between the 1950s and 2000s data sets, we used the 'polygon to raster' function included in the ArcGIS 9.1 Spatial Analyst package to convert digitized forest patches into a raster with pixel size equal to the NLCD 2001 data (30m). We then used the 'raster to polygon' function to convert this raster back to a polygon layer for analysis.

Analyses

Influences of forest vegetation and landscape composition

We examined the influences of forest vegetation and landscape composition changes on changes in the avian community using linear regression models. We examined the changes in relative abundance of birds within guilds organized by habitat use, migratory habit, and the intersection of habitat and migratory habit. We would have preferred to model changes in absolute abundance of ecological guilds rather than relative abundance, but we had insufficient knowledge of abundance from the 1950s (Chapter 1). We also modeled changes in species richness and absolute abundance of American Robins. We examined this species by itself because it experienced the strongest increases in abundance in our study, its absence from 1950s surveys allowed us to estimate its abundance change reliably, and it was abundant enough (37 of 38 sites) to provide data for modeling.

Among the set of possible independent variables, we examined Pearson correlation coefficients and removed one member of each pair of variables with $R \geq 0.5$ to avoid collinearity. We also included two variables with correlation with $R = 0.56$ - forest area within 1 km and forest edge / area ratio within 1 km – because we suspected both to be important predictors of avian communities. The resulting set of eight candidate independent variables included three that characterize landscape changes, four that characterize vegetation structure, and two that represent canopy tree composition (Table 2).

For each of the three dependent variables we constructed Multiple Linear Regression (MLR) models for all possible combinations of independent variables. We calculated the sums of Akaike weights to assess relative importance of each independent variable, selected best models based on Akaike's information criterion for small samples (AICc) (Burnham & Anderson 2002), and performed model diagnostics to verify validity of best models.

Relationships with regional bird dynamics

We compared our species trends results with those observed in the Prairie Hardwood Transition (North American Bird Conservation Initiative (NABCI) Bird Conservation Region (BCR) 23, http://www.nabci-us.org/bcrs.html) and the Boreal Hardwood Transition (NABCI BCR 12) , using North American Breeding Bird Survey (BBS) data from 1967 - 2006 (Sauer et al. 2007). For each species occurring commonly enough to perform reliable trend analyses (detected on at least 5 surveys in both the BBS and our study), we categorized its trends in both the BBS and in our study as follows: increasing ($p<0.05$), unchanged, or decreasing ($p <0.05$). We assembled this information into contingency tables for each bird conservation region and assessed the level of agreement between the studies' trends using weighted

Cohen's Kappa analyses with squared weighting (Cohen 1968). Analyses were performed with the kappa2 function in R (contributed package 'irr'; R Development Core Team 2006).

Avian geographic range changes

We identified thirteen species in our study whose geographic ranges are known to have either expanded in or near southern Wisconsin during the 20th century, and one species – the Black-billed Cuckoo - whose range is known to have contracted from the area (Appendix 1; Poole 2005, Hitch & Leberg 2007). We assessed the changes in richness and relative abundance, and abundance of range-expanding species using paired permutation tests (10,000 runs) with sites as replicates. We performed abundance comparisons using the same sensitivity analysis as used for species and ecological guilds in chapter 1 (i.e., we tested for changes using adjusted abundances from the 1950s, assuming that Bond (1957) sampled 125% as much, the same as, and 50% as much as we did, and assessed significance under the most conservative assumption - 125% for decrease, and 50% for increase).

Effects of West Nile Virus

We identified four species that have likely declined regionally in response to West Nile Virus infection, based on analysis of birds in Illinois (LaDeau et al. 2007): American Crows, American Robins, Blue Jays, and Tufted Titmice (Appendix 1). We examined the changes in relative abundance and abundance of affected species to assess the possible effects of West Nile Virus infection. We performed all statistical analyses with R version 2.4.0 statistical software and contributed packages (R Development Core Team 2006).

Results

Forest vegetation changes

In forest vegetation, canopy trees trended toward later successional stages and more mesic assemblages, tree density decreased, and basal area declined (Table 3, Rogers et al. in press). These changes are consistent with maturing, managed forest stands protected from fire. Mean shrub abundance did not change between the 1950s and the 2000s.

Landscape composition changes

Observed landscape changes include modest increases in mean forest area (~26% to ~33%) and forest edge/area ratio (Table 3). Edge/area ratio calculation is sensitive to data resolution. Our procedure to equalize the potentially different resolutions of the USGS and NLCD data sources minimized effects on calculation of edge/area ratios, but cannot completely remove these effects. We therefore have limited confidence in our estimates for absolute changes in forest edge/area ratios over time. Nevertheless, these values are valid for relative comparisons of change across sites, and are therefore included in models of avian change. The number of houses within 1 km of study sites increased from a mean of 14 in the 1950s to 44 in 2006, mainly due to tremendous housing growth at a few sites, which is reflected in the high standard deviation value for 2006 (1950s median: 7.5, mode 6; 2006 median 17.5; mode 10).

Influences of forest vegetation and landscape changes on avian communities

For each dependent variable modeled, sums of Akaike weights (∑AICw) are presented in Table 4, and best models are summarized in Table 5. Habitat guilds were most sensitive to landscape-level changes. Trends in woodland species relative abundance were negatively related to trends in edge/area ratios (∑AICw = 0.61) and positively related to trends in forest area (∑AICw = 0.57), while trends in urban species were positively related to edge/area ratio changes (∑AICw = 0.63) and negatively with moisture-nutrients status of canopy tree assemblages (∑AICw =0.62). Trends in early successional species were inversely related to trends in forest area within 1 km of sites (∑AICw = 0.86). The best models only explained between 13% and 24% of the total variation in habitat guild changes (Table 5).

Among migratory habit guilds, changes in neotropical migrant species were positively related to trends in forest succession (∑AICw = 0.94) and shrub abundance (∑AICw = 0.97), while resident species were negatively influenced by these variables (weights = 0.99 and 0.95 respectively). The best models for these guilds accounted for between 37% and 46% of the variability in their relative abundance changes. Changes in short-distance migrant relative abundance were not related to the landscape and vegetation variables included in our analysis.

Results for intersected guilds were generally consistent with results from the separate guilds from which they were comprised. The early successional/short-distance migrant guild was an exception in that changes in relative abundance for this guild were most influenced by changes in numbers of houses within 1 km (∑AICw = 0.91, positive relationship), while changes in early succession species and short-distance migrant species were related to forest area and edge/area ratio changes, respectively. Proportions of total variation explained among best models ranged from ≤15% (ES & R) to >40% (W & R).

Changes in species richness were unrelated to the independent variables we examined. No models were better than the null model according to AICc, and sums of Akaike weights indicated no influential independent variables.

Increases in American Robin abundance were influenced most by increases in numbers of houses within 1 km of study sites (∑AICw = 1.00), and were also positively related to the greater proportion of edge in 2001 (∑AICw = 0.91) and forest succession (∑AICw = 0.70). The best models for American Robin abundance explained over half of the observed increase in abundance ($R^2 = 0.55$).

Relationships with regional bird dynamics

Avian community trends in the southern WI woodlots in our study were only weakly related to trends in the two closest Bird Conservation Regions. Table 6 gives weighted kappa results for analysis between our study and a) Prairie Hardwood Transition and b) Boreal Hardwood Transition regions. Given that our study area is contained within the Prairie Hardwood Transition region, we were surprised to find little agreement between trends observed in our study and those documented throughout the greater region by the BBS. We found weak evidence for positive agreement in trend for the entire community between our southern WI woodlots and regional trends (kappa = 0.25, z = 1.7, p = 0.089). Among habitat use guilds, we found weak evidence for concurrence in trends of woodland and urban species between our southern WI woodlots and the Prairie Hardwood Transition (kappa = 0.09, z = 0.53, p = 0.092 and kappa = 0.56, z = 1.74 and p = 0.081, respectively). Among migratory habit guilds, we found evidence for a positive relationship only in resident species (kappa = 0.74, z = 2.42, p = 0.016). Among intersected habitat-migration guilds, only woodland resident species exhibited agreement between study and regional trends (kappa = 0.727, z = 2.27, p = 0.023).

We also found weak agreement between trends in our southern WI woodlots and the Boreal Hardwood Transition region. We found weak evidence for positive agreement in trend for the entire community in our study woodlots and this northern region (kappa = 0.10, z = 1.96, p = 0.050). Among habitat preference guilds, we found evidence for a positive relationship between study and region trends in early succession species (kappa = 0.36, z = 2.25 and p = 0.025). Among migration form guilds, we found weak evidence for a positive relationship only in resident species (kappa = 0.54, z = 1.94, p = 0.051). Among intersected habitat-migration guilds, we found evidence of agreement between study trends and regional trends for woodland resident and early successional neotropical migrant species (kappa = 0.526, z = 1.79, p = 0.073 and kappa = 0.27, z = 2.00, p = 0.046). We found no evidence of agreement between our study trends and regional trends for woodland neotropical migrant species.

Geographic range changes

Relative abundance of range-expanding species increased from a mean value of 0.06 in the 1950s to 0.15 in 2006 (t = 10.39 on 37 d.f., p < 0.0001; Figure 2A). Under the assumption that Bond (1957) sampled only 50% as much as our study (the most conservative assumption for detection of abundance increases), we found strong evidence that range-expanding species increased in abundance (t = 3.8307 on 37 d.f., p = 0.0005), but no evidence of an increase in abundance of species that are not identified as range-expanding (Figure 2B). Species richness increased significantly among range-expanding and not-expanding species (both p < 0.0001; Figure 2C). The southern range limit of the Black-billed Cuckoo is shifting North and contracting away from our study area (Hitch & Leberg 2007). Our observations of Black-billed Cuckoos are consistent with range contraction. We observed this species at fewer sites, lower relative abundance, and lower absolute abundance than in the 1950s, however only the decline in relative abundance was statistically significant.

Effects of West Nile Virus

For the four species in our study found by LaDeau et al (2007) to decline in Illinois as a result of West Nile Virus, we found an increase in frequency of occurrence, relative abundance, and abundance over the period of our study. We therefore have no evidence for significant effects of this disease in our southern Wisconsin woodlots.

Discussion

The avian community changes we observed were consistent with effects of habitat fragmentation and development. Declines in richness and abundance among woodland neotropical migrant species support concerns about non-breeding habitat mortality and effects of breeding habitat change. Given that the study area is highly fragmented and over fifty years has passed, however, we were surprised that some of the changes we observed were not more severe. We found little evidence for other hypotheses that predict avian declines.

Overall, the forest vegetation and landscape changes we measured had limited relationships with ecological guild changes. Importantly, the observed directions of avian and habitat trends were often inconsistent with the relationships indicated in our models, indicating that habitat variables measured were not the most important factors influencing relative abundance trends. For instance, migratory habit guild models showed that changes in forest succession status were positively associated with changes in neotropical migrant relative abundance. However, mean relative abundance of neotropical migrants decreased despite forests trending toward later succession on average. This is not paradoxical. The disagreement reflects that negative drivers not included in the models (e.g., non-breeding habitat mortality effects) were more influential than the positive forest succession effects, so the net trend for neotropical migrants was negative. Forest succession explains some of the variability around this mean decrease, in that sites experiencing the greatest magnitude of succession tended to have smaller decreases in neotropical migrants.

