Avian Species Turnover, Change in Species Composition of Suburban Adapters, and Reduction in Abundance of Suburban Adapters and Urban Invaders in the Central Business District of Rockingham, North Carolina: Comparison of 1994 vs 2021

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Volume 10, 2023 Urban Naturalist No. 58

Urban Naturalist

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Cover Photograph: Four species of exotic urban invaders nested within or on the McNair Furniture Store (the former Everett-McNair Store) in Block 7 in 1994. By 2021, the building's façade on all sides was completely sealed, eliminating their nest sites. This included the new awning supported by 3 topside cables (bottom left of photo), which was of a new design and materials (the flat vinyl underside of the awning eliminated the spaces within its framework). *Passer domesticus* L. (House Sparrow), unexpectedly, was still common in downtown Rockingham in 2021, but they no longer nested at this renamed and restored Arts Richmond building. Photograph © D.B. McNair.

The ***Urban Naturalist*** (ISSN # 2328-8965) is published by the Eagle Hill Institute, PO Box 9, 59 Eagle Hill Road, Steuben, ME 04680-0009. Phone 207-546-2821 Ext. 4, FAX 207-546-3042. E-mail: office@eaglehill.us. Webpage: http://www.eaglehill.us/urna. Published on an article by article basis. **Special issue proposals are welcome**. The *Urban Naturalist* is an open access journal. **Authors**: Submission guidelines are available at http://www.eaglehill.us/urna. **Co-published journals:** The *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, and *Eastern Paleontologist*, each with a separate Board of Editors. The Eagle Hill Institute is a tax exempt 501(c)(3) nonprofit corporation of the State of Maine (Federal ID # 010379899).

Avian Species Turnover, Change in Species Composition of Suburban Adapters, and Reduction in Abundance of Suburban Adapters and Urban Invaders in the Central Business District of Rockingham, North Carolina: Comparison of 1994 vs 2021

Douglas B. McNair[1]

Abstract – Avian species richness within the central business district (42.4-ha plot) at Rockingham, North Carolina in 2021 (18 species) was less than in 1994 (21 species), with a net loss of 3 suburban adapters. A considerable change in species composition of suburban adapters included loss of 2 species, *Turdus migratorius* (American Robin) and *Quiscalus quiscula* (Common Grackle), that no longer breed in this habitat type (but remain in adjacent residential habitat). Except for American Robin and Common Grackle, most counts of individual species in the census plot were not highly concordant with counts from regional Breeding Bird Survey routes. Total breeding density at Rockingham in 2021 (122.2 territories/40 ha) was lower than in 1994 (147.1 territories/40 ha), for both suburban adapters and exotic urban invaders. Species turnover, the change in species composition of suburban adapters, and reduction in abundance of both functional guilds were consistent with a sharp reduction in total mean body mass of suburban adapters (29%), and especially, of exotic urban invaders (55%). Contrary to expectations, the breeding density of suburban adapters was proportionally more abundant in 2021 (67.2%) compared to 1994 (61.4%) because 3 of the 4 species of exotic urban invaders sharply declined in abundance and distribution within the 25-block study area of downtown Rockingham. Building condition has improved over the 27-year interval, but is an insufficient explanation for the decline of *Columba livia* var. *domestica* (Feral Pigeon), *Sturnus vulgaris* (European Starling), and *Haemorhous mexicanus* (House Finch), since *Passer domesticus* (House Sparrow) has increased in abundance. I speculate that selective predation by *Accipiter cooperii* (Cooper's Hawk) on Feral Pigeons and European Starlings and a decline of House Finch after an outbreak of mycoplasmal conjunctivitis reached Rockingham is the most parsimonius explanation for these results.

Introduction

Most long-term community-level studies in urban environments have disproportionately focused on birds (Fidino and Magle 2017). Most of these avian studies have quantified the effects of urbanization on species richness, species turnover, and changes in species composition through time, with most studies solely focused on the breeding bird community (see Shultz et al. 2011 for a non-breeding season study). These long-term studies in urban environments have varied in spatial extent from local to regional comparisons over multiple habitats (e.g., Abrahamczyk et al. 2021, Shultz et al. 2011), which have included rural areas (e.g., Leveau 2022), to a single site comparison with or without extensive habitat changes (Abrahamcyzk et al. 2021, Aldrich and Coffin 1980, Fidino et al. 2022). The duration of these studies has extended to over a century (Fidino and Magle 2017, Fidino et al. 2022; Shultz et al. 2011), but much shorter intervals are typical (≤ 30 years), to as low as an interval of 6 years (Leveau 2022). Studies of breeding bird communities have been continuous (data collected every year), but most have been discontinuous (data not collected every year, often in just 2 years with a long interval between years; Aldrich and Coffin 1980, Abrahamczyk et al. 2021). The studies at continuous

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Associate Editor: Michael Strohbach, Technische Universität Braunschweig.

or discontinous time intervals may stand alone, without corroborating data to inform how species populations may have fluctuated during the time interval (Aldrich and Coffin 1980), or be complemented by independent long-term data sets that cover the duration of the interval that may provide information on annual fluctuations in bird populations. One such long-term data set is the Breeding Bird Survey (BBS) that began in 1966 (USGS 2022). Although designed as a large-scale survey of North American bird assemblages (Schipper et al. 2016), local or regional BBS routes have been used to compare species relative abundance to results from local census plots that used the spot-mapping technique (continuous interval: Brooks and Bonter 2010; discontinuous interval: Curtis and Robinson 2015).

In contrast to most other long-term urban studies in North America which have included habitats such as parks or residential suburbs (Aldrich and Coffin 1980, Fidino et al. 2022), detailed knowledge of the composition of avian communities during the breeding season in central business districts of towns and cities in the Southeast is generally poor (McNair 2021). McNair (2021), using the spot- or territory mapping method, documented species richness, species composition, breeding densities, and the distribution of avian species that nested within the central business district of the City of Rockingham, the county seat of Richmond County, North Carolina, in 1994. These avian species included native suburban adapters such as *Mimus polyglottos* L. (Northern Mockingbird) and exotic urban invaders such as *Passer domesticus* L. (House Sparrow). Breeding bird censuses in the same plot were also conducted for scarce to uncommon species in 3 later years (2012, 2016–2017), but effort was not comparable and generally ignored common species. In addition, McNair (2021) documented information on species turnover based on these later censuses in comparison to 1994. This included the loss of 2 formerly common suburban adapters, *Turdus migratorius* L. (American Robin) and *Quiscalus quiscula* L. (Common Grackle), plus an additional net loss of 5 scarce species of suburban adapters. No urban invaders were lost, although the uncommon *Columba livia* var. *domestica* Gmelin (Feral Pigeon) had declined. However, a year-by-year comparison for all species with 1994 results was lacking.

