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# DECLINES IN ABUNDANCE AND SPECIES RICHNESS OF BIRDS FOLLOWING A MAJOR FLOOD ON THE UPPER MISSISSIPPI RIVER

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ABSTRACT.—We examined the abundance and species richness of birds breeding in floodplain forests of the Upper Mississippi River from 1992 to 1994 to identify effects of a major flood in 1993 on the bird assemblage. Sixty-five study plots were divided into treatments and controls based on whether they were flooded in 1993. Among 84 species observed on all plots, 41 species decreased in abundance from 1992 to 1994, 13 species increased, and numbers of 5 species were unchanged. Sample sizes were inadequate to evaluate trends for 25 species. Species richness declined over the three-year period. The main effect "year" was significant in 20 of the 36 species tested. Cool, wet conditions may have contributed to poor reproductive success in 1993 and resulted in widespread declines in abundance during the year following the flood. Bird abundance increased on most unflooded plots in 1993, probably because birds were displaced from flooded plots. This pattern was most striking for Neotropical migrants, species preferring habitat edges, lower-canopy nesters, and species that forage in the air. We suggest that periodic major flooding maintains suitable floodplain habitat for Prothonotary Warblers (*Protonotaria citrea*) in the face of competition with House Wrens (*Troglodytes aedon*) for nest sites. *Received 30 November 1995, accepted 22 January 1996.*

FLOODPLAINS ARE DYNAMIC HABITATS where periodic flooding creates natural disturbances that set back succession and provide new sites for plant establishment (Peck and Smart 1986, Kupfer and Malanson 1993, Jones et al. 1994, Sparks 1995, Yin and Nelson 1995). Large floodplain forests like those of the Upper Mississippi River are uncommon in northern landscapes (Mitsch and Gosselink 1993) and provide unique habitats that support a high abundance and diversity of birds (Grettenberger 1991, Best et al. 1995, Knutson et al. 1996). Few studies have examined the avifauna of large floodplain forests (Emlen et al. 1986, Decamps et al. 1987, Knutson 1995), and studies of the effects of floods that include pre-flood data are even less common (Knopf and Sedgwick 1987).

Direct effects of flooding on birds nesting in floodplains tend to be minor because spring floods usually recede by mid- to late May. Summer floods are rare and usually of short duration. However, major floods of long duration or high amplitude can create large-scale disturbances that dramatically change vegetative cover (Yin et al. 1994). Bird assemblages may respond to changes in availability of nest sites and food resources caused by these disturbances. Flooding had a major effect on a riparian bird community in Arizona by eliminating cottonwood and willow nesting habitat (Hunter et al. 1987). Depending upon the severity of the disturbance, some species may increase in abundance while others decline. In addition, flooding may maintain suitable habitat for some bird species that are uncommon in drier, less-disturbed habitats.

Rainfall during May to August 1993 in the Upper Mississippi River basin reached historically high levels (ca. twice normal), approximating 75- to 300-year recurrence intervals (Wahl et al. 1993, Interagency Floodplain Management Review Committee 1994). River water levels were well above normal throughout the breeding season (Parrett et al. 1993). We examined the effects of this major flood on the abundance and species richness of birds breeding in floodplain forests by comparing data collected from 1992 to 1994. We considered our data in relation to two hypotheses of how the flood and associated weather patterns affected the floodplain bird assemblage. The Flood Disturbance Hypothesis proposes that the pattern of change in abundance will differ between flooded and unflooded plots because structural

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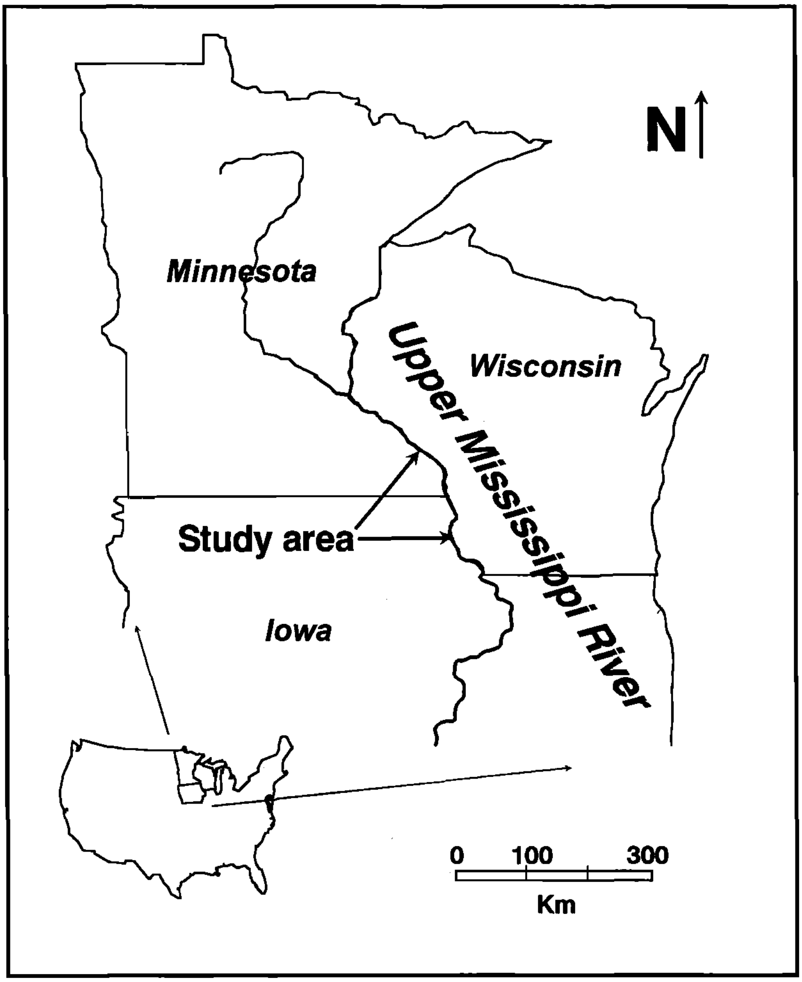


FIG. 1. Location of study area in Pools 6 to 10 of the Upper Mississippi River.

changes in habitat will occur on flooded plots but not on unflooded plots. Bird abundance may increase on unflooded plots the year of the flood as birds seek refuge from adjacent flooded sites. Other possible effects include lower abundance on flooded plots in the year of the flood or the following year. We predicted that edge species, ground and lower-canopy nesters, and ground and lower-canopy feeders would be most affected by these structural changes. We also predicted that species preferring habitats near water, and piscivores, would increase on flooded plots. The Weather Hypothesis proposes that multispecies declines in abundance would be observed on both flooded and unflooded plots, resulting from reduced productivity in wet, cool weather associated with a flood (and not from the flood disturbance itself). We predicted that insectivores would be most affected if weather conditions depressed insect abundance (Rotenberry et al. 1995).