Relationships of migratory habit guilds with forest composition were surprising, given that oak-dominated earlier succession forests harbor greater diversity and densities of insects, a prey base for many neotropical bird species (Rodewald & Abrams 2004). Resident and neotropical migrant relative abundances also responded differently to the abundance of shrubs, with resident changes negatively related and neotropical changes positively related to changes in shrub abundance. These results may reflect habitat needs of the many low-nesting neotropical migrant species (e.g., Indigo bunting, Gray Catbird, Veery) that use shrub structures as substrates or concealment for their nests (Peterjohn & Sauer 1993). Shrubs may also harbor prey for predominantly insectivorous neotropical migrant species.

Models of habitat guild relative abundances had relatively low explanatory power ($R^2 < 0.25$), but relationships were consistent with previously documented avian community patterns and processes in fragmented forests (e.g., Lynch & Whitcomb 1978, Ambuel & Temple 1982, Leck et al. 1988, Askins 1990): woodland species' relative abundance declined with increasing edge/area ratios within 1 km, but this was mitigated by increased forest areas within 1 km. Increases in early successional species were negatively associated with increases in forest area, while urban species relative abundances increased with increasing edge/area ratios. The observed trends in avian habitat guilds are therefore consistent with model relationships for increases in edge/area ratio, but not for the increases in forest area. This suggests that either the edge/area ratio effect was stronger than the forest area effect, or that our models failed to include other important influences. Housing density was surprisingly not influential for urban species as a group, although American Robin abundance was strongly associated with houses. Other urban species such as Mourning Doves may be associated more strongly with agricultural habitats, which our analysis did not quantify, than with houses.

We found little evidence for source-sink dynamics between the extensively forested northern Midwest (i.e., the Boreal Hardwood Transition bird conservation region) and our fragmented forest sites in southern Wisconsin. No correlations existed between woodland neotropical migrant species trends in our study and in the Boreal Hardwood Transition. The positive correlations we did observe - between trends of early succession species in our study and the Boreal Hardwood Transition, and between resident species trends in our study and the Prairie Hardwood Transition, in which our study is located - may reflect the similar habitat trends to those in our study have occurred across these regions (Radeloff et al. 2005) rather than source-sink relationships. We acknowledge two weaknesses in this analysis: first, it tested only for correlations among trends at the level of ecological guilds, and would not detect source-sink relationships that may exist for single species. Second, the trends we compared cover somewhat different time periods, (1950s – 2006 vs. 1967 – 2006).

We found stronger evidence for the importance of geographic range shifts as mechanisms of avian community change, but these affect only relatively few species. We documented increases in the abundance and species richness of range-expanding species. Northward range expansions among several species in our study are likely the result of warming climate conditions (e.g., Blue-winged and Hooded Warblers, Blue-Gray Gnatcatcher; Hitch & Leberg 2007), but conservation efforts (e.g., Wild Turkey) and regional land-use change (e.g., Northern Cardinal) also likely facilitate range expansion for some species.

Although West Nile Virus has altered avian communities across North America since 1999 (LaDeau et al. 2007), we found significant increases among species that are likely to have been affected in the Midwest. This does not exclude the possibility of an effect, however, as the magnitudes of the 50-year increasing trends in these species could mask the effects of recent epidemics.

Observed declines in species richness and abundance among woodland neotropical migrants but not among other woodland species or neotropical species support the non-breeding habitat mortality hypothesis. In our best regression model, only 26% of the relative abundance changes for this guild were related to habitat changes (forest succession, changes in shrub frequency, and changes in edge to area ratio within 1 km). Tropical forest destruction is a likely cause of mortality among woodland neotropical migrant species (Rappole & McDonald 1994).

Extinction debt from previous habitat change may alternatively be responsible for the observed loss of species among woodland neotropical migrants. We cannot definitively distinguish this effect from non-breeding habitat mortality. If extinction debt were important, however, we would expect other woodland species to be affected also. We did not observe decline among woodland species in general. Also, although several woodland neotropical migrants have declined in frequency of occurrence among sites, only the Least Flycatcher was extirpated from all sites.

Our tests of hypothesized ecological mechanisms are not exhaustive, and other mechanisms may explain the avian dynamics we observed. Increases in bird species associated with early successional or urban habitats (e.g. Mourning Doves and American Goldfinches) may reflect population increases due to dynamics in non-forest habitats. If these species' dynamics are in accordance with the ideal free distribution (Fretwell & Lucas 1969), suitability of non-forest habitats would have decreased with increasing densities of birds, thus potentially promoting colonization of forests by species not traditionally associated with forest habitat. Increased availability of bird feeders with higher housing densities near forests may benefit permanent resident species (e.g. Black-capped Chickadees, White-breasted Nuthatches, Northern Cardinals, Downy Woodpeckers) by increasing winter survivorship (Grubb & Cimprich 1990, Egan & Brittingham 1994). Feeders may also allow some short-distance migrants (e.g. American Goldfinches and Mourning Doves) to overwinter, or to return from wintering grounds much earlier in the spring than was possible in the 1950s. Area-sensitive species (e.g. Pileated woodpeckers) may have responded positively to increased forest areas (Keller & Yahner 2007). Some species may have also benefited from increased food availability from exotic invasive species. American Robins, for example, may have benefited from increases in exotic earthworms and fruit-bearing shrubs (*Rhamnus sp.* and *Lonicera sp.*) in forests, although nesting success is lower in exotic than native shrubs (Borgmann & Rodewald 2004, Schmidt & Whelan 1999).

Species whose abundance is positively associated with early successional forest (e.g. American Redstarts) or woodland habitats with lower tree densities (e.g. Baltimore Orioles) may have declined as a result of forest succession between the early 1950s and 2006 (Hunt 1996, Yahner 2003, Davis et al. 2000). Other declining species (e.g. Eastern Wood Pewees, Least Flycatchers, Cerulean Warblers) may have responded to understory vegetation changes resulting from increased deer browsing (DeCalesta 1994). Ground-nesting species (e.g. Ovenbirds) may have declined with reduced leaf litter, important for nest construction and concealment, resulting from increased earthworm abundance (Hale et al. 2006).

Changes in species richness were related to none of the habitat changes that we measured. This is surprising because previous research has shown relationships between avian species richness and forest area (e.g., Ambuel & Temple 1983), housing density (Pidgeon et al 2007, Lepczyk et al. 2008), and vegetation structure (MacArthur & MacArthur 1961, Cody 1981, Bersier & Meyer 1995). We found, however, that increases of range-expanding species accounted for approximately a third of the mean observed increase in species per site (2 of 6).

Finally, avian adaptation to forest fragment habitats is a mechanism that may be driving increases in some species. Although our study contains no genetic evidence for or against this hypothesis, evolution is a common response to anthropogenic change (Carroll et al. 2007). Adaptation through evolution may therefore be an important part of long-term change in relatively stable human-altered habitats. We suggest that further research into this area may offer important insights to avian conservation biology.

Although biotic homogenization has occurred among avian communities and woodland neotropical migrant species have declined, the rate of that decline was less than expected, at least in terms of species richness. Mortality associated with non-breeding habitat is likely a cause of this decline. Breeding habitat configuration and forest composition explain only part of the observed trend, but they do matter. Increasing overall species richness and stable avian abundances also indicate that fragmented forests in southern

Wisconsin continue to be viable avian habitat. More broadly, our study suggests that landscapes significantly altered and developed by people should still be considered as priorities for conservation of biodiversity. If evolutionary adaptation to human-altered habitats is occurring, then we can likely facilitate this process by slowing rates of development and disturbance in these habitats. As much of the planet's land area is settled, disturbed, or fragmented and will remain so for the foreseeable future, we suggest that further research into possible adaptation may offer important insights into conservation biology and help maximize the conservation values of human-altered landscapes.

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Tables

Table 1: Canopy tree species index scores along succession and moisture-nutrients gradients (Peet & Loucks 1977). On the succession gradient, 0 corresponds to the earliest succession (most shade-intolerant) species, and 10 latest succession (most shade-tolerant). On the moisture-nutrients gradient, 0 represents species most strongly associated with xeric, nutrient-poor soils, and 10 represents species most strongly associated with mesic, nutrient-rich soils. Site scores are calculated as averages of species scores, weighted by species' relative basal areas.

Scientific name	**Common name**	**Moisture-nutrients**	**Succession**
Acer negundo	Box Elder	3.1	2.4
Acer rubrum	Red Maple	7.6	4
Acer saccharum	Sugar Maple	10	10
Carpinus caroliniana	American Hornbeam	8	8
Carya cordiformes	Bitternut Hickory	8.2	8.6
Carya ovata	Shagbark Hickory	3.6	8.5
Celtis occidentalis	Common Hackberry	7.8	6
Fagus grandifolia	American Beech	9.5	9.5
Fraxinus pennsylvanica	Green Ash	9	4.7
Juglans cinerea	Butternut	8.1	4.3
Juglans nigra	Black Walnut	7.4	5.7
Ostrya virginiana	American Hophornbeam	9.1	9.8
Populus grandifolia	Bigtooth Aspen	5.9	1.8
Populus tremuloides	Trembling Aspen	2.2	0.9
Prunus serotina	Black Cherry	4.4	9.1
Quercus alba	White Oak	3.8	3.1
Quercus rubra	Northern Red Oak	7.1	0
Quercus macrocarpa	Bur Oak	1.7	2
Quercus velutina	Black Oak	0	2.5
Tilia americana	American Basswood	8.8	6.9
Ulmus americana	American Elm	5.6	6.8
Ulmus rubra	Red Elm	8.3	3.9

Table 2: Summary of independent variables (A) selected and (B) considered but not selected for MLR models of change in ecological guild relative abundances, species richness, and American Robin abundance. After each non-selected variable in B is the number of the selected variable with which it was highly correlated and the sign of the coefficient.

A) selected

Variable	**Description**
Landscape change variables	**Change in:**
1. forest area within 1 km	Forest area within 1 km radius of survey center
2. forest edge / area ratio within 1 km	Forest edge / forest area ratio within 1 km radius of survey center
3. houses within 1 km	Number of houses within 1 km radius of survey center
Canopy Tree composition variables	**Change in:**
4. moisture – nutrients index (Peet & Loucks 1977)	average of species moisture-nutrients scores, weighted by species' relative basal areas
5. successional status index (Peet & Loucks 1977)	average of species succession scores, weighted by species' relative basal areas
Vegetation structure variables	**Change in:**
6. number of trees	Number of tree stems (> 10 cm D.B.H.) per hectare
7. tree basal area	Tree (> 10 cm D.B.H.) basal area per hectare
8. shrub abundance index	Sum of shrub species frequencies of occurrence among 20 1 m^2 quadrats

B) not selected

Variable	**Description**
Landscape change variables	**Change in:**
core forest area within 1 km (1 +)	Forest area > 30 m from forest edge within 1 km radius of survey center
survey patch area (1 +)	Area of forest patch surveyed
survey patch core area (1 +)	Area of forest patch where survey was conducted > 30 m from forest edge
survey patch edge/area ratio (1 -)	Edge to area ratio of forest patch where survey was conducted
roads within 1 km (3 +)	Road length within 1 km radius of survey center
Vegetation structure variables	**Change in:**
Mean basal area (7 +)	Mean basal area per tree stem

Table 3: Mean values, standard deviations, and paired t-test results for landscape and forest vegetation variables, 1950s and 2000s.