Thus, I conducted in 2021 a discontinuous long-term breeding bird census in the central business district of Rockingham, NC—a single site comparison at a single habitat where the rate of urbanization is slow without extensive changes (McNair 2021)—over a typical interval (≤ 30 years; Fidino and Magle 2017) of 27 years (1994 vs 2021). I complemented these repeat censuses by analyses of BBS data from routes in the northern Pee Dee region of the Carolinas that provide information on annual fluctuations in species relative abundance of bird populations that surround Rockingham compared to these species absolute abundance within my local census plot. The first objective of this study is to present a year-by-year comparison (1994 vs 2021) of species richness, species turnover, changes in species composition, and breeding densities of avian species in the central business district (hereafter, called downtown) of the City of Rockingham to advance our understanding of the patterns and processes of biotic homogenization of towns (reviewed in McNair 2021). Repeat censuses of breeding bird census plots have been performed for some habitat types in southeastern North America (e.g., Aldrich and Coffin 1980, Engstrom et al. 1984, Imhof 1995), but not for any core urban environment. A minor shift toward more buildings and less vegetation has occurred within the study plot in downtown Rockingham since 1994 (see methods). Therefore, from greater homogenization of this urban environment, I would expect a decrease in species richness, low species turnover but considerable change in species composition, and a decrease in abundance of suburban adapters in contrast to no change in species richness, no species turnover and no change in species composition, and an increase in abundance for urban invaders between the 2 years. The second objective of this study was to complement this comparison at a small spatial scale by documenting changes in total body mass of both functional guilds (suburban adapters, urban invaders). I expected changes in this aggregate ecosystem property of total biomass (Catano et al. 2020), used as another measure of the local stability of this avian community during the breeding season, to roughly parallel expected changes in the above 4 parameters for suburban adapters and urban invaders, since the degree of urbanization has slightly increased (Abrahamczyk et al. 2021). The final objective of this study was to focus on a comparison of the breeding status, distribution, and nest site characteristics of 4 urban invaders at buildings and other anthropogenic nest sites, except for *Haemorhous mexicanus* P.L. Statius Müller (House Finch) nesting at vegetative nest sites (McNair 2021, 2022a). The most commonly studied small-bodied urban bird worldwide has been the House Sparrow (Fidino and Magle 2017), which has significantly declined in part of their range, including North America where House Sparrows are an invader (Berigan et al. 2020). This study, in addition to information available in McNair (2021, 2022b), provides new information including an unexpected result, on the ecology and demography of the House Sparrow in downtown Rockingham.

Methods

Study area description

The study area includes a portion of the Rockingham Historic District and other buildings listed on the National Register of Historic Places (Turberg and Pezzoni 2008). Most of these historic buildings, of diverse architectural styles, were built in the late 19th and early 20th centuries. The earliest extant commercial building in Richmond County, the Everett-McNair Store, was built in 1871 but the greatest concentration of commercial buildings is from the 1900s–1920s (Turberg and Pezzoni 2008). The oldest structure within the study area is the Leak-Wall House, built in 1853. Some restored historic structures are used for community and business purposes, but despite modest urban renewal efforts over the past 3 decades (Turberg and Pezzoni 2008), which have accelerated over the past decade (J.R. Massey, Jr., Assistant City Manager, City of Rockingham, pers. comm.; McNair 2021), vacant buildings remain. A full description of the study area (42.4 ha; Fig. 1), the central business district of Rockingham, is available in McNair (2021).

The estimated gain in building area within the study area of downtown Rockingham since 1994 (6.59 ha; McNair 2021) compared to 2021 (6.905 ha) is 4.6%. This included construction of new buildings and demolition of old buildings (>50 years). I categorized the landscape matrix of all vascular plant species within the study area into 5 elements: espaliers and trellises, solitary trees, or shrubs usually spaced at least 1.3–1.5 m apart, hedgerows (rows of closely spaced shrubs and/or low-growing trees with an occasional tall tree, which may include exotic species and remnant native vegetation), tree rows, and small woodlots (restricted areas of woodland) which are the most complex element. The estimated loss of vegetation since 1994 has been approximately 6% (McNair 2021; McNair 2021, unpubl. data). The greatest loss of vegetation since 2017 has continued to be hedgerows (McNair 2021), although the greatest proportion of vegetation removed for any of the 5 vegetative elements (McNair 2022a) has been espaliers and trellises.

Avian surveys

Species nomenclature for scientific names, authorities, and common names follows Chesser et al. (2021) and ITIS (2022).

Breeding Bird Census (BBC) data. Avian censuses at Rockingham in 2021 used the spot- or territory-mapping method—the same method used in 1994 (McNair 2021), to estimate densities. The census period in 2021 was 21 consecutive days during the peak breeding period from 23 April to 13 May when I visited the plot 51 times for a total of 90 hours, half of which (50.8%)

began at sunrise. The 21-d census period was colder (1.36° C below normal) and much drier with a total rainfall of 4.14 cm compared to Normals period (1981–2010) means at Hamlet (latitude 34.8863 N, longitude 79.6924 W, 107 m asl), NC (NRCC 2021), which facilitated efficient censuses. In addition to spot-mapping, I used the location of 65 and 41 active nests, respectively, of suburban adapters and urban invaders plus confirmed breeding attempts without direct evidence, but based on observations of behavior, to confirm the number of territories, especially for urban invaders breeding at anthropogenic nest sites (buildings and associated structures). The duration of the census period in 2021 was much shorter compared to 1994. Consequently, the nest data were insufficient to perform analyses for the effects of buildings and vegetation on species richness and the number of nest records, except for comparison of the area of buildings within blocks among all blocks, with and without nests, for 3 species of urban invaders breeding at buildings in 1994 and 2021.

Figure 1 The 25-block study area in downtown Rockingham, Richmond County, North Carolina, with each block represented by a number, largely consists of buildings and other sealed surfaces, with smaller areas of a mixture of native and exotic vegetation, including lawns. The 0.4-km perimeter beyond the study area boundary is designated by a black dashed line. The source of the image is from the North Carolina Orthoimagery Program (date of imagery 8 March 2015) and is used with permission.