## STUDY AREA AND METHODS

The study area included forested floodplain habitat of the Upper Mississippi River (Fig. 1) from near Winona, Minnesota downriver to Guttenburg, Iowa, a distance of about 177 km along the main channel of the river. This section of the river is unrestricted by levees; during high water the river floods some or all of the floodplain forests, depending upon their elevation. The forest community is dominated by silver maple (*Acer saccharinum*). Elm (*Ulmus* spp.), green ash (*Fraxinus pennsylvanica*), swamp white oak (*Quer-*

*cus bicolor*), cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), and river birch (*Betula nigra*) are less abundant (Knutson 1995). The shrub layer is dominated by green ash seedlings, poison ivy (*Toxicodendron radicans*), silver maple seedlings, and prickly ash (*Zanthoxylum americanum*). Wood nettle (*Urtica dioica*) and reed canary grass (*Phalaris arundinaceae*) dominate the herb layer.

We obtained daily water elevation data from the U.S. Army Corps of Engineers gauging station at LaCrosse, Wisconsin (River Mile 696.8) from 1937 to 1994 to assess flood severity at a location near the center of the study area.

We randomly selected 65 plots from forested areas where tree canopy cover was >70% using a 600 × 600-m sampling grid overlaid on digital land-cover maps. Thirty-four plots were under water and 31 were above water at the time of censusing in 1993, which defined our control and treatment groups. Plots were at least 200 m apart, but in most cases were separated by 600 m to several km. Within each study plot, we counted birds at 3 to 10 ($\bar{x}$ = 5.5 ± SE of 0.2) points spaced ≥200 m apart in 1992 (pre-flood), 1993 (flood), and 1994 (post-flood). Plots were censused once between 20 May and 6 July in each year. Logistical considerations prevented us from having equal numbers of points in each plot. Three observers each year collected the census data. The observers were experienced in bird identification and had one week of field training immediately prior to the field season to verify and improve identification skills. Flooded plots were traversed by canoe or kayak.

We calculated the relative abundance of each species for each plot by determining the number of individuals identified within 50 m of the observer over a 10-min period (Ralph et al. 1993) and summing these numbers over all points in the plot. We divided these totals by the number of points in the plot to derive the mean number of individuals per point. For comparison, we report abundances as number of individuals per 10 points. We used the total number of species identified on the plot as our estimate of species richness. To assess flood-response patterns for species with similar characteristics, we classified birds by nesting guild, feeding guild, preferred habitat, territory size, and migration distance. To address management questions, we also classified birds by an overall index of management concern and by population trend.

We used a sign test (Zar 1984) to test the hypothesis that more species decreased in abundance from 1992 to 1994 than increased. All species counted on at least one plot in both 1992 and 1994 were included in this analysis. Changes in relative abundance were analyzed using a two-way ANOVA with repeated measures (Hatcher and Stepanski 1994) on the "year" factor by species and by bird classifications. Only species found on at least five plots in each year were used in the species analysis; all birds were included in the classification analysis. Because of the large number of tests (due to the number of species involved), we adjusted the significance level to $P \leq 0.005$ to control the experiment-wise error rate (Rice 1989, Beal and Khamis 1991).

## RESULTS

In 1993, water elevations were well above normal during May, June, and July, whereas 1992 and 1994 were years of relatively normal water elevations (Fig. 2). No study plot was flooded in 1992 or 1994. We counted 84 species and 19,396 individual birds during the three-year study, 10,963 on flooded plots and 8,433 on unflooded plots. Forty-one species decreased in abundance from 1992 to 1994 (Appendix), 13 species increased, and 5 were unchanged (sign test, $P \leq 0.001$). In the ANOVA analysis, 4 of 36 species had a significant interaction term (plot × year), 11 had a significant main effect of plot (flooded vs. unflooded), and 20 had a significant main effect of year (Table 1). Three species had significant terms for the main effects of plot and year, and a significant interaction term. Mean abundance for all birds showed a significant main effect of year and a significant interaction term on the ANOVA (Table 2). Species richness declined over the three-year period and differed between flooded and unflooded plots (Table 2). When birds were classified by guild and management categories, 6 categories had significant interaction terms and 17 had a significant main effect of year (Table 2). The patterns of change in abundance frequently were marked by an overall decline over the study period (Fig. 3A, C, E, and I) and peaks of abundance on unflooded plots in 1993 (Fig. 3B, D, F and H). However, birds preferring water increased over the study period (Fig. 3G). The four species with significant terms for interaction all showed large increases in abundance on unflooded plots in 1993 (Fig. 4). Three secondary cavity nesters, Prothonotary Warbler (*Protonotaria citrea*), House Wren (*Troglodytes aedon*), and Tree Swallow (*Tachycineta bicolor*) differed in patterns of abundance over the period (Fig. 5). Prothonotary Warblers had higher abundance on flooded plots in all years and decreased abundance on unflooded plots over the study period (Fig. 5A). House Wrens had nearly the reverse of this pattern, with decreased abundance on flooded plots over the

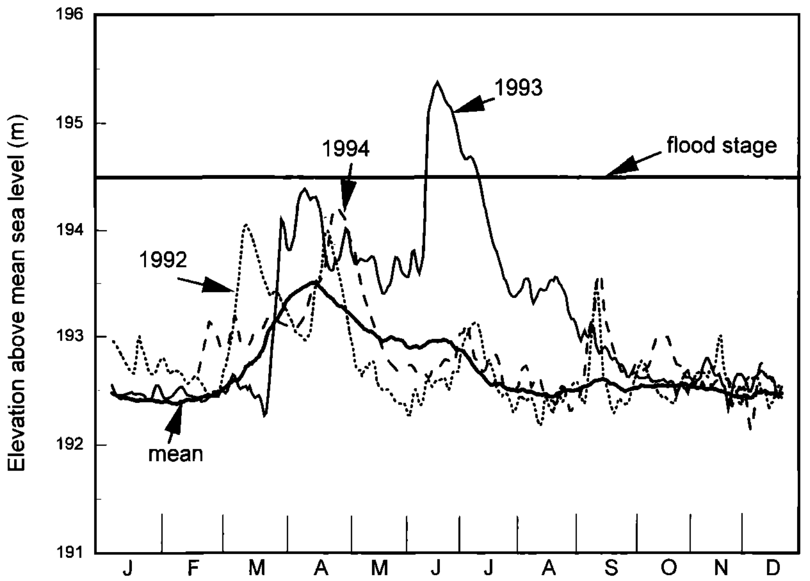


FIG. 2. Hydrograph of daily water elevations recorded at the La Crosse, Wisconsin gauging station, Pool 8 (River Mile 696.85). The mean daily elevation from 1937–1994 (solid bold line) is shown, along with elevations for 1992 (dotted line), 1993 (solid line), and 1994 (dashed line). Horizontal line indicates flood stage. Magnitude of flooding increased below this gauging station.

study period and a large peak in abundance on unflooded plots in 1993 (Fig. 5B). Tree Swallows declined in abundance on all plots in 1993, returning to pre-flood levels in 1994 (Fig. 5C).