	1950s		2006		difference	
	Mean	Stand. Dev.	Mean	Stand. Dev.	t-stat	2-sided p-value
Forest area w/in 1 km (m^2)	8.35E+05	4.94E+05	1.04E+06	7.15E+05	3.2284	0.0026
Forest edge/area w/in 1 km (m/m^2)	0.0151	0.0053	0.0170	0.0075	2.6951	0.0105
Houses w/in 1 km (no.) *	14.18	17.48	43.97	99.48	2.1381	0.0392
Moisture-nutrients index (0-10)	6.38	2.15	7.08	1.86	5.3070	0.0000
Succession index (0-10)	4.84	1.83	6.17	1.65	6.5472	0.0000
Trees per hectare (no.)	384.31	84.86	320.99	76.79	-3.3754	0.0017
Basal area per hectare (cm^2)	2.55E+05	6.31E+04	2.27E+05	8.89E+04	-1.7369	0.0907
Summed shrub frequency **	15.55	10.39	15.08	10.65	-0.2749	0.7849

* increase driven by strong growth at a few sites; median and mode reflect more modest increase: 1950s median 7.5, mode 6; 2006 median 17,5; mode 10

**sum of species frequencies of occurrence among 20 1 m^2 quadrats

Table 4: Sums of Akaike weights of landscape and forest vegetation change variables for models of change in ecological guild relative abundances, species richness, and American Robin abundance. For each dependent variable, we created models including all possible combinations of independent variables, and then obtained the sum of Akaike weights by summing the Akaike weights for all models that included that variable. Values in bold represent the most influential independent variables for corresponding dependent variable.

Change in:	Forest area w/in 1 km	Edge / area w/in 1 km	No. houses w/in 1km	Moisture-nutrients index	Succession index	Trees per hectare	Basal area per hectare	Summed shrub frequency
American Robin								
Stand. Abund. *	0.32	**0.91**	**1.00**	0.32	**0.70**	0.32	0.62	0.33
Habitat use guild (all relative abundance)								
Woodland (W)	**0.57**	**0.61**	0.28	0.27	0.29	0.51	0.33	0.28
Early succ. (ES)	**0.86**	0.32	0.29	0.30	0.49	0.34	0.34	0.30
Urban (U)	0.35	**0.63**	0.40	**0.62**	0.30	0.47	0.31	0.31
Migratory habit guild (all relative abundance)								
Neotropical (NT)	0.29	0.33	0.39	0.35	**0.94**	0.31	0.34	**0.97**
Short-distance (SD)	0.30	0.41	0.27	0.28	0.28	0.45	0.28	0.35
Resident (R)	0.30	0.29	0.50	0.31	**0.99**	0.33	0.49	**0.95**
Intersected guilds (all relative abundance) **								
W & NT	0.34	**0.64**	0.29	0.33	**0.61**	0.43	0.30	**0.64**
W & R	0.45	0.32	0.41	0.34	**0.96**	0.36	0.51	**0.89**
ES & NT	**0.89**	0.34	0.37	0.33	**0.65**	0.29	0.31	0.51
ES & SD	0.34	0.34	**0.92**	0.29	0.34	**0.57**	0.29	0.34
ES & R	**0.76**	0.34	0.31	0.30	0.32	0.35	0.30	0.31
U & SD	0.32	**0.74**	0.42	0.50	0.28	0.36	0.35	0.35
Species Richness								
All species	0.47	0.31	0.30	0.28	0.50	0.28	0.32	0.29

* American Robin abundance standardized by sample effort at each site

** insufficient data for analyses of W & SD, U & NT, and U & R guilds

Table 5: Best multiple linear regression models of change in ecological guild relative abundances, American Robin abundance, and species richness as functions of changes in landscape and forest vegetation variables. For each dependent variable, we created models including all possible combinations of independent variables, and then selected the top 3 models based on Akaike's information criterion for small samples (AICc). A. Coefficients; B. R^2 and AIC_c

Change in:	**Rank**	**Forest area w/in 1 km**	**Edge / area w/in 1 km**	**Houses w/in 1 km**	**Moisture-nutrients index**	**Succ-ession index**	**Trees per hectare**	**Basal area per hectare**	**Summed shrub frequency**	**Y – int**
American Robin										
Abundance *	1		28.26	2.32E-3		0.071		8.18E-7		0.314
	2		28.86	2.25E-3	-0.026	0.076		7.82E-7		0.325
	3		27.36	2.29E-3		0.069		8.41E-7	-1.79E-3	0.318
Habitat										
Woodland (W)	1	1.31E-7					2.57E-4			-0.201
	2		-9.12							-0.172
	3	9.08E-8	-5.13				2.26E-4			-0.185
Early succession (ES)	1	-9.86E-8								0.156
	2	-9.98E-8				0.012				0.141
	3	-1.08E-7				0.015	-1.05E-4			0.132
Urban (U)	1		2.88		-0.017		-8.79E-5			0.056
	2		2.94		-0.017					0.062
	3	3.09E-8	4.25		-0.017					0.053
Migratory habit										
Neotropical (NT)	1					0.037			4.34E-3	-0.280
	2			-1.72E-4		0.036			4.12E-3	-0.273
	3				0.020	0.033			5.11E-3	-0.288
Short-distance (SD)	1									0.087
	2						-1.43E-4			0.078
	3		3.73							0.080
Resident (R)	1			1.78E-4		-0.028		1.71E-7	-2.91E-3	0.179
	2					-0.030		1.56E-7	-3.12E-3	0.186
	3					-0.033			-2.87E-3	0.186

Change in:	**Rank**	**Forest area w/in 1 km**	**Edge / area w/in 1 km**	**Houses w/in 1 km**	**Moisture-nutrients index**	**Succ-ession index**	**Trees per hectare**	**Basal area per hectare**	**Summed shrub frequency**	**Y – int**
Intersected Guilds **										
W & NT	1		-6.25			0.025			2.69E-3	-0.305
	2					0.030			3.32E-3	-0.323
	3		-7.87			0.022				-0.299
W & R	1					-0.025		1.96E-7	-2.68E-3	0.132
	2			1.55E-4		-0.023		2.09E-7	-2.50E-3	0.125
	3	5.06E-8				-0.029			-2.38E-3	0.121
ES & NT	1	-8.88E-8				0.014				0.057
	2	-8.91E-8				0.015			1.19E-3	0.056
	3	-8.50E-8		-1.01E-4		0.013				0.060
ES & SD	1			1.38E-4			-6.13E-5			0.022
	2			1.42E-4						0.026
	3			1.45E-4		0.004	-7.32E-5			0.016
ES & R	1	-3.01E-8								0.055
	2	-3.32E-8					-4.03E-5			0.053
	3	-3.00E-8							-3.16E-4	0.055
U & SD	1		3.95		-0.015					0.053
	2		3.78							0.043
	3		3.65		-0.018			-8.36E-8		0.053
Species Richness										
All species	1	0								6.237
	2	0				-1.032				7.614
	3	3.64E-6				-1.057				6.887

* American Robin abundance standardized by sample effort at each site

** insufficient data for analyses of W & SD, U & NT, and U & R guilds

Change in:	Rank	R^2	AIC_c
American Robin			
Abundance *	1	0.55	3.56
	2	0.55	5.28
	3	0.55	5.30
Habitat			
Woodland (W)	1	0.18	-60.58
	2	0.13	-60.37
	3	0.21	-59.91
Early succession (ES)	1	0.18	-89.88
	2	0.22	-89.75
	3	0.24	-88.84
Urban (U)	1	0.19	-121.63
	2	0.14	-121.60
	3	0.18	-121.02
Migratory habit			
Neotropical (NT)	1	0.37	-75.41
	2	0.39	-74.63
	3	0.39	-74.28
Short-distance (SD)	1	0.00	-81.52
	2	0.04	-81.20
	3	0.04	-81.17
Resident (R)	1	0.46	-96.06
	2	0.42	-95.71
	3	0.39	-95.58
Intersected Guilds **			
W & NT	1	0.26	-62.14
	2	0.20	-61.34
	3	0.19	-61.04
W & R	1	0.36	-94.80
	2	0.39	-94.52
	3	0.35	-94.27
ES & NT	1	0.27	-104.26
	2	0.31	-104.24
	3	0.28	-103.14
ES & SD	1	0.22	-161.58
	2	0.17	-160.92
	3	0.25	-160.81
ES & R	1	0.13	-164.21
	2	0.15	-163.38
	3	0.14	-162.84
U & SD	1	0.17	-119.75
	2	0.11	-119.08
	3	0.20	-118.89
Species Richness			
All species	1	0.00	244.42
	2	0.05	244.46
	3	0.09	244.68

Table 6: Comparisons of avian trends in our study with regional trends from 1967-2006 (BBS, Sauer et al 2007): A. Prairie Hardwood Transition (which includes our study area), and B. the Boreal Hardwood Transition, a largely forested region to the north of our study area. For each sufficiently common species (≥ 5 surveys in both the BBS and our study), we assessed the agreement of categorized trends (increasing ($p < 0.05$), unchanged, or decreasing ($p < 0.05$)) between our study and each region using weighted Kappa analysis (squared weighting).

A. Prairie Hardwood Transition and our study

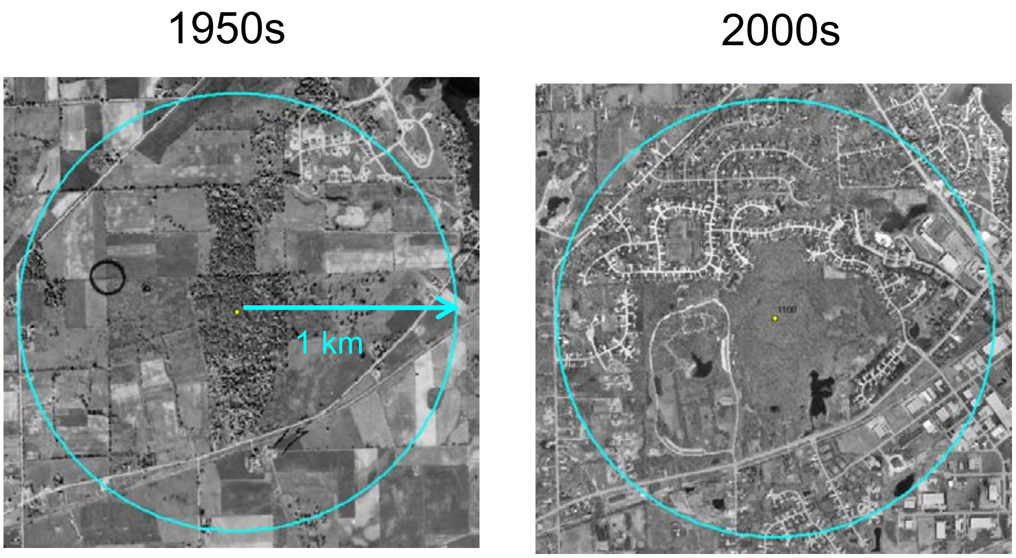
Ecological Guild	**N species**	**kappa**	**z-stat**	**p-value**
All species	46	0.250	1.7017	0.0888
Habitat				
Woodland (W)	27	0.092	0.5311	0.0924
Early succ./scrub (ES)	7	0.300	0.9845	0.3249
Urban (U)	4	0.556	1.7408	0.0817
Migration Form				
Neotropical (NT)	24	0.022	0.1199	0.9046
Short-distance (SD)	12	0.353	1.4821	0.1383
Resident (R)	10	0.737	2.4152	0.0157
Intersected *				
W & NT	17	-0.238	-1.2509	0.2110
W & R	9	0.727	2.2678	0.0233
ES & NT	4	-0.500	-1.1547	0.2482
ES & SD	2	-0.333	-1.4142	0.1573
U & SD	3	0.500	1.5000	0.1336

