Birds of large floodplain forests:

Local and regional habitat associations on the Upper Mississippi River

by

Melinda Gail Knutson

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of the

Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Department: Animal Ecology
Interdepartmental Major: Ecology and Evolutionary Biology

Iowa State University
Ames, Iowa

1995

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

ACKNOWLEDGEMENTS

Many thanks to my husband, David L. Ford, for his love, support and encouragement.

ABSTRACT

I studied local and regional habitat associations of birds breeding in floodplain forests of the Upper Mississippi River (UMR) during 1992-94. Floodplain forests provide breeding season habitat for at least 84 bird species, including floodplain forest specialists, cavitynesters, and some neotropical migrant birds that are experiencing regional population declines. Species richness overall and relative abundances of several groups of birds classified by management risk categories and guild associations declined in 1994. Lowered abundance and species richness in 1994 may have resulted from effects of the 1993 flood.

Overall, vegetation (small scale) factors had a larger influence on bird abundances than landscape matrix (large scale) factors. Bird species richness, and the abundance and richness of hole-nesting and bark-gleaning bird guilds, are associated with a landscape matrix dominated by mature forests. Many species, identified by others as area-sensitive in uplands, do not show these patterns in the floodplain. If relative abundance is a reliable indicator of habitat quality, the UMR floodplain provides important habitat for some area-sensitive species such as the American redstart *(Setophaga ruticilla),* blue-gray gnatcatcher *(Polioptila caerulea),* yellow-throated vireo (*Vireo flavifrons)* and yellow-billed cuckoo (Coccyzus *americanus).*

In an artificial nest study, I found large forest tracts had higher nest predation rates than small forest tracts (52.3% vs. 36.3%) and predation rates decreased over the nesting season. There was no significant difference in predation rates among nests placed 25, 50, 100 or 200 m from the forest edge. Calculated artificial nest "survival" derived from observed predation rates in 1993-94 were comparable with natural nest survival estimates from the same study area in 1992. Vegetation variables measured at the nest site did not differ between intact and depredated nests.

Since we have only begun to study the role of floodplain forests as wildlife habitats on the UMR, the most prudent management recommendation is to conserve the existing forests in as close to their present state as possible, with no additional loss of forest. Restoration of higher-elevation terrace forests would increase tree species diversity and provide additional habitat for birds.

CHAPTER 1. GENERAL INTRODUCTION

Numerous researchers have examined habitat relationships of forest songbirds. Few have studied birds inhabiting large floodplain,forests, especially forests of northern rivers (Emlen et al. 1986, Decamps et al. 1987). Recently, declining trends in songbird populations have been identified, especially for birds that migrate to the Neotropics for the winter season (Robbins et al. 1989b, Askins et al. 1990). Many explanations for these observed patterns have been proposed, including habitat loss either in North America or in the tropics of Central and South America (Finch 1991, Rappole and McDonald 1994). Habitat fragmentation has been linked with declining reproductive success, especially for birds that prefer the interiors of large forest tracts (Whitcomb et al. 1981, Lynch and Whigham 1984, Robbins et al. 1989x). Forest interior bird species suffer high predation and parasitism rates when habitat fragmentation forces them to nest close to the forest edge (Brittingham and Temple 1983, Wilcove 1985, Paton 1994).

The large floodplain forests of the Upper Mississippi River (UMR) are some of the largest tracts of forest in the Midwest to remain relatively undisturbed by human intervention, despite losses from lock and dam construction in the 1930's (Grettenberger 1991). One previous study of birds in these forests indicated that the bird community was diverse and many species present were not common in adjacent upland habitats (En-den et al. 1986).

Freemark et al. (in press) outline a process of conservation and management planning for Neotropical migratory birds with research as a major component. Initial steps include broad-scale analysis of continental distributions of bird species. Intermediate steps involve regional analyses of bird distribution and abundance along habitat gradients. Detailed demographic studies such as nest success or survival estimates are the final steps and are implemented as necessary, due to time and cost limitations. My research on UMR floodplain forest birds falls primarily at the intermediate level of this hierarchical scheme. Because little previous research had focused on this bird community, basic information on species distributions, relative abundance, and year-to-year variation was lacking. I studied this bird community during the breeding seasons of 1992, 1993, and 1994 and measured both large-scale and small-scale habitat features. I wanted to determine how the floodplain forest bird community was distributed across the floodplain and to identify habitats and bird species that should be priorities for conservation and protection. Forest fragmentation influences the distribution of some bird species in upland habitats (Robbins et al. 1989a, Robinson et al. 1995, Freemark et al. in press). I wanted to know if this was also true in the large floodplain forests of the UMR.