## DISCUSSION

The main result of the 1993 flood was a decline in species richness and abundance of birds in 1994. Evidence for the Weather Hypothesis was a significant effect of year in the ANOVA, a decline in abundance during the study period, and a significant decline in abundance for the majority of species from 1992 to 1994 (i.e. more species declining than increasing). As expected, insectivores (represented by lower-canopy gleaners, air hawkers, and bark gleaners) declined in abundance. Resident species were more negatively affected than temperate and Neotropical migrants. Birds of high management concern, interior-edge species, species with medium territory size, and hole nesters also declined. Surprisingly, abundance of ground nesters returned to pre-flood levels in 1994. Ground nesters were not common in the floodplain in any year, perhaps due to threat of flood disturbances. Those that nest in the floodplain seemed minimally affected by flooding. However, piscivores and species preferring habitats near water increased in abundance.

The observed declines in abundance and species richness provide evidence for the Weather Hypothesis. Adverse conditions, perhaps cool, wet weather combined with thunderstorms and high wind, may have led to poor reproduction in 1993 and this reduced bird numbers across all plots, not just flooded plots. The cool, wet weather may have delayed the onset of breeding, reduced clutch size, depressed insect populations, and increased metabolic stress on eggs and nestlings, thus decreasing nesting success for many insectivorous species. Knopf and Sedgwick (1987) noted that two ground/shrub nesters, the Brown Thrasher (*Toxostoma rufum*) and the Eastern Towhee (*Pipilo erythrophthalmus*), showed no significant change in abundance the year of a major flood on the South Platte River, but declined the following year. In contrast, two species that nest and feed in the canopy, the Baltimore Oriole (*Icterus galbula*) and the Orchard Oriole (*I. spurius*), did not follow this pattern. Based on mist-net captures in a coastal California site over an 11-year period, DeSante and Geupel (1987) noted community-wide declines in abundance

TABLE 1. Significance levels of the main effects of plot, year, and plot × year interaction for differences in mean abundance of species between flooded and unflooded plots. Species with at least one significant value are listed first.

| | Species | Plot | Year | Interaction |
|---|---|---|---|---|
| | **Species with significant effects** | | | |
| Great Blue Heron | *Ardea herodias* | 0.29 | 0.0001 | 0.89 |
| Yellow-billed Cuckoo | *Coccyzus americanus* | 0.002 | 0.26 | 0.56 |
| Red-headed Woodpecker | *Melanerpes erythrocephalus* | 0.72 | 0.0002 | 0.11 |
| Red-bellied Woodpecker | *Melanerpes carolinus* | 0.89 | 0.0006 | 0.12 |
| Yellow-bellied Sapsucker | *Sphyrapicus varius* | 0.005 | 0.18 | 0.19 |
| Downy Woodpecker | *Picoides pubescens* | 0.09 | 0.004 | 0.03 |
| Hairy Woodpecker | *Picoides villosus* | 0.41 | 0.001 | 0.48 |
| Northern Flicker | *Colaptes auratus* | 0.67 | 0.0001 | 0.83 |
| Eastern Wood-Pewee | *Contopus virens* | 0.07 | 0.0008 | 0.66 |
| Great Crested Flycatcher | *Myiarchus crinitus* | 0.001 | 0.003 | 0.001 |
| Tree Swallow | *Tachycineta bicolor* | 0.15 | 0.001 | 0.30 |
| Blue Jay | *Cyanocitta cristata* | 0.007 | 0.001 | 0.03 |
| American Crow | *Corvus brachyrhynchos* | 0.44 | 0.0005 | 0.04 |
| Black-capped Chickadee | *Parus atricapillus* | 0.10 | 0.0009 | 0.94 |
| White-breasted Nuthatch | *Sitta carolinensis* | 0.06 | 0.0001 | 0.09 |
| Brown Creeper | *Certhia americana* | 0.008 | 0.0002 | 0.02 |
| Gray Catbird | *Dumetella carolinensis* | 0.0001 | 0.007 | 0.33 |
| Yellow-throated Vireo | *Vireo flavifrons* | 0.0007 | 0.12 | 0.99 |
| Warbling Vireo | *Vireo gilvus* | 0.10 | 0.002 | 0.41 |
| Yellow Warbler | *Dendroica petechia* | 0.09 | 0.14 | 0.002 |
| Prothonotary Warbler | *Protonotaria citrea* | 0.0001 | 0.02 | 0.16 |
| Common Yellowthroat | *Geothlypis trichas* | 0.002 | 0.0001 | 0.0001 |
| Northern Cardinal | *Cardinalis cardinalis* | 0.0003 | 0.007 | 0.02 |
| Rose-breasted Grosbeak | *Pheucticus ludovicianus* | 0.0001 | 0.005 | 0.0005 |
| Song Sparrow | *Melospiza melodia* | 0.11 | 0.0001 | 0.84 |
| Red-winged Blackbird | *Agelaius phoeniceus* | 0.09 | 0.0003 | 0.14 |
| Common Grackle | *Quiscalus quiscula* | 0.005 | 0.40 | 0.74 |
| Brown-headed Cowbird | *Molothrus ater* | 0.001 | 0.07 | 0.09 |
| American Goldfinch | *Carduelis tristis* | 0.06 | 0.0004 | 0.26 |
| | **Species with no significant effects** | | | |
| Wood Duck | *Aix sponsa* | 0.26 | 0.01 | 0.32 |
| House Wren | *Troglodytes aedon* | 0.02 | 0.07 | 0.04 |
| Blue-gray Gnatcatcher | *Polioptila caerulea* | 0.15 | 0.03 | 0.32 |
| American Robin | *Turdus migratorius* | 0.16 | 0.10 | 0.62 |
| Red-eyed Vireo | *Vireo olivaceus* | 0.99 | 0.18 | 0.42 |
| American Redstart | *Setophaga ruticilla* | 0.81 | 0.17 | 0.27 |
| Baltimore Oriole | *Icterus galbula* | 0.69 | 0.21 | 0.74 |

during years of extremely high rainfall. Finch (1991) found delayed, asynchronous egg laying in House Wrens in flooded habitats compared with adjacent habitats unaffected by floods. Clutch size for both populations declined in flood years. Lack (1954:25) noted higher nestling mortality for Common Swifts (*Apus apus*) during wet summers. Emergent insects likely represent a major food resource for insectivorous birds nesting in floodplains. According to a study on the Upper Mississippi River in 1993, flooding stimulated high abundance of aquatic invertebrates in some habitats (inundated grasses), whereas other habitats (flooded forests and open water) had low abundances (Theiling et al. 1994). Water depths >0.5 m were associated with low densities of aquatic invertebrates. Depths of 1 m or more were common in our flooded plots.