B. Boreal Hardwood Transition and our study

Ecological Guild	**N species**	**Kappa**	**z-stat**	**p-value**
All species	44	0.098	1.9596	0.0500
Habitat				
Woodland (W)	26	0.104	1.3176	0.1044
Early succession (ES)	7	0.364	2.2450	0.0248
Urban (U)	4	0.200	0.6667	0.5050
Migration form				
Neotropical (NT)	22	0.027	0.3442	0.7307
Short-distance (SD)	12	0.073	0.9988	0.3179
Resident (R)	10	0.545	1.9365	0.0528
Intersected *				
W & NT	16	-0.032	-0.2761	0.7825
W & R	9	0.526	1.7928	0.0730
ES & NT	4	0.273	2.0000	0.0455
ES & SD	2	0.333	1.4142	0.1573
U & SD	3	0.400	0.8660	0.3865

* insufficient data for W & SD, ES & R, U & NT, and U & R guilds

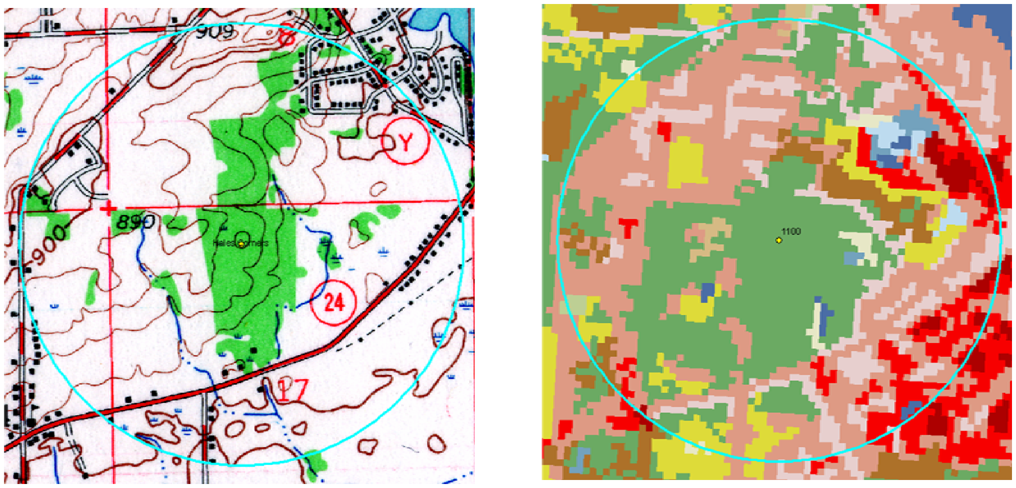
Figures


1950s

2000s

historic aerial photograph

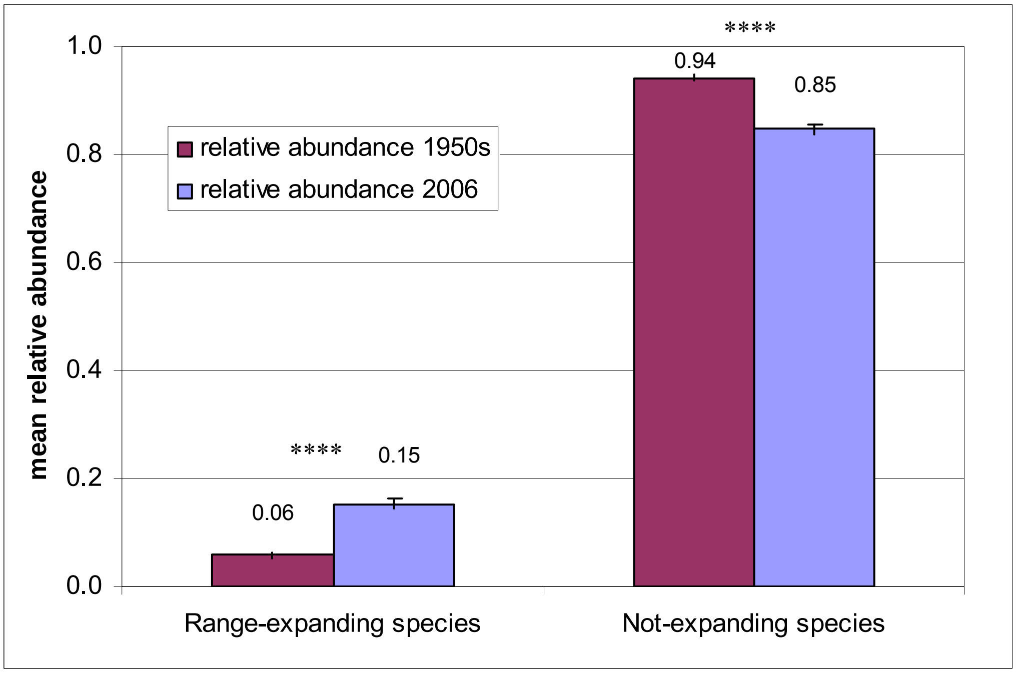
USGS DOQQ aerial photograph



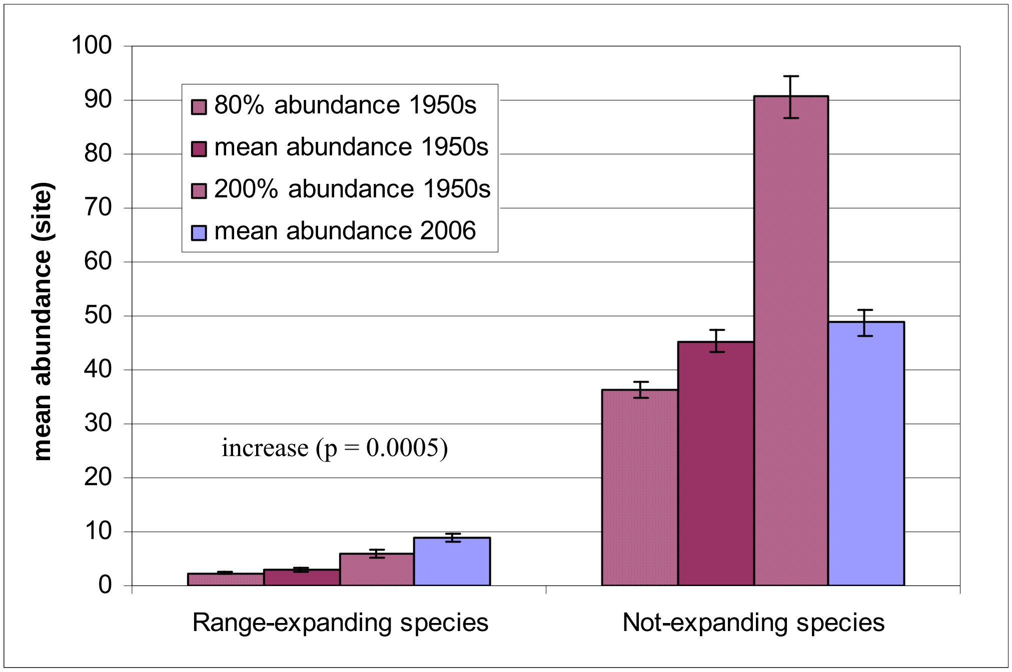
USGS Topographic map

N.L.C.D. 2001

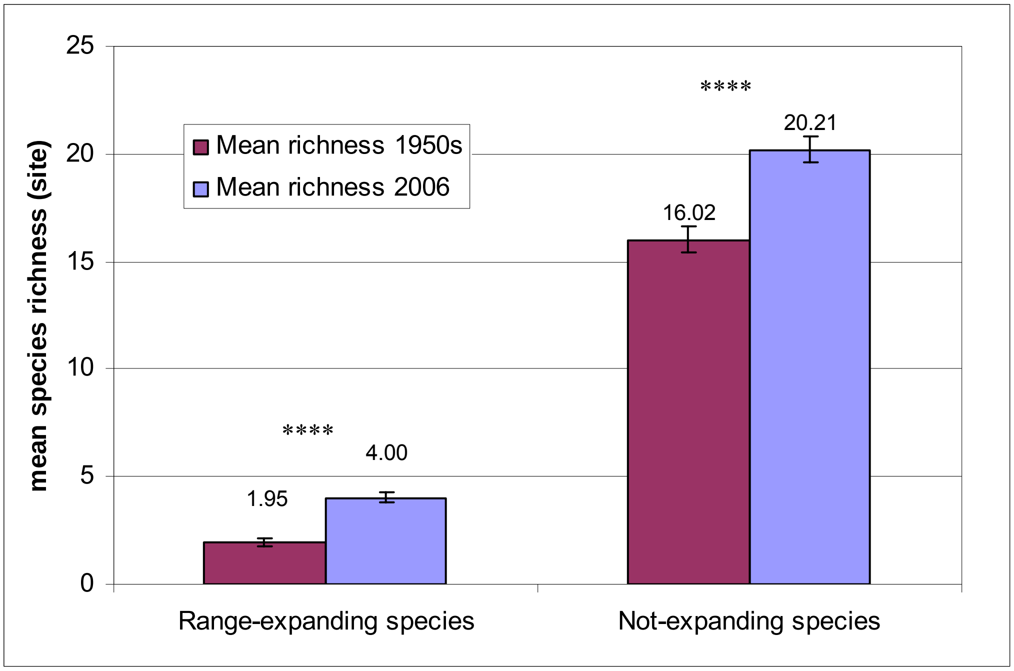
Figure 1: Examples of landscape data sources for both time periods. We estimated housing and road densities within 1 km based on USGS topographic maps from the 1950s and USGS digital orthophoto quarter quadrangles taken from 1992 - 2000. We estimated forest cover within 1 km and forest patch sizes from USGS topographic maps (1950s) and the 2001 National Land Cover Database.



A. Relative abundance



B. Absolute abundance



C. Species richness

Figure 2: Changes in (A) relative abundance, (B) absolute abundance, and (C) site-level species richness of range-expanding species. We identified species in our study whose geographic ranges are known to have expanded in or near southern Wisconsin during the 20th century (Poole 2005, Hitch & Leberg 2007). Absolute abundance comparisons are based on conservative assumptions about Bond's (1957) sampling effort: Bond sampled 1) 125% as much as we did (scaled to 80% abundance), 2) the same amount as we did (100% abundance), and 3) 50% as much as we did (scaled to 200% abundance). Under most conservative assumptions, absolute abundance of range-expanding species increased ($p = 0.0005$), but not-expanding species did not change.