Breeding Bird Survey (BBS) data. The BBS is a large-scale, long-term survey that provides information on the relative abundance of birds along roadside routes based on 3-min counts at 50 stops 0.8 km apart (Sauer et al. 2019, USGS 2022). Sauer et al. (2019) provide information for online analysis of BBS data through 2019. However, I used the BBS operations website (USGS 2022) to extract raw bird count data from 1990 through 2021 from 12 individual BBS routes within or near the northern Pee Dee region of the Carolinas (McNair 2016) that surround Rockingham, NC (Appendix 1). Coverage on 10 of these 12 routes did not begin until the 1990s, corresponding with my BBC study at Rockingham in 1994, and most routes were run in 2021, when my repeat census was conducted. Nonetheless, route surveys from 1990 to 2021 varied in the quality of information based on potential confounding factors such as differences among physiographic provinces, the span of years routes were run, the number of years run (median = 22 years; range = 12–28), and observer ability. Furthermore, most stops on each of the 12 BBS routes are located in rural, not urban areas. Thus, urban areas are undersampled by these routes. Secondly, bird habitat information is not provided by BBS data, unlike BBC data which is associated with specific measured habitats, such as at downtown Rockingham. Thus, population estimates of relative abundance of avian species provided by BBS data within or near the northern Pee Dee region will be strongly biased toward habitats in rural areas and may not represent population changes that have occurred for these species over a 27-year interval in downtown Rockingham because I could not match my census plot with any BBS route except for road-bias. With these caveats, BBS data is the only source that provides systematic long-term information for this region that covers the 27-year interval of my BBC study in downtown Rockingham.

Data analysis

Breeding Bird Census (BBC) data. I calculated species richness (number of different species present), species turnover (the sum of the difference in the loss and gain of species composition between the 2 years), and densities of breeding birds for both functional guilds (suburban adapters, urban invaders) for the entire 25-block study area (McNair 2021) to examine homogenization of the avian community between the years 1994 and 2021 in downtown Rockingham. I also calculated Bray-Curtis dissimilarity indices for species abundance data to compare avian community changes among the 2 species groups (suburban adapters and urban invaders) between the 2 years. In addition, intense search effort directed toward the number and location of nest records at anthropogenic nest sites allowed me to closely document the distribution of urban invaders breeding in the study area. Thus, I compared the area of buildings within blocks among all blocks with and without nests using Mann-Whitney U tests for 3 species of urban invaders breeding at buildings in 1994 and 2021.

I extracted data on mean body mass (g), used as another measure of the local stability of this avian community during the breeding season, matched to adult sex and to the geographic region of southeastern North America if available, from species accounts in Birds of the World (Cornell Lab of Ornithology 2022) for all species except *Charadrius vociferus* L. (Killdeer), for which I used Brunton (1988). I calculated total mean body mass for all birds and by functional guild or subgroup thereof for each year, 1994 vs 2021, by multiplying the number of breeding pairs for each sex for each species by their mean body mass. I then tested for significant differences in total biomass of breeding species between the 2 years using a 2-tailed paired Wilcoxon signed-rank test for all species as well as suburban adapters with and without American Robin and Common Grackle, respectively.

Breeding Bird Survey (BBS) data. I extracted data for 15 species that occurred on a minimum of 3 breeding territories during at least 1 of the 2 years in my BBC study area. All of these species are easily detected by sight or sound. First, I removed 45 outliers from the total of 3720

Table 1 Number of territories, territories per 40 hectares, and percent change in the number of territories between 2 years (1994, 2021) for 25 avian species that had established territories[1] within the 25-block area in downtown Rockingham, North Carolina.

Scientific name (Common name)	1994 Territories	2021 Territories	1994 Territories/ 40 ha	2021 Territories/ 40 ha	1994 vs 2021 Percent change (%)[2]
SUBURBAN ADAPTERS					
Zenaida macroura L. (Mourning Dove)	15.5	14	14.6	13.2	Decrease: 9.7%
Chaetura pelagica L. (Chimney Swift)	1	3	0.9	2.8	Increase
Charadrius vociferus L. (Killdeer)	1	1	0.9	0.9	No change
Melanerpes carolinus L. (Red-bellied Woodpecker)	1	0	0.9	0	Decrease
Myiarchus crinitus L. (Great Crested Flycatcher)	1	0.5	0.9	0.5	Decrease
Tyrannus tyrannus L. (Eastern Kingbird)	0	1	0	0.9	Increase
Lanius ludovicianus L. (Loggerhead Shrike)	1	0	0.9	0	Decrease
Cyanocitta cristata L. (Blue Jay)	1	0	0.9	0	Decrease
Corvus brachyrhynchos (C.L. Brehm, 1822) (American Crow)	0	1	0	0.9	Increase
Poecile carolinensis (Audubon, 1834) (Carolina Chickadee)	0	3.5	0	3.3	Increase
Sitta pusilla Latham (Brown-headed Nuthatch)	1	0	0.9	0	Decrease
Thryothorus ludovicianus Latham (Carolina Wren)	8	12.5	7.6	11.8	Increase: 56.3%
Turdus migratorius L. (American Robin)	13.5	0	12.7	0	Decrease: locally extirpated
Dumetella carolinensis L. (Gray Catbird)	6	8	5.7	7.5	Increase: 33.3%
Toxostoma rufum L. (Brown Thrasher)	9	6.5	8.5	6.1	Decrease: 27.8%
Mimus polyglottos L. (Northern Mockingbird)	11	18	10.4	17	Increase: 63.6%
Spizella passerina (Bechstein, 1798) (Chipping Sparrow)	0	3	0	2.8	Increase
Icterus spurius L. (Orchard Oriole)	1	2	0.9	1.9	Increase
Quiscalus quiscula L. (Common Grackle)	18	0	17.0	0	Decrease: locally extirpated
Cardinalis cardinalis L. (Northern Cardinal)	6	13	5.7	12.3	Increase: 117%
Passerina caerulea L. (Blue Grosbeak)	1	0	0.9	0	Decrease
Subtotal	96	87	90.3	82.1[3]	Decrease: 9.4%
URBAN INVADERS					
Columba livia var. *domestica* Gmelin (Feral Pigeon)	5	1	4.7	0.9	Decrease
Sturnus vulgaris L. (European Starling)	22	9	20.8	8.5	Decrease: 59.1%
Passer domesticus L. (House Sparrow)	20	28	18.9	26.4	Increase: 40%
Haemorhous mexicanus P.L. Statius Müller (House Finch)	13	4.5	12.3	4.2	Decrease: 65.4%
Subtotal	60	42.5	56.7	40.1[3]	Decrease: 29.2%
TOTAL	156	129.5	147.1[3]	122.2[3]	DECREASE: 17.0%