Three other studies conducted in 1993 on the Upper Mississippi River provide direct evidence for low productivity in birds. Great Blue Herons (*Ardea herodias*) in our study area initiated nesting two weeks later in 1993 and had smaller clutch sizes than herons in northern study areas less affected by the flood (Custer et al. 1996). Red-shouldered Hawks (*Buteo lineatus*) in the study area experienced low reproduction during 1993 compared with the previous nine years (36% vs. 75% nest success, 0.45

TABLE 2. Significance levels of the main effects of plot, year, and plot × year interaction for differences in species richness; mean abundance of all birds pooled and birds classified by guild; management status; and population status.

| Class | Plot | Year | Interaction |
|---|---|---|---|
| Species richness | 0.01 | 0.0002 | 0.3903 |
| All birds | 0.71 | 0.0001 | 0.0003 |
| **Migration status**[a] | | | |
| Resident | 0.85 | 0.0001 | 0.20 |
| Temperate migrant | 0.18 | 0.0003 | 0.46 |
| Neotropical migrant | 0.77 | 0.0001 | 0.0009 |
| **Population trend**[b] | | | |
| Stable or increasing | 0.49 | 0.0001 | 0.002 |
| Mixed | 0.25 | 0.01 | 0.0009 |
| Decreasing | 0.27 | 0.007 | 0.93 |
| **Management status**[c] | | | |
| Low | 0.76 | 0.0001 | 0.009 |
| Medium | 0.85 | 0.49 | 0.16 |
| High | 0.40 | 0.0001 | 0.11 |
| **Habitat preference**[d] | | | |
| Interior forest | 0.83 | 0.41 | 0.10 |
| Interior-edge | 0.24 | 0.0001 | 0.09 |
| Edge | 0.53 | 0.03 | 0.002 |
| Near water | 0.14 | 0.0001 | 0.18 |
| **Territory size**[e] | | | |
| <2 ha | 0.53 | 0.01 | 0.009 |
| 2–5 ha | 0.73 | 0.0001 | 0.08 |
| >5 ha | 0.84 | 0.0006 | 0.21 |
| **Nesting location**[e] | | | |
| Ground | 0.64 | 0.0001 | 0.03 |
| Lower canopy | 0.24 | 0.11 | 0.003 |
| Upper canopy | 0.08 | 0.28 | 0.30 |
| Hole | 0.21 | 0.0001 | 0.42 |
| Other | 0.04 | 0.16 | 0.24 |
| **Foraging guild**[f] | | | |
| Carnivore | 0.72 | 0.19 | 0.78 |
| Piscivore | 0.37 | 0.0001 | 0.80 |
| Ground gleaner | 0.66 | 0.73 | 0.03 |
| Lower canopy gleaner | 0.72 | 0.0001 | 0.008 |
| Upper canopy gleaner | 0.60 | 0.0007 | 0.43 |
| Air hawker | 0.27 | 0.001 | 0.003 |
| Bark gleaner | 0.02 | 0.0001 | 0.45 |

[a] Resident birds were defined as wintering in the study area and temperate migrants as wintering in the southern latitudes of the United States. Neotropical migrants were defined as wintering primarily south of the United States (Thompson et al. 1993).

[b] Based on long-term (1966–1994) and short-term (1980–1994) Breeding Bird Survey trends in the Upper Midwest. Species with no trend or increasing population trends were classified as stable or increasing, respectively. Species that showed both an increase and a decrease in either long- or short-term trends were classified as mixed. Species that showed significant decreases in both long- and short-term trends were classified as decreasing.

[c] Based on scores of Thompson et al. (1993). Species with a mean overall score of 1 to 1.99 were classified as low, 2 to 2.99 were classified as medium, and 3 to 5 were classified as high.

[d] Based on Whitcomb et al. (1981), Freemark and Merriam (1986), Thompson et al. (1993).

[e] Based on Schoener (1968), Bellrose (1976), Whitcomb et al. (1981), Blake and Karr (1984), Hayden and Faaborg (1985), Emlen et al. (1986), Freemark and Merriam (1986), Ehrlich et al. (1988), Robbins et al. (1989), and Poole et al. (1992-1995). When no data on territory size were available, data for closely related taxa were used (i.e. Schoener 1968, Dunning 1993).

[f] Based on De Graaf et al. (1985).

vs. 1.61 fledglings per nest; Stravers and McKay 1993). Nesting success of Prothonotary Warblers in 1993 was one-third of that in 1994, and 36% of the nesting cavities were flooded (Flaspohler 1996).

The second major pattern we observed was increased abundance on unflooded plots in 1993, while abundance on flooded plots remained stable or declined. Differences in abundance between flooded and unflooded plots (significant plot × year interaction) provided evidence for the Flood Disturbance Hypothesis. A plausible interpretation is that many species were displaced from adjacent flooded habitats to unflooded habitats. As expected, edge species and lower-canopy nesters showed this effect. This pattern also was observed for all individuals pooled, Neotropical migrants, birds with stable or mixed population status, and birds that forage in the air. Contrary to our expectations, ground nesters showed only a weak increase on unflooded plots, along with lower-canopy gleaners. Birds that did not increase in abundance on unflooded plots may either benefit from flooding (e.g. water-loving and piscivorous species) or exhibit strong attachment to their territories, regardless of flooding conditions. For example, we repeatedly observed Song Sparrows (*Melospiza melodia*) singing over flooded territories.

Some species and bird categories seemed to be responding to preexisting habitat differences in flooded and unflooded plots that persisted throughout the study period; these birds showed a significant plot effect. Vegetation data collected in 1992 showed that tree and snag density, snag size, canopy cover, and herbaceous cover were similar between flooded and unflooded plots (M. G. Knutson unpubl. data). However, flooded plots had larger trees and fewer shrubs than unflooded plots. The higher species richness on flooded plots is accounted for by differences in the number of sampling points between flooded ($\bar{x}$ = 5.7 ± SE of 0.2) and unflooded ($\bar{x}$ = 4.9 ± 0.2) plots. It is