The study area consisted of forested habitat in river navigation Pools 6-10 of the UMR floodplain (NW Universal Transverse Mercator (UTM) E602000, N4883000; SE UTM E660000, N4738000). The area extends from near Winona, MN in the north to Guttenburg, IA in the south, a distance of about 177 km, following the main channel of the river (Figure 1). We randomly selected 62 plots from forested (> 70% tree canopy cover) land within Pools 6-9 using a 600 m X 600 m sampling grid overlaid on classified geographic information systems (GIS) land cover maps obtained from the Environmental Management Technical Center, National Biological Service, Onalaska, WI. In addition, 5 large forested plots selected from the largest contiguous tracts of forest identified in Pools 6-10 were included to ensure that large tracts were represented. In the following chapters, the number of plots used in the analyses vary because a few plots were not sampled in each year and we measured vegetation on only 56 plots.

My avian habitat study began with a detailed inventory of the flora and vegetation structure of the floodplain forests collected in conjunction with bird census data. This information is useful in understanding floodplain forest successional processes in light of changes in hydrology as well as changed biotic conditions due to Dutch elm disease and other factors. Animals other than birds, such as bats and squirrels also depend upon these forests, so baseline habitat information may prove useful for the management of other species as well.

I collected census data on the bird community from the same plots for three years. Information on natural annual variation in census data is useful for planning future monitoring efforts. If land managers understand how bird abundance and distributions vary from year to year, they will be able to identify changes outside the normal limits of annual variation. This capability should enable managers to act more quickly to address problems. In 1993, most of the forests of the UMR were flooded from mid-June through July. This natural event gave me a unique opportunity to examine how the bird community responded to a major flood. I obtained census data during the flood and compared bird distributions and abundances with data from before and after the flood.

I used multivariate analyses to identify patterns in bird species richness and relative abundance associated with floodplain habitat features at two scales, the plot and the region surrounding the plot in UMR forests. I examined relationships between the bird community and specific habitat features, including forest fragmentation. I identified area-sensitive species and area-sensitive bird classifications based on guild membership or management risk. I compared the influence of vegetation (plot) or landscape matrix (region surrounding the plot) variables on bird species distribution, and identified floodplain forest habitat sub-types important for conservation and management.

Because predation is thought to be a major cause of reproductive failure in natural songbird populations, I conducted an experimental study of nest predation using artificial nests. I contrasted large and small floodplain forest tracts to test whether patterns of predation differ between forest sizes.

Dissertation organization

The dissertation is organized with the chapters as papers to be submitted for publication in scientific journals. Erwin E. Klaas, my major professor, is a co-author on these papers. R. Michael Erwin is a co-author for Chapter 4. 1 planned and conducted the research with consultation from Dr. Klaas and Dr. Erwin. References from the literature cited in Chapters l and 7 are listed after the General Conclusions.