[1]Based on minimum territory size from spot-mapping of 0.5.
[2]Percent change only calculated for species with a minimum of 3 territories in both years.
[3]Corrects for rounding errors.

counts (1.2%). Even after data transformation, not all data for all species approximated a normal distribution, so I used non-parametric statistics to evaluate the BBS data (parametric statistics provided similar results). I calculated the median number of birds for each species on each route for all the years run and for only the last 6 years a route was run, respectively; these 2 year-groups are not independent. From these median numbers of individual routes, I next calculated the median number of birds for each species over all routes for each of these 2 year-groups, respectively. I then calculated the ratio of the median number of birds of the 2 year-groups for each species to obtain an estimate of recent proportional population change. I also conducted Spearman's correlation analyses on count data over all years to obtain a positive or negative population trend, regardless of significance, on each of the 12 routes for the 15 species. I then used a 2-tailed binomial test (sign test) to examine the null hypothesis of no difference among the routes in the direction of population trends (e.g., P = 1.0 with 6 positive and 6 negative trends) for each of these species.

All analyses, including descriptive statistics, were performed with statistical software available from VasserStats (2022) and Real Statistics Using Excel (Zaiontz 2022).

Results

BBC at Rockingham

Species richness, species turnover, and species composition. A total of 25 species nested in downtown Rockingham over the 2 years, 1994 and 2021, with 14 species (10 suburban adapters, 4 urban invaders) present both years (Table 1). Total species richness and species richness for suburban adapters in 1994 (21 species: 17 suburban adapters and 4 urban invaders) was greater compared to 2021 (18 species: 14 suburban adapters and 4 urban invaders). Thus, species turnover in 1994 compared to 2021 was a net loss of 3 suburban adapters. The change in species presence-absence between the 2 years was 35% for suburban adapters, whereas it was 0% for urban invaders (no change in species composition). Two of these suburban adapters (American Robin and Common Grackle) no longer breed in this habitat type (but remain in adjacent residential areas). Five species of suburban adapters that nested as single pairs in 1994 did not nest in 2021, whereas 4 species of suburban adapters not nesting in 1994 did nest in 2021, 2 of which had at least 3 territorial pairs (Table 1).

In 2021, 62 other avian species visited but did not nest within the Rockingham plot (Appendix 2). This included a pair of *Molothrus ater* Boddaert, 1783 (Brown-headed Cowbird) which flew over the plot on 30 April.

Breeding densities. Total breeding density in 1994 (147.1 territories/40 ha) and for each functional guild (suburban adapters: 90.3 territories/40 ha; urban invaders: 56.7 territories/40 ha) was greater compared to total breeding density in 2021 (122.2 territories/40 ha) and for each functional guild (suburban adapters: 82.1 territories/40 ha; urban invaders: 40.1 territories/40 ha) (Table 1). The total percent decrease in breeding density in 2021 relative to 1994 was 17%, but much higher for urban invaders (29.2%) compared to suburban adapters (9.4%). Thus, the breeding density of suburban adapters was proportionally greater in 2021 (67.2%) compared to 1994 (61.4%). Excluding American Robin and Common Grackle breeding populations, breeding densities of all other suburban adapters in 2021 increased 34.9%.

Breeding densities in 1994 compared to 2021 increased for 11 species (10 suburban adapters and 1 urban invader) and decreased for 13 species (10 suburban adapters and 3 urban invaders); the breeding density for 1 species did not change (Table 1). According to Bray-Curtis dissimilarity indices, similarity between the 2 years was higher for urban invaders (0.33) than for suburban adapters (0.40), but strong changes in abundance occurred for a number of species in both functional guilds. The most pronounced increase in breeding densities was for 3 suburban adapters: *Cardinalis cardinalis* L. (Northern Cardinal), Northern Mockingbird, and *Thryothorus ludovicianus* Latham (Carolina Wren), whereas the next highest increase was for House Sparrow (40%)—an urban invader. Excluding loss of 2 species (American Robin and Common Grackle) that no longer breed in this habitat type, the most pronounced decrease in breeding densities between 1994 and 2021 was for 2 urban invaders: *Sturnus vulgaris* L. (European Starling) and House Finch. Otherwise, the greatest decrease was for a suburban adapter, *Toxostoma rufum* L. (Brown Thrasher).

Body mass. The total mean body mass for all birds of both functional guilds was 38.7% less in 2021 compared to 1994 (Table 2). Nonetheless, the change in total biomass between the 2 years was not significant (Wilcoxon signed-rank tests for all species: $n_{s/r}$ = 24, W = 44, P = 0.53; all suburban adapters: $n_{s/r}$ = 20, W = 0, P = 1.0; suburban adapters excluding American Robin and Common Grackle: $n_{s/r}$ = 18, W = −39, P = 0.40). The total loss of mean body mass for urban invaders was (813 g) more than for suburban adapters, a comparative loss of 16.7%, but the percent decline of mean body mass of urban invaders was almost twice as much (55.1% versus 28.6% for suburban adapters; Table 2). Thus, the mean body mass of suburban adapters was proportionally more dominant in 2021 (74%) compared to 1994 (61.6%). Excluding the collapse of American Robin and Common Grackle breeding populations, mean body mass of all other suburban adapters increased 21.6% in 2021.

Distribution. The distribution of 3 urban invaders (Feral Pigeon, European Starling, and House Finch) nesting at anthropogenic nest sites in 1994 sharply declined between 1994 and 2021, whereas the distribution of House Sparrow remained unchanged at 12 blocks (Table 3). House Sparrows nested within the same 10 blocks both years, whereas in 1994 they also nested in blocks 13 and 19, and in 2021 they nested in blocks 4 and 24.