APPENDICES

Appendix 1: Scientific name, ecological guild membership, evidence for geographical range-expansion, and evidence for population declines due to West Nile Virus by species. Habitat use abbreviations are W: woodland, ES: early succession / scrub, U: Urban. Migration form abbreviations are NT: neotropical, SD: short-distance, R: resident. Range change abbreviations: EX: Expanded, C: Contracted

Species	Scientific name	Periods detected	Habitat use[1]	Migration form[1]	range changes[2]	WNV effect[3]
Northern Bobwhite	*Colinus virginianus*	2006	ES	R		
Ruffed Grouse	*Bonasa umbellus*	1950s	W	R		
Ring-necked Pheasant	*Phasianus colchicus*	2006		R		
Wild Turkey	*Meleagris gallopavo*	2006	W	R	EX	
Mourning Dove	*Zenaida macroura*	2006	U	SD		
Cooper's Hawk	*Accipiter cooperii*	both	W	SD	EX	
Red-tailed Hawk	*Buteo jamaicensis*	both		SD		
Red-shouldered Hawk	*Buteo lineatus*	both	W	SD		
Broad-winged Hawk	*Buteo platypterus*	2006	W	NT		
Barred Owl	*Strix varia*	both	W	R		
Great Horned Owl	*Bubo virginianus*	both		R		
Yellow-billed Cuckoo	*Coccyzus americanus*	both	W	NT		
Black-billed Cuckoo	*Coccyzus erythropthalmus*	both	W	NT	C	
Hairy Woodpecker	*Picoides villosus*	both	W	R		
Downy Woodpecker	*Picoides pubescens*	both	W	R		
Pileated Woodpecker	*Dryocopus pileatus*	2006	W	R	EX	
Red-headed Woodpecker	*Melanerpes erythrocephalus*	both		SD		
Red-bellied Woodpecker	*Melanerpes carolinus*	both	W	R	EX	
Northern Flicker	*Colaptes auratus*	both		SD		
Ruby-thr. Hmmngbrd.	*Archilochus colubris*	both	W	NT		
Great Crested Flycatcher	*Myiarchus crinitus*	both	W	NT		
Eastern Phoebe	*Sayornis phoebe*	2006		SD		
Eastern Wood-Pewee	*Contopus virens*	both	W	NT		
Acadian Flycatcher	*Empidonax virescens*	both	W	NT		
Alder Flycatcher	*Empidonax alnorum*	2006	ES	NT	EX	
Least Flycatcher	*Empidonax minimus*	1950s	W	NT		
Blue Jay	*Cyanocitta cristata*	both	U	SD		Y
American Crow	*Corvus brachyrhynchos*	both		SD		Y
Brown-headed Cowbird	*Molothrus ater*	both		SD		
Red-winged Blackbird	*Agelaius phoeniceus*	2006		SD		
Baltimore Oriole	*Icterus galbula*	both		NT		
House Finch	*Carpodacus mexicanus*	2006	U	SD	EX	
American Goldfinch	*Carduelis tristis*	both	ES	SD		
Chipping Sparrow	*Spizella passerina*	2006	U	NT		
Field Sparrow	*Spizella pusilla*	2006	ES	SD		
Song Sparrow	*Melospiza melodia*	2006	ES	SD		

Eastern Towhee	*Pipilo erythrophthalmus*	both	ES	SD		
Northern Cardinal	*Cardinalis cardinalis*	both	ES	R	EX	
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	both	W	NT		
Indigo Bunting	*Passerina cyanea*	both	ES	NT		
Scarlet Tanager	*Piranga olivacea*	both	W	NT		
Cedar Waxwing	*Bombycilla cedrorum*	2006		SD		
Red-eyed Vireo	*Vireo olivaceus*	both	W	NT		
Yellow-throated Vireo	*Vireo flavifrons*	both	W	NT		
Blue-headed Vireo	*Vireo solitarius*	2006	W	NT	EX	
Blue-winged Warbler	*Vermivora pinus*	2006	ES	NT	EX	
Cerulean Warbler	*Dendroica cerulea*	both	W	NT		
Chestnut-sided Warbler	*Dendroica pensylvanica*	2006	ES	NT		
Blck.-thr. Green Warbler	*Dendroica virens*	2006	W	NT		
Ovenbird	*Seiurus aurocapilla*	both	W	NT		
Mourning Warbler	*Oporornis philadelphia*	2006	ES	NT	EX	
Common Yellowthroat	*Geothlypis trichas*	2006	ES	NT		
Hooded Warbler	*Wilsonia citrina*	2006	W	NT	EX	
American Redstart	*Setophaga ruticilla*	both	W	NT		
Gray Catbird	*Dumetella carolinensis*	both	ES	NT		
House Wren	*Troglodytes aedon*	both	ES	NT		
White-breasted Nuthatch	*Sitta carolinensis*	both	W	R		
Tufted Titmouse	*Baeolophus bicolor*	both	W	R	EX	Y
Black-capped Chickadee	*Poecile atricapillus*	both	W	R		
Blue-gray Gnatcatcher	*Polioptila caerulea*	both	W	NT	EX	
Wood Thrush	*Hylocichla mustelina*	both	W	NT		
Veery	*Catharus fuscescens*	both	W	NT		
American Robin	*Turdus migratorius*	2006	U	SD		Y

[1] Peterjohn and Sauer (1993)
[2] Based on findings of Hitch & Leberg (2007) and Poole (2005)
[3] Based on findings of LaDeau et al (2007) for Illinois

Appendix 2: Geographic locations (Wisconsin Transverse Mercator (WTM) projection), dates, start times, observers, weather conditions at start time, numbers of sample units completed, and numbers of individuals detected by species for two surveys conducted at each of 38 southern Wisconsin forest sites during summer 2006.

Curtis site number	**1000**		**1002**		**1005**		**1007**		**1008**	
WTM Easting[1]	565672.7557		553423.0486		539861.1792		667477.2528		665830.7171	
WTM Northing[1]	229058.0661		273762.5795		266598.9768		350524.3225		353884.4211	
Date (all 2006)	5/25	6/23	5/23	6/23	5/23	6/22	6/10	7/2	6/10	7/2
Start time (A.M. CDT)	5:50	8:40	5:38	6:30	7:45	5:40	7:10	5:26	5:40	7:20
Observer[2]	AO	AO	AO	JN	AO	JN	JN	JN	JN	JN
Cloud cover[3]	10	2	0	0	0	10	0	11	0	11
Temperature[4]	4	4	1	4	2	2	4	4	4	5
Wind speed[5]	2	3	2	0	2	1	2	1	2	1
Sample units[6]	3	2	4	3	2	3	4	3	4	4
Northern Bobwhite	0	0	0	0	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	0	0	0	0	0	0
Wild Turkey	0	0	0	0	0	0	0	0	0	0
Mourning Dove	0	0	0	0	0	0	0	2	0	0
Cooper's Hawk	0	0	0	0	0	0	0	0	0	0
Red-tailed Hawk	0	1	0	0	0	0	0	0	1	0
Red-shouldered Hawk	0	0	0	0	0	0	0	2	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	0	0	0
Barred Owl	0	0	0	0	0	0	0	0	1	1
Great Horned Owl	0	0	0	0	0	0	0	0	0	0
Yellow-billed Cuckoo	1	0	0	0	0	1	0	1	0	2
Black-billed Cuckoo	0	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	2	1	0	1	0	0	1	1	0	0
Downy Woodpecker	0	1	0	1	0	0	0	1	1	3
Pileated Woodpecker	0	0	0	0	0	0	0	0	0	0
Red-headed Woodpecker	0	0	0	0	0	1	0	1	0	0
Red-bellied Woodpecker	1	1	2	2	0	1	1	1	0	1
Northern Flicker	0	0	0	1	0	0	0	2	1	0
Ruby-thr. Hummingbird	0	0	0	0	0	1	0	0	0	0
Great Crested Flycatcher	0	2	0	0	0	2	0	0	0	1
Eastern Phoebe	1	0	0	0	0	0	0	0	0	0
Eastern Wood-Pewee	2	2	2	2	0	2	2	4	3	4
Acadian Flycatcher	0	0	0	0	0	0	0	1	1	2
Alder Flycatcher	0	0	0	0	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0
Blue Jay	0	1	0	1	0	1	3	2	2	1
American Crow	0	0	1	1	0	2	2	2	3	3
Brown-headed Cowbird	2	0	0	0	1	1	1	1	1	1
Red-winged Blackbird	0	0	0	0	0	0	0	0	0	0
Baltimore Oriole	0	0	0	0	0	0	0	0	1	0
House Finch	0	0	0	0	0	0	0	0	0	0

American Goldfinch	0	0	0	0	0	2	2	1	0	3
Chipping Sparrow	0	0	0	0	0	0	0	0	0	0
Curtis site number	**1000 cont'd**		**1002 cont'd**		**1005 cont'd**		**1007 cont'd**		**1008 cont'd**	
Date (all 2006)	5/25	6/23	5/23	6/23	5/23	6/22	6/10	7/2	6/10	7/2
Field Sparrow	0	0	0	0	0	0	0	0	0	0
Song Sparrow	0	0	0	0	0	0	0	0	0	0
Eastern Towhee	0	0	0	0	0	0	0	0	0	0
Northern Cardinal	3	1	6	3	1	0	1	1	1	1
Rose-breasted Grosbeak	0	0	1	2	0	0	1	0	1	0
Indigo Bunting	0	0	2	1	0	0	1	1	1	0
Scarlet Tanager	0	0	0	0	1	3	1	3	1	2
Cedar Waxwing	1	0	0	0	0	0	0	2	0	1
Red-eyed Vireo	1	0	4	2	4	3	4	6	5	6
Yellow-throated Vireo	0	0	0	0	0	1	0	0	1	0
Blue-headed Vireo	0	0	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	0	0	0	0
Cerulean Warbler	0	0	0	0	0	0	0	0	0	0
Chestnut-sided Warbler	0	0	0	0	0	0	0	0	1	0
Black-thr. Green Warbler	0	0	0	0	0	0	0	0	0	0
Ovenbird	0	0	4	1	2	0	3	2	4	6
Mourning Warbler	0	0	0	0	0	0	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0	0	0	0	0
Hooded Warbler	0	0	0	0	0	0	0	0	0	0
American Redstart	0	0	0	0	0	0	0	0	2	0
Gray Catbird	1	1	0	0	0	0	0	0	0	0
House Wren	4	3	1	1	0	0	0	0	0	0
White-breasted Nuthatch	1	1	1	1	1	1	1	1	0	1
Tufted Titmouse	0	0	1	0	0	0	0	0	0	1
Black-capped Chickadee	0	3	2	2	1	0	0	1	2	1
Blue-gray Gnatcatcher	0	0	3	1	1	1	0	0	0	1
Wood Thrush	1	2	1	1	0	0	1	1	1	0
Veery	1	0	0	0	0	0	0	0	0	0
American Robin	2	1	2	0	0	2	2	0	2	2
Total	24	21	33	24	12	25	27	40	37	44

Curtis site number	**1009**		**1014**		**1016**		**1017**		**1018**	
WTM Easting	655664.5639		666389.0352		646096.3605		650929.6299		658041.8288	
WTM Northing	309750.3408		278572.2218		275970.8808		285606.9036		263940.4593	
Date (all 2006)	6/10	6/30	6/13	6/29	6/13	6/29	6/13	6/30	6/12	6/30
Start time (A.M. CDT)	7:03	5:50	6:05	7:48	5:29	8:10	8:10	5:27	5:35	8:05
Observer	JN	JN	JN	JN	AO	AO	AO	AO	AO	AO
Cloud cover	0	0	0	3	0	0	0	3	0	0
Temperature	4	3	3	5	1	4	4	2	1	4
Wind speed	1	0	1	0	2	1	1	3	3	1
Sample units	5	5	2	2	5	5	5	5	3	4
Northern Bobwhite	0	0	0	0	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	0	0	0	0	0	0
Wild Turkey	0	0	0	0	0	0	0	1	0	0
Mourning Dove	1	2	0	0	0	0	0	0	0	1
Cooper's Hawk	0	0	0	0	0	1	0	0	0	0
Red-tailed Hawk	0	0	0	0	0	0	0	0	0	0
Red-shouldered Hawk	0	0	0	0	0	0	0	0	0	0
Broad-winged Hawk	2	0	0	0	1	0	0	0	0	0
Barred Owl	0	0	0	0	0	0	0	0	0	0
Great Horned Owl	0	0	0	0	0	0	0	0	0	0
Yellow-billed Cuckoo	1	2	0	0	0	0	0	0	0	0
Black-billed Cuckoo	0	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	1	0	1	1	0	2	2	1	0	2
Downy Woodpecker	0	2	0	0	0	2	0	2	0	2
Pileated Woodpecker	0	0	0	0	0	0	0	0	0	0
Red-headed Woodpecker	0	0	0	0	0	0	0	0	0	0
Red-bellied Woodpecker	1	2	1	1	0	0	2	2	0	0
Northern Flicker	0	0	0	0	0	0	0	0	0	0
Ruby-thr. Hummingbird	0	0	0	0	0	0	2	1	0	0
Great Crested Flycatcher	0	4	1	1	0	0	0	1	1	2
Eastern Phoebe	0	0	0	0	0	0	0	0	0	0
Eastern Wood-Pewee	2	5	3	2	2	1	5	5	1	4
Acadian Flycatcher	4	3	0	0	2	0	1	2	0	0
Alder Flycatcher	0	0	0	0	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0
Blue Jay	0	1	0	0	3	2	3	0	3	4
American Crow	4	2	0	2	0	1	0	0	0	0
Brown-headed Cowbird	2	0	0	0	0	1	1	2	1	0
Red-winged Blackbird	0	0	0	0	0	0	0	0	0	0
Baltimore Oriole	0	0	0	0	0	0	0	0	1	1
House Finch	0	0	0	0	0	0	1	0	0	0
American Goldfinch	3	2	3	1	3	1	3	4	1	0
Chipping Sparrow	0	2	1	1	5	2	0	0	0	0
Field Sparrow	0	0	0	0	0	0	0	0	0	0
Song Sparrow	0	0	0	0	0	0	0	0	0	0