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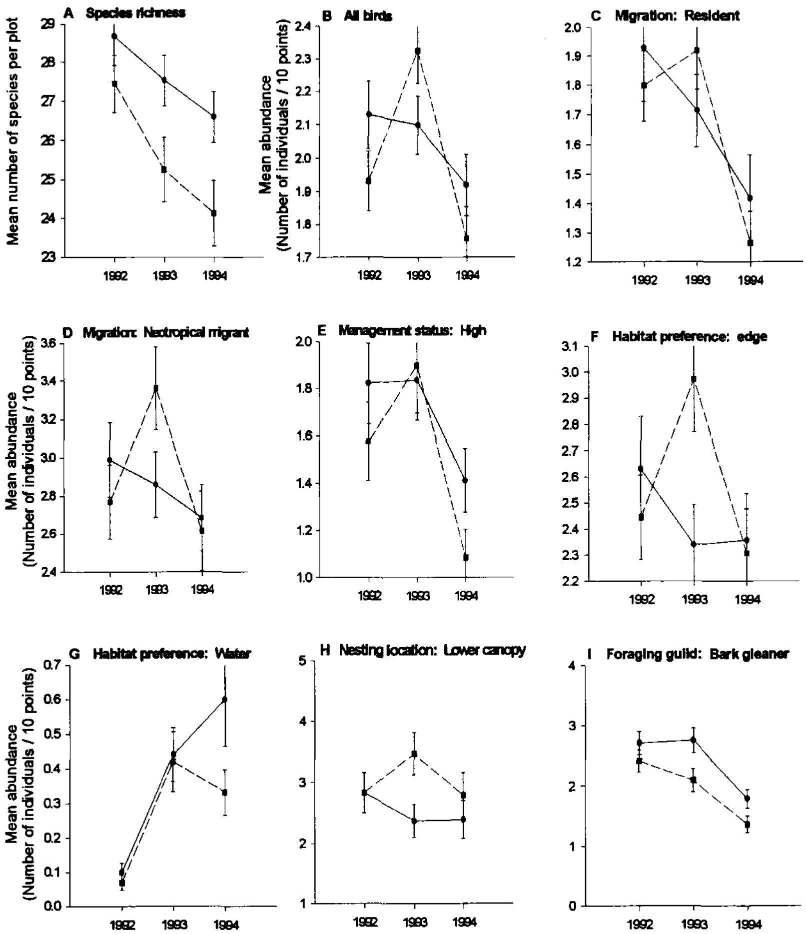


FIG. 3. (A) Mean number of species per plot (± SE) and (B-I) mean abundance (number of individuals per 10 points ± SE) on flooded (solid line) and unflooded (dashed line) plots for birds classified by guild, management status, and population status. All categories shown have at least one significant ($P \leq 0.005$) term for plot, year, or year × plot interaction.

likely that unflooded plots were of higher elevation than flooded plots, but these differences are not large (1 to 2 m), and elevation data of sufficient precision to make this comparison are not available.

Three species showed significant effects of year, plot, and year × plot interaction (Great Crested Flycatcher [*Myiarchus crinitus*], Rose-breasted Grosbeak [*Pheucticus ludovicianus*], and Common Yellowthroat [*Geothlypis trichas*]), and one additional species showed a significant interaction effect (Yellow Warbler [*Dendroica petechia*]; Fig. 4). For these species, abundances rose in 1993 on unflooded plots and fell to low levels in 1994 on all plots. Philopatry under flooded conditions for these species apparently is low. All of these species are Neotropical migrants, have stable or mixed population trends, small to medium territory sizes, and are diverse in their nesting and foraging requirements. An affinity for edge or interior-edge habitats is one trait shared by these four species that might explain the above patterns. Although the species use shrubby edge habitats in different ways, they may abandon flooded areas when edge habitats disappear with flooding.

The three secondary cavity nesters, Prothonotary Warbler, House Wren, and Tree Swallow, are potential competitors for nest cavities in the Upper Mississippi River floodplain. They are commonly found nesting in the same

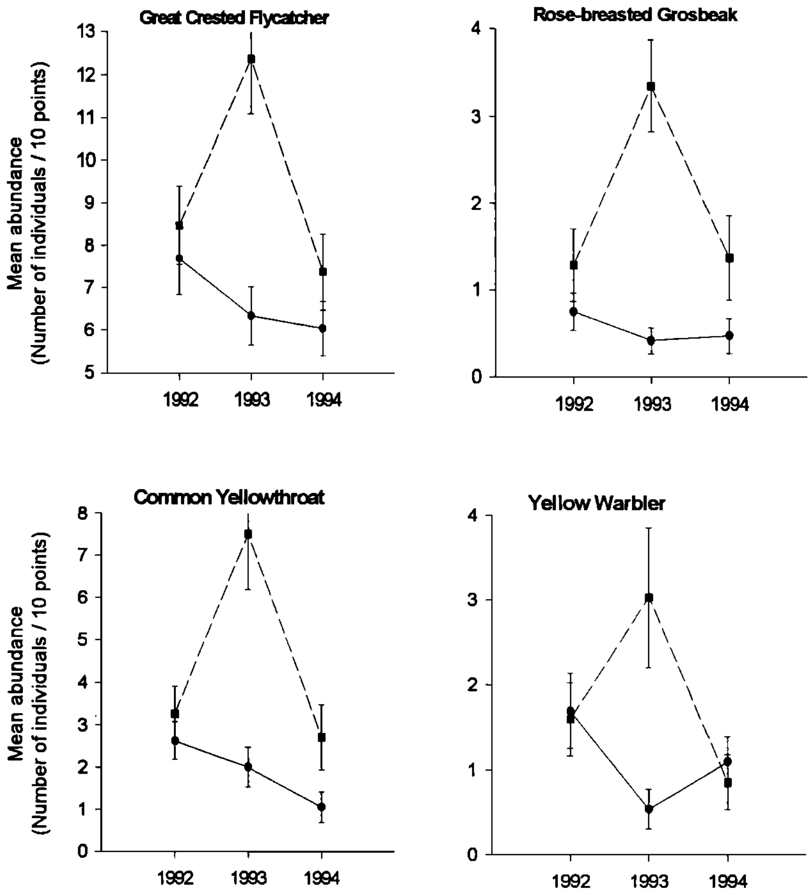


FIG. 4. Mean abundance (number of individuals per 10 points ± SE) on flooded (solid line) and unflooded (dashed line) plots for four species with a significant ($P \leq 0.005$) term for plot × year interaction.

habitats in the study area. The Prothonotary Warbler is found only in large floodplain forests and major tributaries of the Upper Mississippi River in this region. House Wrens and Prothonotary Warblers have been shown to compete for nest sites, and the wrens frequently are successful in obtaining nesting cavities (Walkinshaw 1941, Petit 1989, Brush 1994). We observed House Wren destruction of Prothonotary Warbler nests with subsequent wren oc-

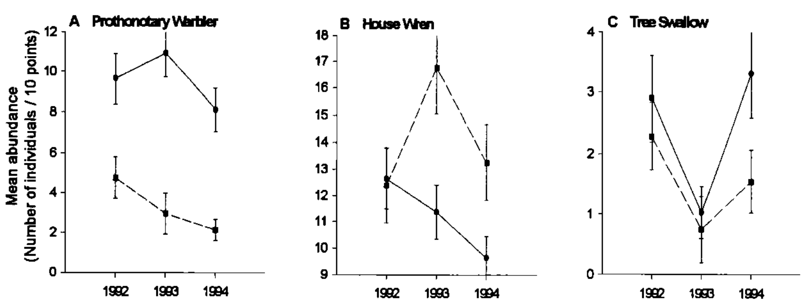


FIG. 5. Mean abundance (number of individuals per 10 points ± SE) on flooded (solid line) and unflooded (dashed line) plots for three species that are potential nest site competitors in Upper Mississippi River floodplain forests.