Anthropogenic nest sites of urban invaders. Blocks with anthropogenic nest sites of House Sparrows contained a greater area of buildings in both years (median = 0.37–0.40 ha, n = 12) compared to blocks without nests (median = 0.17 ha, n = 13; 1994: Mann-Whitney U = 29, P = 0.008; 2021: U = 30, P = 0.009). Blocks with anthropogenic nest sites of European Starlings contained a greater area of buildings in 1994 (median = 0.37 ha, n = 12) compared to blocks without nests (median = 0.14 ha, n = 13; Mann-Whitney U = 23, P = 0.003), but not in 2021 (median = 0.33 ha, n = 6) compared to blocks without nests (median = 0.24, n = 19; U = 39, P = 0.27). Blocks with anthropogenic nest sites of House Finches in 1994 did not contain a greater area of buildings (median = 0.27, n = 12) compared to blocks without nests (median = 0.19, n = 13; Mann-Whitney U = 71.5, P = 0.72), but too few nests were present in 2021 to permit a

Table 2 Total mean body mass (g) of the avian breeding community by functional guild in 1994 and 2021 within the 42.4-ha breeding bird census (BBC) plot at Rockingham, North Carolina

Functional guild	Mean body mass (g)		
	1994	2021	Difference (percentage gain or loss)
All birds in both functional guilds	22,991	14,084	−8,907 (−38.7%)
All urban invaders	8,824	3,964	−4,860 (−55.1%)
All suburban adapters	14,167	10,120	−4,047 (−28.6%)
Suburban adapters: only including *Turdus migratorius* and *Quiscala quiscula*	5,843	0	−5,843 (−100%)
Suburban adapters: excluding *Turdus migratorius* and *Quiscala quiscula*	8,324	10,120	+1,796 (+21.6%)

test. Of the 73 and 41 active nest sites of the 4 urban invaders in 1994 and 2021, respectively, 70 (96%) and 37 (90%) were in buildings (and associated structures) >50 years old; only 1 European Starling nest site, 4 House Sparrow nest sites (3 in newer signs in 2021), and 1 House Finch nest site were in younger buildings.

BBS from the northern Pee Dee region

The median number of birds based on BBS data from the northern Pee Dee region of the Carolinas was low (< 5 birds/route) for 3 of the 15 avian species (suburban adapter: Gray Catbird; urban invaders: Feral Pigeon and House Finch) considered herein (Table 4). Recent proportional population changes for these 3 species were 0% and their sample sizes from individual BBS routes for positive and negative population trends were too low to perform 2-tailed binomial tests.

Of the remaining 12 more numerous species, 3 of 4 species (2 suburban adapters: American Robin and Common Grackle, and 1 urban invader: House Sparrow) with the greatest recent proportional population declines on BBS surveys from the northern Pee Dee region, at least 45%, also had significant negative population trends among all 12 BBS routes (2-tailed binomial tests; Table 4), regardless of the number of significant trends (Spearman's correlation tests) on individual routes. Based on BBS data, the severe recent population decline of the fourth species (Chimney Swift), approached significance. Otherwise, the most recent proportional population decline from the Pee Dee region was just under 23% for Brown Thrasher, which was not significant (Table 4). In contrast, no significant increases occurred for any of the 3 species with recent positive population trends. The greatest recent proportional population increase for any species on these BBS surveys from the northern Pee Dee region was for Carolina Wren, at almost 12%. The most anomalous result for any species from BBS data was for Chipping Sparrow, whose recent proportional population change was a slight decrease, yet had a positive trend on 9 of the 12 individual BBS routes.

Discussion

Any conclusions generated from a single site study in 1 novel habitat for southeastern North America are limited. Regardless, the 2 functional guilds of avian species that have nested in

Table 3. Number of blocks where breeding was confirmed for 4 species of exotic urban invaders nesting at buildings in 1994 and 2021 within the 25-block study area at Rockingham, North Carolina.

Scientific name (Common name)	Number of blocks 1994	2021	1994 vs 2021: Percent change (%)
Columba livia var. *domestica* Gmelin (Feral Pigeon)	7	1[1]	Decrease: 85.7%
Sturnus vulgaris L. (European Starling)	12	6[2]	Decrease: 50%
Passer domesticus L. (House Sparrow)	12	12	No Change
Haemorhous mexicanus P.L. Statius Müller (House Finch)	12	2[3]	Decrease: 83.3%

[1]Breeding confirmed in block 1 in both years.
[2]Breeding confirmed in 5 of the 6 blocks in 2021 in both years; breeding confirmed in block 21 only in 2021.
[3]Breeding confirmed in both blocks (12, 20) in 2021 in both years.

Table 4. Median number of birds, the recent proportional population change in the median number of birds (+ = increase; − = decrease), and the number of positive and negative population trends over 12 Breeding Bird Survey (BBS) routes for 15 avian species that had at least 3 breeding territories in 1 or both years (1994, 2021) on the 42.4 ha plot in downtown Rockingham, North Carolina. The 2-tailed binomial test analyses the number of positive and negative trends (regardless of statistical significance) for each species. See methods section for full explanation in text.

Species	Median number	Recent proportional population change (%)[1]	Positive trend[2,3]	Negative trend[2,3]	2-tailed binomial test (*P*)
SUBURBAN ADAPTERS					
Zenaida macroura L. (Mourning Dove)	41.5	-5.4	6 (2)	6 (2)	1.0
Chaetura pelagica L. (Chimney Swift)	10	-52.5	2 (2)	9 (6)	0.065
Poecile carolinensis (Audubon, 1834) (Carolina Chickadee)	7.75	+6.4	6 (1)	6 (3)	1.0
Thryothorus ludovicianus Latham (Carolina Wren)	25.25	+11.9	6 (2)	6 (3)	1.0
Turdus migratorius L. (American Robin)	8.5	-50.0	2	10 (4)	**0.04**
Dumetella carolinensis L. (Gray Catbird)	0	0	2	3 (3)	No test[4]
Toxostoma rufum L. (Brown Thrasher)	7.75	-22.6	4 (1)	8 (4)	0.39
Mimus polyglottos L. (Northern Mockingbird)	30	-16.7	7 (1)	5 (1)	0.77
Spizella passerina (Bechstein, 1798) (Chipping Sparrow)	18.75	-4.0	9 (2)	3 (1)	0.15
Quiscalus quiscula L. (Common Grackle)	18.25	-45.2	1	11 (8)	**0.006**
Cardinalis cardinalis L. (Northern Cardinal)	40.75	+1.1	8 (4)	4	0.39
URBAN INVADERS					
Columba livia var. *domestica* Gmelin (Feral Pigeon)	0	0	1	2	No test[4]
Sturnus vulgaris L. (European Starling)	11	-18.2	3 (1)	8 (4)	0.23
Passer domesticus L. (House Sparrow)	5	-70.0	2	8 (5)	**0.02**
Haemorhous mexicanus P.L. Statius Müller (House Finch)	1.5	0	5 (2)	3	No test[4]

[1]Recent proportional change is the ratio of the grand median number of birds for each species over all 12 routes for all years run compared to only the last 6 years run, respectively.
[2]Determined by Spearman's correlation analyses. Individual BBS routes were omitted when count data were inadequate to calculate a reliable trend.
[3]Number of significant trends on individual routes is in parentheses.
[4]Sample size too small (< 10 routes) to use this test.