Eastern Towhee	0	0	0	0	0	0	0	0	0	0
Curtis site number	**1009 cont'd**		**1014 cont'd**		**1016 cont'd**		**1017 cont'd**		**1018 cont'd**	
Date (all 2006)	6/10	6/30	6/13	6/29	6/13	6/29	6/13	6/30	6/12	6/30
Northern Cardinal	3	4	2	2	1	1	1	3	0	3
Rose-breasted Grosbeak	0	1	0	0	0	0	0	0	0	0
Indigo Bunting	0	0	0	1	0	0	0	0	3	0
Scarlet Tanager	1	1	0	0	1	3	0	1	1	0
Cedar Waxwing	0	0	0	0	2	0	0	0	0	0
Red-eyed Vireo	6	5	3	2	5	8	5	9	1	4
Yellow-throated Vireo	0	0	1	0	0	0	5	2	0	1
Blue-headed Vireo	0	0	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	0	0	0	0
Cerulean Warbler	2	0	0	0	0	0	2	0	0	0
Chestnut-sided Warbler	0	1	0	0	1	0	0	0	0	0
Black-thr. Green Warbler	0	0	0	0	2	3	0	0	0	0
Ovenbird	4	5	1	0	4	5	4	3	1	2
Mourning Warbler	0	0	0	0	0	0	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0	0	0	0	0
Hooded Warbler	0	1	0	0	1	2	2	4	0	0
American Redstart	1	2	0	0	0	1	0	0	0	0
Gray Catbird	0	0	0	0	0	0	0	0	0	0
House Wren	1	0	0	0	0	0	0	0	0	0
White-breasted Nuthatch	3	4	1	2	0	4	7	4	2	2
Tufted Titmouse	0	0	0	0	0	0	0	1	0	0
Black-capped Chickadee	7	3	1	3	3	6	5	2	1	0
Blue-gray Gnatcatcher	0	3	1	1	0	0	6	6	0	0
Wood Thrush	0	0	0	0	1	4	1	2	0	3
Veery	0	0	0	0	0	0	0	0	0	0
American Robin	1	0	1	2	0	0	3	0	1	0
Total	50	57	21	22	37	50	61	58	18	31

Curtis site number	**1019**		**1020**		**1021**		**1023**		**1024**	
WTM Easting	620366.6302		611785.3112		600484.7465		482105.3647		473273.3799	
WTM Northing	353289.9760		373918.3627		376032.4645		347184.4931		357639.1741	
Date (all 2006)	6/9	7/2	6/8	7/3	6/8	7/3	6/7	7/6	6/6	7/6
Start time (A.M. CDT)	7:00	5:30	7:00	5:22	5:26	7:04	5:50	7:50	8:00	5:32
Observer	AO	AO	AO	JN	AO	JN	AO	JN	JN	JN
Cloud cover	10	2	2	0	1	0	0	5	10	5
Temperature	3	5	4	3	4	4	4	4	4	2
Wind speed	3	2	1	1	1	2	1	0	1	0
Sample units	5	5	5	5	3	2	5	4	5	5
Northern Bobwhite	0	0	0	0	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	0	0	0	0	0	0
Wild Turkey	0	0	0	1	0	0	2	0	0	0
Mourning Dove	0	0	0	1	0	0	0	1	1	0
Cooper's Hawk	1	0	0	0	0	0	0	0	0	0
Red-tailed Hawk	0	0	0	0	0	0	0	1	0	0
Red-shouldered Hawk	0	0	0	0	0	0	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	0	1	0
Barred Owl	0	0	0	1	0	0	0	0	0	1
Great Horned Owl	0	0	0	0	0	0	0	0	1	0
Yellow-billed Cuckoo	0	0	0	1	0	1	0	1	0	0
Black-billed Cuckoo	0	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	1	3	1	0	0	0	0	0	2	1
Downy Woodpecker	2	0	5	2	0	1	0	2	1	2
Pileated Woodpecker	0	0	0	0	0	0	0	0	0	0
Red-headed Woodpecker	0	0	0	0	0	0	0	0	0	0
Red-bellied Woodpecker	2	1	2	2	1	0	0	0	1	0
Northern Flicker	0	0	0	0	1	0	0	1	0	0
Ruby-thr. Hummingbird	0	0	0	0	0	0	0	0	0	0
Great Crested Flycatcher	6	3	2	2	0	0	0	0	0	0
Eastern Phoebe	0	0	0	0	0	0	0	0	1	0
Eastern Wood-Pewee	7	4	7	7	3	1	3	5	5	5
Acadian Flycatcher	0	0	0	0	0	0	3	2	2	2
Alder Flycatcher	0	0	0	0	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0
Blue Jay	1	2	4	2	2	1	1	2	2	3
American Crow	0	1	1	2	2	2	0	0	2	3
Brown-headed Cowbird	1	1	1	0	0	1	3	1	3	2
Red-winged Blackbird	0	0	0	0	0	0	0	0	0	0
Baltimore Oriole	0	0	0	0	0	0	0	0	0	0
House Finch	0	0	0	0	0	0	0	0	0	0
American Goldfinch	1	2	0	3	0	0	1	3	0	0
Chipping Sparrow	0	0	0	0	0	0	0	0	0	2
Field Sparrow	0	0	0	0	0	0	0	0	0	0
Song Sparrow	0	0	0	0	0	0	0	0	0	0

Eastern Towhee	0	0	0	0	0	0	0	0	1	0
Curtis site number	**1019 cont’d**		**1020 cont’d**		**1021 cont’d**		**1023 cont’d**		**1024 cont’d**	
Date (all 2006)	6/9	7/2	6/8	7/3	6/8	7/3	6/7	7/6	6/6	7/6
Northern Cardinal	4	1	0	2	3	2	1	1	0	1
Rose-breasted Grosbeak	1	0	1	0	1	1	2	1	4	2
Indigo Bunting	0	0	1	1	1	1	3	1	1	0
Scarlet Tanager	0	2	2	0	0	0	0	3	0	2
Cedar Waxwing	2	0	5	0	1	0	0	0	0	0
Red-eyed Vireo	11	11	4	6	4	4	5	8	7	7
Yellow-throated Vireo	1	0	0	0	0	0	0	0	0	3
Blue-headed Vireo	1	1	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	0	0	0	0
Cerulean Warbler	0	0	0	0	0	0	0	0	0	0
Chestnut-sided Warbler	0	0	0	0	0	0	0	0	0	0
Black-thr. Green Warbler	0	0	0	0	0	0	0	0	0	0
Ovenbird	0	0	0	0	0	0	4	3	3	7
Mourning Warbler	0	0	0	0	0	0	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0	0	0	0	0
Hooded Warbler	0	0	0	0	0	0	0	0	0	0
American Redstart	0	0	0	0	0	0	1	3	0	0
Gray Catbird	0	0	0	0	0	0	0	0	0	0
House Wren	4	4	5	6	7	2	0	0	0	0
White-breasted Nuthatch	1	2	3	4	1	1	1	4	1	6
Tufted Titmouse	0	0	0	1	0	0	0	0	0	1
Black-capped Chickadee	4	2	0	3	0	1	0	1	1	1
Blue-gray Gnatcatcher	3	2	0	0	0	0	1	3	5	1
Wood Thrush	1	2	2	0	0	0	2	1	1	1
Veery	0	0	0	0	0	0	0	0	0	0
American Robin	4	1	2	0	0	1	1	0	4	3
Total	59	45	48	47	27	20	34	48	50	56

Curtis site number	**1026**		**1027**		**1032**		**1033**		**1034**	
WTM Easting	443907.3724		556631.5208		564127.3376		557889.4780		545275.0547	
WTM Northing	355545.8007		310820.6938		228526.5895		241745.7739		230951.4459	
Date (all 2006)	6/7	7/7	5/29	6/24	6/1	6/19	5/25	6/22	6/8	6/19
Start time (A.M. CDT)	5:33	8:05	7:45	5:33	5:29	6:45	7:50	5:30	7:45	5:35
Observer	JN	JN	AO	AO	AO	JN	AO	AO	JN	JN
Cloud cover	0	0	2	8	6	1	10	5	3	0
Temperature	4	6	7	2	4	5	4	4	5	4
Wind speed	1	1	3	1	0	3	3	2	1	1
Sample units	5	5	5	5	4	3	5	5	2	2
Northern Bobwhite	0	0	0	0	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	0	0	0	0	0	0
Wild Turkey	1	0	0	0	0	0	0	3	2	0
Mourning Dove	0	0	0	0	0	0	0	0	0	0
Cooper's Hawk	0	0	0	0	0	0	0	0	0	0
Red-tailed Hawk	0	0	0	1	0	0	0	1	0	0
Red-shouldered Hawk	0	0	0	0	0	0	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	0	0	0
Barred Owl	0	0	0	0	0	0	0	0	0	0
Great Horned Owl	0	0	0	0	0	0	0	0	0	0
Yellow-billed Cuckoo	0	1	2	3	1	0	0	0	1	0
Black-billed Cuckoo	0	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	1	0	3	0	0	0	1	3	0	0
Downy Woodpecker	0	2	1	2	0	0	0	2	1	1
Pileated Woodpecker	0	0	1	1	0	0	0	0	0	0
Red-headed Woodpecker	1	0	0	0	0	0	0	0	0	0
Red-bellied Woodpecker	1	1	1	1	1	1	2	2	0	0
Northern Flicker	0	1	0	0	0	0	0	1	0	1
Ruby-thr. Hummingbird	0	0	0	0	0	0	0	0	0	0
Great Crested Flycatcher	0	0	5	1	1	1	4	2	0	0
Eastern Phoebe	0	0	0	0	1	0	0	0	0	0
Eastern Wood-Pewee	3	4	4	4	1	2	3	4	2	2
Acadian Flycatcher	1	0	0	0	0	1	0	0	0	0
Alder Flycatcher	0	0	0	0	0	0	1	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0
Blue Jay	2	3	1	1	3	2	6	5	1	0
American Crow	1	0	2	0	1	0	1	6	2	1
Brown-headed Cowbird	2	2	1	0	0	0	2	1	2	2
Red-winged Blackbird	0	0	0	0	0	0	0	0	0	0
Baltimore Oriole	0	0	1	0	0	0	0	1	0	0
House Finch	0	0	0	0	0	0	0	0	0	0
American Goldfinch	0	4	0	1	0	2	0	1	0	1
Chipping Sparrow	0	0	0	0	0	0	0	0	0	0
Field Sparrow	0	0	0	0	0	0	0	0	0	0
Song Sparrow	0	0	0	0	0	0	0	0	0	0