cupation of the cavities (M. G. Knutson unpubl. data). We also found that the abundance of Prothonotary Warblers was positively correlated with the presence of mature, open-canopy forest; large, tall trees and snags; and a sparse understory (Knutson 1995). The abundance of House Wrens was not strongly correlated with any of the habitat variables we measured. Brush (1994) found that Prothonotary Warblers prefer wetter, less fragmented forests than do House Wrens. The abundance patterns we observed for these three species were quite different (Fig. 5), indicating that flooding may influence habitat suitability differently. The differences in abundance patterns, especially for Prothonotary Warblers and House Wrens, provide evidence that flooding disturbances may maintain habitat differences that translate into different niches for these two species. House Wren avoidance of the lowest-elevation (i.e. frequently inundated) sites may allow Prothonotary Warblers to coexist when they occupy the same region (Brush 1994). Periodic major flooding may maintain suitable floodplain habitat for Prothonotary Warblers in the face of competition from House Wrens for nesting sites.

From a management perspective, severe flooding does negatively impact the abundance of birds of high management concern, such as Neotropical migrants, as well as resident species such as woodpeckers. However, flood disturbance also may maintain habitat for some species of high management concern, like the Prothonotary Warbler. We were unable to determine the duration of declines in abundance and richness after a major flood. Our data indicate that while declines in abundance and richness were present, the magnitude of change was small. For many species, abundance returned to nearly pre-flood levels the year following the flood. If bird abundance and richness rebound quickly after a disturbance event, then the long-term effects on the bird assemblage are minimal. The displacement of individuals from flooded to unflooded plots that we observed was limited to the flood year and thus posed little long-term threat to the avifauna. However, if the amplitude and duration of the flood are severe enough that a large percentage of the canopy trees die, then major changes in the bird assemblage could occur. Reports from Mississippi River habitats in southern Iowa, northern Missouri, and Illinois (K. McKay pers. comm.) indicate that the habitat and the bird community have changed as a result of the extreme 1993 flooding that occurred there. In some parts of our study area, sapling mortality was 7.2% and tree mortality 1.7% one year after the flood, whereas sapling mortality reached 70–80% and tree mortality 18–37% in floodplain areas south of our study area (southern Iowa, northern Missouri, and Illinois; Yin et al. 1994). Yin et al. (1994) determined that post-flood tree and sapling mortality was directly related to the duration and amplitude of flooding, which increased from north to south on the Upper Mississippi River in 1993. Floodplain bird management ultimately is tied to watershed land-use patterns and riverine engineering modifications that together influence the timing, frequency, amplitude, and severity of water-level fluctuations. As we observed, flood disturbances within normal limits can be positive for some bird species, but severe flooding reduces both abundance and species richness of the avifauna.

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APPENDIX. Number of plots and abundance (no. individuals per 10 points; SE in parentheses) of species in 1992, 1993, and 1994 ($n = 65$). Species are classified by guild associations and management risk categories.[a]

| Species | No. of plots 1992 | No. of plots 1993 | No. of plots 1994 | Abundance 1992 | Abundance 1993 | Abundance 1994 | Migration | Population | Status | Habitat | Territory | Nesting | Foraging |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pied-billed Grebe *Podilymbus podiceps* | 0 | 4 | 0 | — | 0.1 (0.0) | — | T | M | L | W | M | O | O |
| Great Blue Heron *Ardea herodias* | 12 | 35 | 28 | 0.4 (0.3) | 1.7 (0.3) | 1.9 (0.3) | T | S | L | W | L | UC | P |
| Great Egret *Ardea alba* | 0 | 0 | 1 | — | — | 0.1 (0.1) | T | S | L | W | L | UC | P |
| Green Heron *Butorides virescens* | 0 | 1 | 1 | — | 0.0 (0.0) | 0.0 (0.0) | T | M | L | W | L | UC | P |
| Canada Goose *Branta canadensis* | 0 | 0 | 3 | — | — | 0.4 (0.2) | T | S | L | W | L | G | G |
| Wood Duck *Aix sponsa* | 6 | 24 | 21 | 0.3 (0.3) | 1.1 (0.3) | 1.7 (0.3) | T | S | L | W | L | H | G |
| Mallard *Anas platyrhynchos* | 2 | 15 | 8 | 0.1 (0.2) | 1.1 (0.2) | 0.5 (0.2) | T | S | L | W | L | G | G |
| Hooded Merganser *Lophodytes cucullatus* | 1 | 1 | 0 | 0.0 (0.0) | 0.1 (0.0) | — | T | ND | L | W | L | H | P |
| American White Pelican *Pelecanus erythrorhynchos* | 0 | 2 | 0 | — | 0.2 (0.0) | — | T | ND | L | W | L | O | P |
| Black Tern *Chlidonias niger* | 0 | 1 | 0 | — | 0.0 (0.0) | — | N | ND | H | W | L | O | A |
| Sandhill Crane *Grus canadensis* | 1 | 0 | 4 | 0.0 (0.0) | — | 0.1 (0.0) | N | ND | L | W | L | O | G |
| Wild Turkey *Meleagris gallopavo* | 1 | 0 | 1 | 0.0 (0.0) | — | 0.0 (0.0) | R | S | L | IE | L | G | G |
| Bald Eagle *Haliaeetus leucocephalus* | 2 | 1 | 3 | 0.1 (0.0) | 0.0 (0.0) | 0.1 (0.0) | R | M | H | W | L | UC | P |
| Red-tailed Hawk *Buteo jamaicensis* | 0 | 0 | 1 | — | — | 0.0 (0.0) | R | S | L | E | L | UC | C |
| Red-shouldered Hawk *Buteo lineatus* | 2 | 1 | 2 | 0.1 (0.0) | 0.0 (0.0) | 0.1 (0.0) | R | M | H | I | L | UC | C |
| Sora *Porzana carolina* | 0 | 2 | 0 | — | 0.1 (0.0) | — | T | M | L | W | S | O | G |
| Killdeer *Charadrius vociferus* | 0 | 1 | 2 | — | 0.0 (0.0) | 0.1 (0.0) | T | S | L | E | S | G | G |
| American Woodcock *Scolopax minor* | 2 | 0 | 0 | 0.1 (0.0) | — | — | T | D | L | E | M | G | G |
| MourningDove *Zenaida macroura* | 16 | 14 | 4 | 1.0 (0.2) | 0.5 (0.2) | 0.1 (0.2) | R | M | L | E | M | UC | G |
| Black-billed Cuckoo *Coccyzus erythropthalmus* | 1 | 1 | 2 | 0.0 (0.0) | 0.0 (0.0) | 0.1 (0.0) | N | M | H | IE | M | LC | LC |
| Yellow-billed Cuckoo *Coccyzus americanus* | 25 | 19 | 16 | 1.4 (0.2) | 0.9 (0.2) | 0.7 (0.2) | N | D | H | IE | M | LC | LC |
| Great Horned Owl *Bubo virginianus* | 1 | 0 | 0 | 0.0 (0.0) | — | — | R | S | L | IE | L | UC | C |
| Barred Owl *Strix varia* | 5 | 2 | 1 | 0.1 (0.0) | 0.1 (0.0) | 0.0 (0.0) | R | S | L | I | L | H | C |
| Chimney Swift *Chaetura pelagica* | 7 | 5 | 2 | 0.2 (0.1) | 0.2 (0.1) | 0.1 (0.1) | N | D | M | E | S | H | A |
| Ruby-throated Hummingbird *Archilochus colubris* | 12 | 0 | 3 | 0.4 (0.1) | — | 0.1 (0.1) | N | S | M | IE | M | UC | LC |
| Belted Kingfisher *Ceryle alcyon* | 4 | 5 | 1 | 0.1 (0.1) | 0.2 (0.1) | 0.0 (0.1) | T | M | L | W | L | O | P |
| Red-headed Woodpecker *Melanerpes erythrocephalus* | 28 | 10 | 12 | 1.2 (0.1) | 0.4 (0.1) | 0.4 (0.1) | R | D | L | IE | L | H | B |
| Red-bellied Woodpecker *Melanerpes carolinus* | 47 | 53 | 41 | 2.9 (0.4) | 4.3 (0.4) | 2.5 (0.4) | R | S | L | IE | L | H | B |