downtown Rockingham showed a negative outcome, loss of 2 suburban adapters, and a positive outcome of a pronounced decrease of 3 urban invaders. McNair (2021) previously documented the loss of American Robin and Common Grackle, so their continued absence in 2021 was expected even though they were formerly (1994) 2 of the 3 most abundant suburban adapters. Except for robins and grackles, most counts of individual species in the census plot were not highly concordant with counts from regional Breeding Bird Survey routes. Otherwise, species composition on the census plot after 27 years has not shifted except for gain or loss of scarce suburban adapters, which was a net loss of 1 species. Consequently, species turnover of suburban adapters was not as severe as suggested before (McNair 2021). However, despite only a slight increase in the degree of urbanization at Rockingham, the change in species composition of suburban adapters was considerable, which has been a typical temporal trend of long-term studies in urban (and non-urban) environments regardless of the scale of investigation and the many factors that can contribute to these changes (Abrahamczyk et al. 2021, Aldrich and Coffin 1980, Fidino and Magle 2017, Fidino et al. 2022, Schipper et al. 2016, Shultz et al. 2011). Despite these losses of suburban adapters at Rockingham, their breeding density, and even more so mean body mass, were proportionally more abundant in 2021 compared to 1994. These unexpected results occurred because 3 of the 4 species of exotic urban invaders sharply declined in abundance and distribution within the 25-block study area of downtown Rockingham. Thus, all measures (species richness, species composition, breeding densities, and distribution) have documented an absolute loss of biodiversity in 2021 compared to 1994. However, the proportional increase of suburban adapters vis-a-vis urban invaders was positive, so the loss of local stability through loss of biomass in this avian community during the breeding season (Catano et al. 2020) is less negative and impactful than it otherwise would have been. Only a minor loss of vegetation and a minor gain in the area of buildings has occurred in downtown Rockingham, so small-scale changes in habitat are not sufficient to explain changes in abundance of different species groups. Extant vegetative habitat remains structurally suitable for nesting suburban adapters and 1 urban invader (House Finch; McNair 2022a; McNair 2021–2022, unpubl. data). Buildings and associated structures also remain structually suitable for several suburban adapters and all urban invaders. Consequently, other than structural features of habitat, what has driven changes in avian community composition in downtown Rockingham after 27 years?

McNair (2021) previously documented that building area was positively associated with the number of nest records at buildings for 2 urban invaders (European Starling and House Sparrow), which this study has reaffirmed by directly comparing building area of blocks with and without nest records of these 2 species in 1994. This comparison remained true for House Sparrows in 2021, but not for European Starlings as their abundance and distribution plummeted, even though total building area in downtown Rockingham slightly increased. The relationship of building area with building condition is inexact, but building condition in downtown Rockingham, which has many historic buildings (see study area description), has improved over the 27-year interval (McNair 2021, this study). Nonetheless, most active nests were in older buildings which still contain many cavities, crevices, and ledges. Consequently, building condition is an insufficient explanation for the decline of Feral Pigeon, European Starling, and House Finch, since the most numerous and widespread urban invader in 2021, the House Sparrow, has increased in abundance though its distribution was stable and still truncated at 12 blocks.

Feral Pigeon. Feral Pigeons have declined in downtown Rockingham as a result of improvements in building condition that eliminated some nest sites (McNair 2021), but also from predation by *Accipiter cooperii* (Bonaparte, 1828) (Cooper's Hawk). Cooper's Hawk has sharply increased during spring in the Piedmont of North Carolina since the 1990s (Sauer et al. 2019, Westphal 2006); their potential effect of increased predation on pigeons and other species would be greatest in eastern North America where their population decline was the steepest (B.A.

Millsap, pers. comm.). Feral Pigeons have been preferred prey of female Cooper's Hawks in suburban and urban environments (Millsap 2018, Roth and Lima 2003), where most predation occurs outside the breeding season since females do little hunting while breeding (B.A. Millsap, pers. comm.). This decline of Feral Pigeons in downtown Rockingham since the mid-2010s has continued to the present; several pairs of Cooper's Hawk breed in residential and semi-residential areas of Rockingham, with 1 pair located within 0.5 km of the study plot (McNair 2021, unpubl. data). Cooper's Hawk predation may now be the main factor in driving the decline of Feral Pigeons.

European Starling. European Starlings, based on differences in their annual indices of abundance on Breeding Bird Survey routes from 1994 to 2019 which do not impart information on habitat, have declined 39% in North Carolina (Sauer et al. 2019). Their recent proportional decline on routes in the northern Pee Dee region of the Carolinas has been 18% (this study). These declines are less than their decline in downtown Rockingham. European Starling may also be a preferred prey species of Cooper's Hawks (Roth and Lima 2003), whose adult mass is 82 g (Millsap et al. 2013), although European Starlings were not captured in urban areas of Albuquerque, New Mexico where they are uncommon (Millsap 2018). Most studies in urban and rural areas at different seasons have documented that columbids and passerines with mass greater than ~ 70 g, such as American Robin (77 g; Millsap et al. 2013), are preferred prey of Cooper's Hawks (Errington 1933, Millsap 2018, Millsap et al. 2013). Females take larger prey than males (Millsap 2018), especially in urban areas where a smaller variety of prey is more abundant and available (Estes and Mannan 2003, Millsap 2018, Roth et al. 2008). Most Cooper's Hawk predation during the breeding season is on nestling birds (B.A. Millsap, pers. comm.), so Cooper's Hawk predation on fledged young and adult starlings at other times of the year would be more likely to depress their populations. Smaller prey that is 45–49 g, such as Northern Mockingbirds and Northern Cardinals, have usually not been main prey items except in some rural areas (Millsap et al. 2013). Even smaller prey, such as House Sparrows 28 g and House Finches 21 g, have only constituted incidental prey of Cooper's Hawks (Millsap 2018, Roth and Lima 2003). Northern Mockingbirds and Northern Cardinals were the 2 most abundant suburban adapters in downtown Rockingham in 2021, suggesting female Cooper's Hawks are only killing larger species. However, Mourning Doves, preferred prey of female Cooper's Hawks in urban areas (op. cit.), remain common as breeding birds in downtown Rockingham. Thus, Cooper's Hawk predation is apparently not solely responsible for the sharp decline of European Starlings in downtown Rockingham.