Eastern Towhee	1	0	0	0	0	0	0	0	0	0
Curtis site number	**1026 cont'd**		**1027 cont'd**		**1032 cont'd**		**1033 cont'd**		**1034 cont'd**	
Date (all 2006)	6/7	7/7	5/29	6/24	6/1	6/19	5/25	6/22	6/8	6/19
Northern Cardinal	3	1	0	3	1	1	2	5	2	2
Rose-breasted Grosbeak	3	1	0	0	2	2	4	2	1	0
Indigo Bunting	3	3	0	0	2	0	3	4	1	0
Scarlet Tanager	1	5	4	3	1	0	0	1	0	0
Cedar Waxwing	1	3	2	0	2	0	1	0	0	0
Red-eyed Vireo	5	6	7	9	5	2	5	3	1	1
Yellow-throated Vireo	3	1	1	1	0	0	0	0	0	0
Blue-headed Vireo	0	0	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	0	0	0	0
Cerulean Warbler	0	0	0	0	0	0	0	0	0	0
Chestnut-sided Warbler	0	0	0	0	0	0	0	0	0	0
Black-thr. Green Warbler	0	0	0	0	0	0	0	0	0	0
Ovenbird	4	6	1	4	0	0	1	0	0	0
Mourning Warbler	0	0	0	0	0	0	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0	0	0	0	0
Hooded Warbler	0	0	0	0	0	0	0	0	0	0
American Redstart	3	0	0	0	0	0	2	0	0	0
Gray Catbird	0	0	0	0	0	0	1	2	0	0
House Wren	0	0	1	0	2	2	3	5	2	1
White-breasted Nuthatch	2	0	2	1	0	0	1	2	2	0
Tufted Titmouse	0	1	1	3	0	0	0	0	0	0
Black-capped Chickadee	3	3	0	7	0	1	0	1	0	2
Blue-gray Gnatcatcher	0	1	3	4	0	1	0	0	0	0
Wood Thrush	0	0	1	0	0	1	1	0	0	0
Veery	0	0	0	0	0	0	2	0	0	0
American Robin	2	3	0	1	3	3	1	1	1	1
Total	47	52	45	51	27	22	47	58	21	15

Curtis site number	**1041**		**1052**		**1055**		**1064**		**1067**	
WTM Easting	553964.2278		556871.5342		567713.9260		565718.7957		550139.8920	
WTM Northing	275172.1969		247962.6479		241777.1261		243690.0669		257345.8203	
Date (all 2006)	5/20	6/25	6/8	6/20	5/22	6/24	5/22	6/24	5/20	6/25
Start time (A.M. CDT)	5:34	7:55	6:00	7:30	7:40	5:38	5:36	7:35	7:55	5:30
Observer	AO	AO	JN	JN	AO	JN	AO	JN	AO	AO
Cloud cover	0	6	0	1	0	1	0	9	0	2
Temperature	2	4	4	4	2	3	0	5	3	4
Wind speed	1	0	1	1	0	0	0	0	0	0
Sample units	5	5	3	3	5	5	5	5	5	5
Northern Bobwhite	0	0	0	0	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	0	0	0	0	0	0
Wild Turkey	0	0	0	0	1	0	0	0	0	0
Mourning Dove	0	0	2	2	0	1	0	1	0	0
Cooper's Hawk	0	0	0	0	0	1	0	0	0	0
Red-tailed Hawk	0	0	0	0	3	0	0	0	0	0
Red-shouldered Hawk	0	0	0	0	0	0	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	0	0	0
Barred Owl	0	2	0	0	0	0	0	1	0	0
Great Horned Owl	0	0	0	0	0	0	0	0	0	0
Yellow-billed Cuckoo	0	0	1	0	0	0	1	2	0	1
Black-billed Cuckoo	0	0	0	0	0	0	0	0	2	0
Hairy Woodpecker	2	0	0	1	1	1	1	1	2	0
Downy Woodpecker	0	1	0	0	1	3	0	0	1	3
Pileated Woodpecker	0	0	0	1	0	0	0	0	1	1
Red-headed Woodpecker	0	0	0	0	4	2	0	0	0	0
Red-bellied Woodpecker	3	3	3	1	4	2	0	3	4	3
Northern Flicker	0	0	2	1	0	0	0	1	0	1
Ruby-thr. Hummingbird	0	2	0	0	0	0	0	1	1	0
Great Crested Flycatcher	3	0	1	1	1	0	3	1	1	0
Eastern Phoebe	0	0	0	0	0	0	0	0	0	0
Eastern Wood-Pewee	1	6	3	3	1	4	0	6	0	7
Acadian Flycatcher	0	0	0	0	0	1	0	0	0	0
Alder Flycatcher	0	0	0	0	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0
Blue Jay	1	4	2	2	3	2	1	2	4	3
American Crow	0	1	0	0	3	1	1	1	0	2
Brown-headed Cowbird	6	4	0	0	3	2	3	2	5	2
Red-winged Blackbird	0	0	0	0	0	0	0	0	0	0
Baltimore Oriole	0	0	1	0	0	0	1	0	0	0
House Finch	0	0	0	0	0	0	0	0	0	0
American Goldfinch	1	2	0	0	0	2	0	0	0	0
Chipping Sparrow	0	0	0	0	0	1	0	0	0	0
Field Sparrow	0	0	0	0	0	0	0	0	0	0
Song Sparrow	0	0	0	0	0	0	0	0	0	0

Eastern Towhee	0	0	0	0	0	0	0	0	0	0
Curtis site number	**1041 cont'd**		**1052 cont'd**		**1055 cont'd**		**1064 cont'd**		**1067 cont'd**	
Date (all 2006)	5/20	6/25	6/8	6/20	5/22	6/24	5/22	6/24	5/20	6/25
Northern Cardinal	0	1	4	3	4	4	3	5	0	2
Rose-breasted Grosbeak	2	0	0	1	1	3	5	4	0	0
Indigo Bunting	3	1	2	0	0	0	4	2	0	0
Scarlet Tanager	1	2	0	2	7	2	2	0	4	4
Cedar Waxwing	0	0	0	0	0	1	0	0	0	0
Red-eyed Vireo	4	5	1	2	4	5	4	7	5	8
Yellow-throated Vireo	1	0	0	0	1	1	0	0	1	0
Blue-headed Vireo	0	0	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	0	0	1	0
Cerulean Warbler	0	0	0	0	2	0	0	0	0	0
Chestnut-sided Warbler	0	0	0	0	0	0	0	0	2	0
Black-thr. Green Warbler	3	0	0	0	1	0	0	0	2	0
Ovenbird	3	2	0	0	0	0	0	0	1	0
Mourning Warbler	0	0	0	0	0	0	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0	0	0	0	0
Hooded Warbler	1	1	0	0	0	0	0	0	0	0
American Redstart	0	1	0	0	1	0	0	0	0	0
Gray Catbird	1	1	0	0	0	0	1	2	1	0
House Wren	0	4	3	3	0	0	0	0	1	1
White-breasted Nuthatch	5	8	2	3	4	5	2	3	5	5
Tufted Titmouse	0	1	0	0	0	2	0	1	0	1
Black-capped Chickadee	0	6	0	1	6	4	2	3	1	2
Blue-gray Gnatcatcher	6	5	0	0	1	0	3	3	1	2
Wood Thrush	0	1	2	1	2	3	2	5	3	3
Veery	2	1	0	0	0	0	1	0	0	0
American Robin	1	0	2	1	1	1	3	2	2	0
Total	50	65	31	29	60	54	43	59	51	51

Curtis site number	**1084**		**1085**		**1086**		**1093**		**1095**	
WTM Easting	568600.3157		553480.2632		612411.9157		430400.8735		591161.9800	
WTM Northing	230529.8980		310770.3920		293573.7095		342840.8755		330072.0600	
Date (all 2006)	5/30	6/23	5/29	6/24	6/4	6/19	6/6	7/8	6/3	6/19
Start time (A.M. CDT)	5:45	6:25	5:39	7:27	5:25	5:50	9:10	5:36	5:30	8:15
Observer	AO	AO	AO	AO	AO	AO	AO	JN	AO	AO
Cloud cover	5	2	0	10	8	0	10	5	5	2
Temperature	5	3	7	3	5	4	5	3	4	6
Wind speed	1	2	3	1	2	1	0	0	0	3
Sample units	5	5	5	5	5	5	5	5	5	5
Northern Bobwhite	0	0	0	0	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	0	0	0	0	0	0
Wild Turkey	0	0	0	0	0	0	0	0	1	0
Mourning Dove	0	0	0	0	0	0	0	2	0	0
Cooper's Hawk	0	0	0	0	1	0	0	0	0	0
Red-tailed Hawk	0	0	0	0	0	0	0	1	0	0
Red-shouldered Hawk	0	0	0	0	0	0	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	0	0	0
Barred Owl	0	0	0	0	0	0	0	0	0	0
Great Horned Owl	0	0	0	0	0	0	0	0	0	0
Yellow-billed Cuckoo	2	0	1	0	0	0	0	1	0	0
Black-billed Cuckoo	0	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	1	4	0	1	1	0	1	0	1	0
Downy Woodpecker	0	1	0	2	0	2	1	3	0	1
Pileated Woodpecker	0	0	1	0	0	0	0	1	1	0
Red-headed Woodpecker	1	1	1	0	0	0	0	0	0	0
Red-bellied Woodpecker	4	5	4	0	0	1	1	1	1	0
Northern Flicker	1	1	0	0	0	0	2	2	0	0
Ruby-thr. Hummingbird	0	0	0	0	0	0	0	0	1	1
Great Crested Flycatcher	1	3	1	0	1	3	0	0	0	0
Eastern Phoebe	0	0	0	0	0	0	2	1	0	0
Eastern Wood-Pewee	4	5	4	3	5	4	1	4	6	4
Acadian Flycatcher	0	0	2	2	1	2	0	0	0	0
Alder Flycatcher	0	0	0	0	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0
Blue Jay	4	6	1	1	0	1	3	2	1	0
American Crow	0	0	1	3	2	3	0	2	3	0
Brown-headed Cowbird	1	3	1	3	0	0	4	2	4	1
Red-winged Blackbird	0	0	0	0	0	1	0	0	0	0
Baltimore Oriole	1	1	0	0	0	0	0	0	0	0
House Finch	0	0	0	0	0	0	0	0	0	0
American Goldfinch	0	0	0	0	2	3	0	1	0	0
Chipping Sparrow	0	0	0	0	1	0	0	0	0	0
Field Sparrow	0	0	0	0	0	0	0	1	0	0
Song Sparrow	0	0	0	0	1	0	0	0	0	0