APPENDIX. Continued.

| Species | No. of plots 1992 | 1993 | 1994 | Abundance 1992 | 1993 | 1994 | Migration | Population | Status | Habitat | Territory | Nesting | Foraging |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Yellow-bellied Sapsucker *Sphyrapicus varius* | 58 | 57 | 56 | 6.1 (0.5) | 5.6 (0.5) | 4.5 (0.5) | T | ND | L | IE | M | H | B |
| Downy Woodpecker *Picoides pubescens* | 51 | 40 | 44 | 3.7 (0.3) | 1.8 (0.3) | 2.5 (0.3) | R | M | L | IE | M | H | B |
| Hairy Woodpecker *Picoides villosus* | 39 | 19 | 19 | 1.9 (0.2) | 0.7 (0.2) | 0.9 (0.2) | R | S | L | I | L | H | B |
| Northern Flicker *Colaptes auratus* | 39 | 45 | 12 | 2.9 (0.3) | 3.0 (0.3) | 0.5 (0.3) | R | D | L | IE | M | H | B |
| Pileated Woodpecker *Dryocopus pileatus* | 9 | 2 | 11 | 0.3 (0.1) | 0.1 (0.1) | 0.4 (0.1) | R | S | L | I | L | H | B |
| Eastern Wood-Pewee *Contopus virens* | 59 | 59 | 60 | 7.5 (0.5) | 7.2 (0.5) | 4.6 (0.5) | N | D | H | IE | M | UC | A |
| Acadian Flycatcher *Empidonax virescens* | 4 | 2 | 2 | 0.2 (0.1) | 0.1 (0.1) | 0.1 (0.1) | N | D | H | I | S | UC | A |
| Least Flycatcher *Empidonax minimus* | 3 | 8 | 2 | 0.1 (0.1) | 0.2 (0.1) | 0.1 (0.1) | N | D | M | E | S | UC | A |
| Willow Flycatcher *Empidonax traillii* | 2 | 1 | 0 | 0.0 (0.0) | 0.0 (0.0) | — | N | ND | M | E | S | LC | A |
| Eastern Phoebe *Sayornis phoebe* | 0 | 2 | 2 | — | 0.0 (0.0) | 0.1 (0.0) | T | S | L | IE | S | O | A |
| Great Crested Flycatcher *Myiarchus crinitus* | 60 | 63 | 61 | 8.9 (0.7) | 9.4 (0.7) | 6.7 (0.6) | N | M | H | IE | M | H | A |
| Eastern Kingbird *Tyrannus tyrannus* | 2 | 1 | 0 | 0.1 (0.0) | 0.0 (0.0) | — | N | D | M | E | M | LC | A |
| Purple Martin *Progne subis* | 2 | 0 | 0 | 0.0 (0.0) | — | — | N | D | H | E | S | H | A |
| Tree Swallow *Tachycineta bicolor* | 36 | 10 | 29 | 2.7 (0.4) | 0.9 (0.4) | 2.4 (0.4) | T | M | L | E | S | H | A |
| Blue Jay *Cyanocitta cristata* | 40 | 44 | 27 | 2.7 (0.4) | 3.2 (0.4) | 1.6 (0.4) | R | D | L | IE | M | UC | UC |
| American Crow *Corvus brachyrhynchos* | 29 | 39 | 22 | 1.8 (0.4) | 3.2 (0.4) | 1.2 (0.4) | R | S | L | E | L | UC | G |
| Black-capped Chickadee *Parus atricapillus* | 42 | 40 | 25 | 2.6 (0.3) | 2.9 (0.3) | 1.1 (0.3) | R | M | L | IE | M | H | LC |
| Tufted Titmouse *Parus bicolor* | 1 | 0 | 1 | 0.1 (0.0) | — | 0.0 (0.0) | R | S | L | IE | M | H | LC |
| White-breasted Nuthatch *Sitta carolinensis* | 56 | 54 | 35 | 4.6 (0.4) | 5.3 (0.4) | 2.3 (0.4) | R | M | L | IE | L | H | B |
| Brown Creeper *Certhia americana* | 30 | 17 | 10 | 1.7 (0.2) | 0.7 (0.2) | 0.3 (0.2) | R | S | L | I | M | H | B |
| Carolina Wren *Thryothorus ludovicianus* | 2 | 5 | 2 | 0.1 (0.1) | 0.2 (0.1) | 0.1 (0.1) | R | S | L | IE | S | LC | LC |
| House Wren *Troglodytes aedon* | 61 | 63 | 66 | 13.6 (0.9) | 13.9 (0.9) | 11.3 (0.9) | N | S | L | E | S | H | LC |
| Winter Wren *Troglodytes troglodytes* | 0 | 0 | 1 | — | — | 0.0 (0.0) | T | S | L | I | M | G | G |
| Blue-gray Gnatcatcher *Polioptila caerulea* | 46 | 50 | 54 | 4.1 (0.5) | 3.8 (0.5) | 5.2 (0.5) | N | S | M | IE | S | UC | UC |
| Eastern Bluebird *Sialia sialis* | 2 | 0 | 0 | 0.1 (0.0) | — | — | T | S | L | E | S | H | G |
| Veery *Catharus fuscescens* | 9 | 7 | 4 | 0.4 (0.1) | 0.2 (0.1) | 0.2 (0.1) | N | D | H | I | S | G | G |
| Wood Thrush *Hylocichla mustelina* | 2 | 4 | 2 | 0.1 (0.1) | 0.1 (0.1) | 0.0 (0.1) | N | M | H | IE | S | LC | G |
| American Robin *Turdus migratorius* | 62 | 61 | 58 | 9.0 (0.7) | 6.6 (0.7) | 8.3 (0.7) | T | S | L | E | S | UC | G |
| Gray Catbird *Dumetella carolinensis* | 47 | 40 | 41 | 5.5 (0.6) | 3.4 (0.6) | 3.2 (0.6) | N | S | M | E | S | LC | G |