House Finch. The decline of the House Finch population, near or at its peak in North Carolina in 1994 (McNair 2021, Sauer et al. 2019), would be expected after an outbreak of mycoplasmal conjunctivitis reached Rockingham after 1994 (Badyaev et al. 2012, Hochachka and Dhondt 2000, McNair 2021). House Finches frequently nested in vegetative nest sites in 1994 (McNair 2022a), including the same period censused as in 2021 (McNair, unpubl. data), but I did not document House Finches breeding in any vegetative nest sites in 2021, despite arduous search effort in sites that are easy to examine. This absence suggests buildings are preferred nest sites of House Finches in urban environments, notwithstanding that building area was not different between blocks with and without their nests in 1994.

House Finches had the narrowest breadth of use of the 5 vegetative landscape elements in which to nest in downtown Rockingham, using only espaliers and trellises or isolated trees and tall shrubs, usually at low heights (McNair 2022a). Fewer espaliers and trellises than before were present in downtown Rockingham in 2021, yet isolated trees and tall shrubs remain common. This includes *Lagerstroemia indica* L. (Crapemyrtle), which have increased in number, especially along the streetscape (221 trees large enough to be potentially suitable for nesting birds in 17 blocks; McNair 2021, unpubl. data). House Finches nested in 6 Crapemyrtles in

1994, but not in 2021 when their breeding density was low. Though Badyaev et al. (2012) stated that House Finches do not compete with native species for nest sites, McNair (2021) suggested that some nest-site competition may exist with Northern Mockingbirds, which are increasing in urban areas of southeastern North America, at Gainesville, Florida (Hanauer et al. 2010, Stracey and Robinson 2012) and at Rockingham (this study). Northern Mockingbird had the highest breeding density of any suburban adapter in downtown Rockingham in 2021, when they again nested in Crapemyrtles (4 active nests). Nonetheless, the sharp decrease in House Finches is highly unlikely to be from nest-site competition with Northern Mockingbirds. Even at buildings, House Finches only nested within 2 blocks in 2021.

House Sparrow. Berigan et al. (2020) emphasized that the pattern of steady decline of House Sparrow populations in urban areas of eastern North America since 1995 varied based on geographic location. In the Maritime Provinces of Canada, Erskine (2006) documented a sharp decline of urban populations before House Sparrows declined in rural areas, whereas in southeastern North America at Gainesville, Florida, House Sparrow populations remained most numerous in the central business district (Burnett and Moulton 2015). House Sparrows have declined in the Piedmont of North Carolina (Sauer et al. 2019), including urban areas (Hendrickson and Ferebee 1994, Westphal 2006), and they declined significantly on BBS routes in the northern Pee Dee region of the Carolinas (this study) even though urban areas are undersampled. Thus, the increase of House Sparrows in downtown Rockingham during the breeding season in 2021 was unexpected, although, as suggested by Burnett and Moulton (2015), central business districts may serve as repositories for urban House Sparrows in southeastern North America.

McClure et al. (2011) found no evidence for competitive exclusion during the breeding season between House Sparrows and House Finches at a local scale in southeastern North America, and if it did occur, they stated it was not important enough to affect their spatial distribution. The spatial distribution of House Sparrows in downtown Rockingham did not expand, but their abundance did increase while House Finches sharply declined in abundance and distribution. The reciprocal response in abundance may offer modest support for the interpretation of Cooper et al. (2007), although they may have overstated their case concerning nest-site competition at buildings. These 2 species' nest sites and nest types at buildings and associated structures in downtown Rockingham were different. I obtained no evidence of usurpation or interference that impacted loss of nests or prevention of breeding except for possible loss of 2 nests of House Finches under metal awnings where they attached to vertical concrete walls of buildings in 1994. In contrast, House Sparrows appropriated 2 nest sites in 2 blocks that were formerly used by European Starlings in 1994, which could have contributed to the increase of House Sparrows in 2021.

Avian community composition. Predation by Cooper's Hawk has probably to some extent altered avian community composition in downtown Rockingham of at least the largest urban invader, the Feral Pigeon, but to what extent remains to be positively determined for European Starling and the larger suburban adapters. The Common Grackle, itself an avian predator, had already had a long-term decline in southeastern North America before its disappearance from downtown Rockingham (McNair 2021). Grackles still breed in nearby residential areas, as do American Robins. Both species formerly nested at the greatest heights in vegetation of any of the suburban adapters in downtown Rockingham (McNair 2022a). Adult birds and their nest contents may have been at greater risk from Cooper's Hawk predation and a suite of other avian predators (e.g., crows), because they nested in more exposed habitat (cf., Abrahamczyk et al. 2021). However, the Mourning Dove remains common in downtown Rockingham and the northern Pee Dee region of the Carolinas. Smaller species of suburban adapters that are also abundant habitat generalists with stable populations in the northern Pee Dee region actually increased at

Rockingham in 2021 compared to 1994, especially Carolina Wren, Northern Mockingbird, and Northern Cardinal which are also common in urban areas of Gainesville, Florida (Stracey and Robinson 2012). The abundance of small-bodied birds of suburban adapters and 1 urban invader (House Sparrow) in downtown Rockingham strongly suggests that habitat remains structurally suitable (McNair 2022a), and that they are not particularly vulnerable to Cooper's Hawk predation or a suite of other avian nest predators (see Stracey and Robinson 2012 for alternative explanations). Nonetheless, the influence of nest predation on avian community composition in this urban environment (see following paragraph) and whether the loss of American Robin and Common Grackle is independent of predation by Cooper's Hawk remains to be resolved (McNair 2022a). One other major factor that has influenced avian species composition in downtown Rockingham was disease (Hochachka and Dhondt 2000) which sharply diminished the House Finch, which in turn may have mediated an increase in House Sparrows released from mild effects of interspecific competition. Abrahamczyk et al. (2021) documented sharp declines of 2 suburban adapters, *Turdus merula* L. (Common Blackbird) and *Chloris chloris* L. (European Greenfinch) in an urban district at Bonn, Germany, from disease outbreaks.