Eastern Towhee	0	0	0	0	0	0	2	1	0	0
Curtis site number	**1084 cont'd**		**1085 cont'd**		**1086 cont'd**		**1093 cont'd**		**1095 cont'd**	
Date (all 2006)	5/30	6/23	5/29	6/24	6/4	6/19	6/6	7/8	6/3	6/19
Northern Cardinal	2	5	1	4	4	5	3	3	0	5
Rose-breasted Grosbeak	3	4	0	0	1	0	6	2	0	0
Indigo Bunting	2	2	2	1	0	1	4	3	6	3
Scarlet Tanager	2	4	1	2	0	1	1	1	1	0
Cedar Waxwing	0	0	0	0	1	1	0	0	0	0
Red-eyed Vireo	5	2	8	5	5	6	3	7	12	8
Yellow-throated Vireo	0	1	1	0	1	2	1	2	0	0
Blue-headed Vireo	0	0	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	3	0	0	0
Cerulean Warbler	1	0	1	0	0	0	0	0	0	0
Chestnut-sided Warbler	0	0	0	1	0	0	0	0	0	0
Black-thr. Green Warbler	0	0	0	0	0	1	0	0	0	0
Ovenbird	0	1	2	3	0	0	1	1	0	0
Mourning Warbler	0	0	1	0	0	0	0	0	0	0
Common Yellowthroat	0	0	0	1	0	0	0	2	0	0
Hooded Warbler	0	0	0	0	0	0	0	0	0	0
American Redstart	0	0	1	2	1	3	3	3	0	0
Gray Catbird	2	2	1	1	0	0	1	3	0	0
House Wren	1	1	0	3	2	3	1	1	3	8
White-breasted Nuthatch	4	2	2	4	1	2	1	2	2	2
Tufted Titmouse	1	0	3	0	0	0	1	0	1	0
Black-capped Chickadee	2	4	0	5	2	6	0	6	2	1
Blue-gray Gnatcatcher	2	1	2	2	1	1	1	1	2	4
Wood Thrush	2	2	0	1	0	0	1	7	0	0
Veery	0	0	0	0	0	0	0	0	0	0
American Robin	1	0	1	3	0	3	1	4	1	0
Total	50	61	44	53	34	55	49	73	49	38

Curtis site number	**1100**		**1103**		**1106**		**1107**		**1108**	
WTM Easting	670052.4712		694671.6774		590963.6019		533218.2640		559871.8857	
WTM Northing	271335.5412		244759.8824		249835.9325		238649.6478		254782.5351	
Date (all 2006)	6/13	6/29	6/12	7/1	6/11	6/20	6/1	7/6	6/1	6/20
Start time (A.M. CDT)	7:15	5:35	8:20	5:27	7:05	5:25	7:40	5:29	8:10	5:45
Observer	JN	JN	AO	AO	AO	AO	AO	AO	JN	JN
Cloud cover	0	0	0	0	7	1	3	0	2	0
Temperature	4	3	3	5	2	3	5	3	5	4
Wind speed	1	0	4	2	3	0	0	0	2	1
Sample units	5	5	5	4	5	5	5	5	3	3
Northern Bobwhite	0	0	0	0	0	0	0	2	0	0
Ruffed Grouse	0	0	0	0	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	1	0	0	0	0	0
Wild Turkey	0	0	0	0	5	0	0	1	0	0
Mourning Dove	0	0	0	0	0	0	0	0	0	2
Cooper's Hawk	0	0	0	0	1	1	0	0	0	0
Red-tailed Hawk	0	0	0	0	1	0	0	0	0	0
Red-shouldered Hawk	0	0	0	0	0	0	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	0	0	0
Barred Owl	0	0	0	0	0	0	0	0	0	0
Great Horned Owl	0	1	0	0	0	0	0	0	0	0
Yellow-billed Cuckoo	0	0	0	0	1	0	0	1	0	1
Black-billed Cuckoo	0	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	1	2	1	0	0	0	1	1	1	0
Downy Woodpecker	4	3	1	1	1	1	1	1	0	0
Pileated Woodpecker	0	0	0	0	0	0	0	0	0	0
Red-headed Woodpecker	0	1	0	0	0	0	0	0	0	0
Red-bellied Woodpecker	4	2	1	0	1	3	4	3	2	2
Northern Flicker	0	0	0	0	0	1	1	0	1	1
Ruby-thr. Hummingbird	1	0	0	1	0	0	0	0	0	0
Great Crested Flycatcher	2	1	4	0	0	1	3	1	0	1
Eastern Phoebe	0	0	0	0	0	0	0	0	0	0
Eastern Wood-Pewee	4	3	2	2	1	1	3	4	2	3
Acadian Flycatcher	0	1	0	0	0	0	0	0	0	0
Alder Flycatcher	0	0	0	0	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0	0	0	0	0
Blue Jay	2	2	1	0	1	2	6	6	1	2
American Crow	1	1	1	1	2	3	1	0	0	0
Brown-headed Cowbird	0	1	1	2	0	3	3	0	1	0
Red-winged Blackbird	0	0	0	0	0	0	0	0	0	0
Baltimore Oriole	0	0	0	0	1	0	1	1	0	0
House Finch	0	0	0	0	0	0	0	0	0	0
American Goldfinch	6	2	0	1	0	1	0	0	0	0
Chipping Sparrow	0	0	0	0	0	0	0	0	0	0
Field Sparrow	0	0	0	0	0	0	1	0	0	0
Song Sparrow	0	0	0	0	0	0	0	0	0	0

Eastern Towhee	0	0	0	0	0	1	0	0	0	0
Curtis site number	**1100 cont'd**		**1103 cont'd**		**1106 cont'd**		**1107 cont'd**		**1108 cont'd**	
Date (all 2006)	6/13	6/29	6/12	7/1	6/11	6/20	6/1	7/6	6/1	6/20
Northern Cardinal	4	4	0	3	6	5	2	5	2	2
Rose-breasted Grosbeak	0	1	0	0	0	3	1	0	3	3
Indigo Bunting	1	2	0	2	2	3	10	3	2	1
Scarlet Tanager	0	3	0	0	1	1	0	2	0	0
Cedar Waxwing	0	0	2	0	1	0	1	0	0	0
Red-eyed Vireo	7	6	5	9	4	2	0	0	2	1
Yellow-throated Vireo	0	0	0	0	0	1	0	0	1	1
Blue-headed Vireo	0	0	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	0	0	0	0
Cerulean Warbler	0	0	0	0	0	0	0	0	0	0
Chestnut-sided Warbler	0	0	0	0	0	0	0	0	0	0
Black-thr. Green Warbler	0	0	0	0	0	0	0	0	0	0
Ovenbird	0	2	3	1	0	0	0	0	0	0
Mourning Warbler	0	0	1	0	0	0	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0	0	0	0	0
Hooded Warbler	0	0	3	4	0	0	0	0	0	0
American Redstart	0	1	0	0	0	0	0	0	1	0
Gray Catbird	0	0	0	0	0	0	2	3	2	1
House Wren	0	0	0	0	0	1	2	2	1	1
White-breasted Nuthatch	2	4	0	2	1	1	2	4	1	3
Tufted Titmouse	0	0	0	0	1	1	0	0	1	0
Black-capped Chickadee	1	4	0	0	3	5	1	2	0	0
Blue-gray Gnatcatcher	2	2	1	0	3	1	0	0	0	0
Wood Thrush	0	3	0	0	0	1	0	0	2	1
Veery	0	0	0	0	0	0	0	0	0	0
American Robin	8	4	1	0	6	1	0	1	1	2
Total	50	56	28	29	44	44	46	43	27	28

Curtis site number	**1109**		**1112**		**1185**	
WTM Easting	544958.3201		432293.4775		527648.3400	
WTM Northing	269758.3543		362477.7910		234054.4600	
Date (all 2006)	6/1	6/23	6/7	7/7	6/2	7/7
Start time (A.M. CDT)	5:45	7:50	8:00	5:38	7:35	5:41
Observer	JN	JN	JN	JN	JN	AO
Cloud cover	1	0	0	0	0	0
Temperature	4	5	5	4	4	3
Wind speed	1	1	1	0	2	0
Sample units	3	3	5	4	3	5
Northern Bobwhite	0	0	0	0	0	0
Ruffed Grouse	0	0	0	0	0	0
Ring-necked Pheasant	0	0	0	0	0	0
Wild Turkey	0	0	0	0	0	0
Mourning Dove	1	1	0	0	0	0
Cooper's Hawk	0	0	0	0	0	0
Red-tailed Hawk	0	0	0	0	0	0
Red-shouldered Hawk	0	0	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0
Barred Owl	0	0	1	0	0	0
Great Horned Owl	0	0	0	0	0	0
Yellow-billed Cuckoo	2	1	0	0	0	0
Black-billed Cuckoo	0	0	0	0	0	0
Hairy Woodpecker	0	0	0	1	0	0
Downy Woodpecker	0	1	0	2	0	1
Pileated Woodpecker	0	0	0	0	0	1
Red-headed Woodpecker	0	0	0	0	0	0
Red-bellied Woodpecker	1	2	1	0	0	2
Northern Flicker	1	0	0	0	0	2
Ruby-thr. Hummingbird	0	0	0	0	0	0
Great Crested Flycatcher	1	1	0	0	2	0
Eastern Phoebe	0	0	0	0	0	0
Eastern Wood-Pewee	2	2	4	3	4	2
Acadian Flycatcher	0	0	0	0	3	1
Alder Flycatcher	0	0	0	0	0	0
Least Flycatcher	0	0	0	0	0	0
Blue Jay	2	2	0	1	0	2
American Crow	0	1	2	1	0	1
Brown-headed Cowbird	0	0	3	5	1	0
Red-winged Blackbird	0	0	0	0	0	0
Baltimore Oriole	0	0	0	0	0	0
House Finch	0	0	0	0	0	0
American Goldfinch	0	0	0	1	5	0
Chipping Sparrow	0	0	0	0	0	0
Field Sparrow	0	0	0	0	0	0
Song Sparrow	0	0	0	0	0	0

Eastern Towhee	0	0	0	1	0	0
Curtis site number	**1109 cont’d**		**1112 cont’d**		**1185 cont’d**	
Date (all 2006)	6/1	6/23	6/7	7/7	6/2	7/7
Northern Cardinal	1	2	2	3	5	1
Rose-breasted Grosbeak	1	1	1	4	0	0
Indigo Bunting	2	2	1	2	0	0
Scarlet Tanager	0	0	0	1	3	1
Cedar Waxwing	0	0	0	0	0	0
Red-eyed Vireo	3	3	6	7	3	4
Yellow-throated Vireo	0	0	1	2	1	0
Blue-headed Vireo	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0
Cerulean Warbler	0	0	0	0	0	0
Chestnut-sided Warbler	0	0	0	0	0	0
Black-thr. Green Warbler	0	0	0	0	0	0
Ovenbird	0	0	2	4	0	0
Mourning Warbler	0	0	0	0	0	0
Common Yellowthroat	0	0	0	0	0	0
Hooded Warbler	0	0	0	0	0	0
American Redstart	0	0	6	1	0	0
Gray Catbird	0	0	0	2	0	0
House Wren	2	4	0	0	8	4
White-breasted Nuthatch	2	2	2	5	1	1
Tufted Titmouse	1	4	2	2	0	1
Black-capped Chickadee	0	0	3	2	1	2
Blue-gray Gnatcatcher	0	0	1	2	7	2
Wood Thrush	2	1	0	1	1	2
Veery	0	0	0	0	0	0
American Robin	1	0	4	4	0	1
Total	25	30	42	57	45	31

1 Approximate center of forest patch where survey took place

2 Observers: Anders Olson (AO); Joseph Nadolski (JN)

3 Cloud cover codes: 0: 0% - 9% of sky clouded; 1: 10%-19%, 2: 20%-29%; 3: 30%-39%; 4: 40%-49%; 5: 50%-59%; 6: 60%-69%; 7: 70%-79%; 8: 80%-89%; 9: 90%-99%; 10: 100%

4 Temperature codes: 0: 40F-44F; 1: 45F-49F; 2: 50F-54F; 3: 55F-59F; 4: 60F-64F; 5: 65F-69F; 6: 70F-74F; 7: 75F-79F

5 Wind speed codes: 0: <1 mile per hour (mph); 1: 1mph-3mph; 2: 4mph-7mph; 3: 8mph-12mph; 4: 13mph-18mph

6 Indicates number of sample units (5 minute point transect + 5 minute walking transect) completed during survey