APPENDIX. Continued.

| Species | No. of plots 1992 | 1993 | 1994 | Abundance 1992 | 1993 | 1994 | Migration | Population | Status | Habitat | Territory | Nesting | Foraging |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Brown Thrasher *Toxostoma rufum* | 2 | 0 | 0 | 0.1 (0.1) | — | — | T | D | L | E | M | G | G |
| Cedar Waxwing *Bombycilla cedrorum* | 9 | 1 | 3 | 0.3 (0.1) | 0.1 (0.1) | 0.1 (0.1) | R | S | L | E | M | UC | A |
| European Starling *Sturnus vulgaris* | 7 | 1 | 3 | 0.3 (0.1) | 0.0 (0.1) | 0.2 (0.1) | R | D | L | E | S | H | G |
| Yellow-throated Vireo *Vireo flavifrons* | 33 | 39 | 33 | 1.9 (0.3) | 2.2 (0.3) | 1.3 (0.3) | N | S | H | IE | S | UC | UC |
| Warbling Vireo *Vireo gilvus* | 39 | 53 | 49 | 4.6 (0.7) | 6.8 (0.7) | 5.6 (0.7) | N | D | M | IE | M | UC | UC |
| Red-eyed Vireo *Vireo olivaceus* | 31 | 36 | 30 | 1.8 (0.3) | 2.2 (0.3) | 1.6 (0.3) | N | S | M | IE | S | UC | UC |
| Yellow Warbler *Dendroica petechia* | 27 | 21 | 21 | 1.7 (0.3) | 1.7 (0.3) | 1.0 (0.3) | N | S | L | E | S | LC | LC |
| Yellow-throated Warbler *Dendroica dominica* | 2 | 0 | 0 | 0.1 (0.0) | — | — | N | S | M | IE | S | UC | UC |
| Cerulean Warbler *Dendroica cerulea* | 6 | 10 | 1 | 0.2 (0.1) | 0.4 (0.1) | 0.0 (0.1) | N | D | H | I | S | UC | UC |
| American Redstart *Setophaga ruticilla* | 59 | 59 | 61 | 21.6 (1.7) | 20.2 (1.6) | 22.7 (1.6) | N | M | M | I | S | LC | LC |
| Prothonotary Warbler *Protonotaria citrea* | 53 | 44 | 46 | 7.9 (0.9) | 7.1 (0.8) | 5.2 (0.8) | N | S | H | IE | S | H | LC |
| Ovenbird *Seiurus aurocapillus* | 3 | 7 | 1 | 0.2 (0.1) | 0.2 (0.1) | 0.0 (0.1) | N | S | H | I | S | G | G |
| Common Yellowthroat *Geothlypis trichas* | 45 | 44 | 27 | 3.1 (0.6) | 4.6 (0.5) | 1.8 (0.5) | N | M | M | E | S | G | LC |
| Scarlet Tanager *Piranga olivacea* | 5 | 3 | 0 | 0.1 (0.1) | 0.2 (0.1) | — | N | S | H | I | M | UC | UC |
| Northern Cardinal *Cardinalis cardinalis* | 50 | 53 | 46 | 4.0 (0.5) | 5.1 (0.5) | 3.3 (0.5) | R | S | L | IE | S | LC | G |
| Rose-breasted Grosbeak *Pheucticus ludovicianus* | 22 | 29 | 14 | 1.1 (0.3) | 1.8 (0.3) | 0.9 (0.3) | N | M | H | IE | M | UC | UC |
| Indigo Bunting *Passerina cyanea* | 18 | 3 | 2 | 1.0 (0.1) | 0.1 (0.1) | 0.0 (0.1) | N | D | M | E | M | LC | LC |
| Eastern Towhee *Pipilo erythrophthalmus* | 1 | 0 | 0 | 0.0 (0.0) | — | — | T | D | L | IE | M | LC | G |
| Chipping Sparrow *Spizella passerina* | 1 | 0 | 0 | 0.0 (0.0) | — | — | N | S | L | E | S | LC | G |
| Field Sparrow *Spizella pusilla* | 1 | 2 | 0 | 0.0 (0.1) | 0.1 (0.1) | — | T | D | L | E | S | G | G |
| Song Sparrow *Melospiza melodia* | 56 | 62 | 55 | 5.7 (0.7) | 10.5 (0.7) | 6.7 (0.7) | T | S | L | E | S | G | LC |
| Swamp Sparrow *Melospiza georgiana* | 0 | 2 | 0 | — | 1.7 (0.1) | — | T | S | L | W | S | O | G |
| Red-winged Blackbird *Agelaius phoeniceus* | 45 | 52 | 41 | 4.7 (0.8) | 7.5 (0.8) | 4.8 (0.8) | T | D | L | E | S | LC | G |
| Common Grackle *Quiscalus quiscula* | 51 | 47 | 56 | 9.8 (1.6) | 7.2 (1.5) | 9.4 (1.5) | R | D | L | E | S | UC | G |
| Brown-headed Cowbird *Molothrus ater* | 54 | 39 | 52 | 3.9 (0.5) | 3.3 (0.5) | 4.8 (0.5) | R | M | L | E | L | O | G |
| Baltimore Oriole *Icterus galbula* | 59 | 56 | 59 | 6.1 (0.6) | 5.9 (0.6) | 7.0 (0.6) | N | D | M | E | M | UC | UC |
| American Goldfinch *Carduelis tristis* | 34 | 28 | 7 | 2.5 (0.4) | 1.4 (0.3) | 0.3 (0.3) | R | M | L | E | S | LC | LC |

[a] Migration: R = resident, T = temperate migrant, N = Neotropical migrant; Population: S = stable, increasing, M = mixed, D = decreasing, ND = no data; Management status: L = low, M = medium, H = high; Habitat preference: I = interior forest, IE = interior-edge, E = edge, W = near water; Territory size: S = < 2 ha, M = 2–5 ha, L = > 5 ha; Nesting location: G = ground, LC = lower canopy, UC = upper canopy, H = hole, O = other. Foraging guild: C = carnivore (vertebrates other than fish), P = piscivore, G = ground gleaner, grazer, forager, LC = lower canopy/shrub gleaner, hawker, forager, UC = upper canopy gleaner, hawker, forager, A = air hawker, sallier, screener, B = bark gleaner, excavator.