These 2 factors, predation and disease, are top-down processes with the former predicting reduced survivorship in urban and suburban habitats (Evans et al. 2015). This reduced survival is consistent with apparent low nest survival of suburban adapters and 1 urban invader nesting in vegetation in downtown Rockingham in 1994 (McNair 2022a). However, the predation paradox hypothesizes that whereas the number of synanthropic vertebrate predators increases with urbanization, the greater availability of anthropogenic food subsidies, a bottom-up process, depresses nest predation rates (Fischer et al. 2012, Rodewald et al. 2011). I believe the predation paradox is unlikely to be important in downtown Rockingham, since the evidence for generalist predators switching from natural to anthropogenic food sources is weak. First, biomass and avian abundance, including suburban adapters, decreased in 2021, which can increase predation pressure and thus elevate, not depress, nest predation rates. Second, the Brown-headed Cowbird, an avian predator is absent and the Common Grackle no longer occurs in downtown Rockingham during the breeding season, except as an infrequent visitor. So while its near absence should now depress nest predation rates, the number of vertebrate predators has decreased, not increased in this urban environment. Third, unlike 1994 (McNair 2021), anthropogenic food subsidies were less available in 2021 when bird feeders were absent. The only grocery store closed, which eliminated a heavily used and poorly maintained dumpster and other trash receptacles used by businesses, and collection by the City of Rockingham improved to reduce food pilferage by animals, and food trays provided by humans for free-ranging *Felis catus* L. (Domestic Cat) were only present at 2 locations (blocks 4 and 12). Fourth, abundant fruits, from native and exotic plants in downtown Rockingham, may be available during autumn and winter (McNair 2021–2022, unpubl. data), but are much scarcer during the breeding season when fruiting exotic plants would not contribute that much additional anthropogenic food (McNair 2021). These above factors would reduce both the number of synanthropic vertebrate predators and anthropogenic food subsidies, thus diminishing applicability of the predation paradox in downtown Rockingham.

Acknowledgments

I thank J.R. Massey, Jr. (current Assistant City Manager, City of Rockingham) for sharing information, B. Norling for preparing Figure 1, and B.A. Millsap, M.T. Stanback, M. Strohbach, and 2 anonymous individuals for their reviews of the submitted version of the manuscript.

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Appendix 1. The physiographic province, name, Breeding Bird Survey (BBS) route number, state, years covered since 1990, and number of years run for 12 BBS routes within or near the northern Pee Dee region of North and South Carolina that surrounds Rockingham, NC.

Province[1]	**Name**	**BBS route number**	**State**	**Years**	**Years run**
P	Wilgrove	63216	NC	1995–2021	22
P	Oakboro	63017	NC	1990–2019[2]	17
P	Biscoe	63215	NC	1990–2017	22
S	Lake Surf	63314	NC	1998–2021	18
S	Hamlet	63207	NC	1995–2021	24
S	Raeford	63900	NC	1990–2019	25
S	Sandhills	80900	SC	1994–2021	27
S/I	Mount Pisgah	80053	SC	1999–2021	14
I	Bethel	63315	NC	2002–2021	12
I	Rowland	63106	NC	1990–2021	28
I	Bennettsville	80054	SC	1999–2017	15
I	Dillon	80010	SC	1990–2021[2]	24

[1]P = Piedmont; S = Sandhills; I = Inner Coastal Plain.
[2]BBS route run before 1990, but these data are excluded.

Appendix 2. List of 59 avian species that visited but did not nest within the Rockingham breeding bird census plot (42.4 ha) from 23 April to 13 May 2021.

***Scientific name* (Common name)**

Aix sponsa L. (Wood Duck)

Coccyzus americanus L. (Yellow-billed Cuckoo)

Chordeiles minor J.R. Forster (Common Nighthawk)

Archilochus colubris L. (Ruby-throated Hummingbird)

Ardea herodias L. (Great Blue Heron)

Butorides virescens L. (Green Heron)

Coragyps atratus (Bechstein, 1793) (Black Vulture)

Cathartes aura L. (Turkey Vulture)

Accipiter striatus Vieillot (Sharp-shinned Hawk)

Accipiter cooperii (Bonaparte, 1828) (Cooper's Hawk)

Haliaeetus leucocephalus L. (Bald Eagle)

Ictinia mississippiensis A. Wilson (Mississippi Kite)

Buteo lineatus Gmelin (Red-shouldered Hawk)

Buteo platypterus Vieillot (Broad-winged Hawk)

Buteo jamaicensis Gmelin (Red-tailed Hawk)

Megascops asio L. (Eastern Screech-Owl)

Strix varia Barton (Barred Owl)

Megaceryle alcyon L. (Belted Kingfisher)

Melanerpes carolinus L. (Red-bellied Woodpecker)

Dryobates pubescens L. (Downy Woodpecker)

Colaptes auratus L. (Northern Flicker)

Dryocopus pileatus L. (Pileated Woodpecker)

Contopus virens L. (Eastern Wood-Pewee)

Empidonax virescens Vieillot (Acadian Flycatcher)

Sayornis phoebe Latham (Eastern Phoebe)

Vireo griseus Boddaert (White-eyed Vireo)

Vireo flavifrons Vieillot (Yellow-throated Vireo)

Vireo olivaceus L. (Red-eyed Vireo)

Cyanocitta cristata L. (Blue Jay)

Corvus ossifragus A. Wilson (Fish Crow)

Corvus corax L. (Common Raven)

Stelgidopteryx serripennis Audubon (Northern Rough-winged Swallow)

Progne subis L. (Purple Martin)

Hirundo rustica L. (Barn Swallow)

Baeolophus bicolor L. (Tufted Titmouse)

Troglodytes aedon (Vieillot, 1809) (House Wren)

Polioptila caerulea L. (Blue-gray Gnatcatcher)

Sialia sialis L. (Eastern Bluebird)

Catharus ustulatus (Nuttall, 1840) (Swainson's Thrush)

Hylocichla mustelina Gmelin (Wood Thrush)

Bombycilla cedrorum Vieillot (Cedar Waxwing)

Spinus tristis L. (American Goldfinch)

Zonotrichia albicollis Gmelin (White-throated Sparrow)

Pipilo erythrophthalmus L. (Eastern Towhee)

Agelaius phoeniceus L. (Red-winged Blackbird)

Molothrus ater Boddaert (Brown-headed Cowbird)

Quiscalus quiscula L. (Common Grackle)

Geothlypis trichas L. (Common Yellowthroat)

Setophaga ruticilla L. (American Redstart)

Setophaga americana L. (Northern Parula)

Setophaga petechia J.F. Gmelin (Yellow Warbler)

Setophaga striata J.R. Forster (Blackpoll Warbler)

Setophaga pinus L. (Pine Warbler)

Setophaga coronata L. (Yellow-rumped Warbler)

Setophaga dominica L. (Yellow-throated Warbler)

Setophaga discolor (Vieillot, 1809) (Prairie Warbler)

Piranga rubra L. (Summer Tanager)

Passerina caerulea L. (Blue Grosbeak)

Passerina cyanea L. (Indigo Bunting)