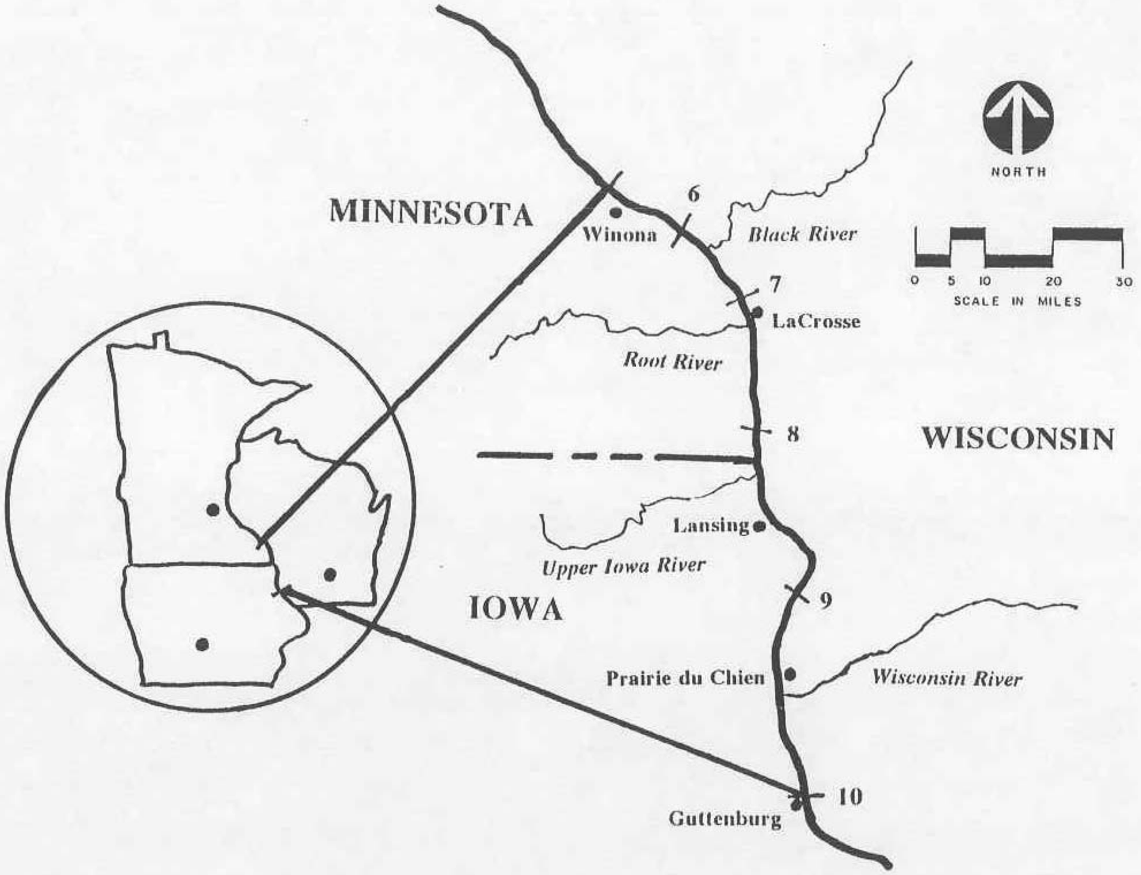

Figure 1. Location of our Upper Mississippi River study area (NW UTM: E602000, N4883000; SE UTM: E660000, N4738000) Numbers indicate locks and dams.

CHAPTER 2. PLANT DOMINANCE AND STRUCTURE OF UPPER MISSISSIPPI RIVER FLOODPLAIN FORESTS: HOW POTENTIAL CHANGES AFFECT BIRDS

A paper to be submitted to the American Midland Naturalist

Melinda G. Knutson[1, 2] and Erwin E. Klaas[1]

Abstract

Lock and dam construction, agriculture, and urban development on the Upper Mississippi River have resulted in the conversion of about half of the presettlement floodplain forests to non-forested habitats. The remaining forests have changed in species composition and structure; species richness is lower and tree density has declined. A. *saccharinwn is* the dominant tree species, followed by *Ulmur* spp., *Fraxinus pennsylvanica,* and *Quercus bicolor.* The sapling layer is dominated by *Ulmus* spp. and *F. pennsylvanica,* followed by *A. saccharinum, Celtis occidentalis,* and *Q. bicolor. Ulmus* spp. and *F. pennsylvanica* each have a large cohort of saplings, whereas *A. saccharinum* has few saplings. *Populus deltoides* has declined in importance along with some hardwood species. We found that tree sizes were similar to those in the presettlement forests, but present forests had fewer trees. This may be due to the effects of hydrologic changes on tree growth or to continued die-off of *Ulmus* spp. caused by Dutch elm disease. Presumably, *A. saccharinum* has filled the canopy gap left by *Ulmus* spp. by increasing in size but not in seedling establishment. Although the relative dominance of the three floodplain forest co-dominants, *A. saccharinum, F. pennsylvanica,* and *Ulmus* spp. has changed, their combined dominance in UMR floodplain forests has changed little in the last 150 years. Historically they comprised about 65%; today they make up about 75% of these forests. We observed changes in tree species dominance and sapling composition that may signal a major change in forest structure. The present tall, closed-canopy forests could be replaced by forests with smaller trees and more grass and shrub habitats. Future changes in forest height and structure could have corresponding effects on floodplain forest birds. Many members of the bird community are heavily dependent upon the present tall-canopied forests for breeding and feeding and would be adversely affected by large-scale change toward a small-stature forest, especially upper-canopy nesters and feeders and cavity-nesting birds. Forest management should focus on encouraging natural forest successional.

---

[1] Graduate student and Professor, respectively, Iowa State University, Department of Animal Ecology and National Biological Service, Iowa Cooperative Fish and Wildlife Research Unit, Ames, IA. Research conducted and manuscript written by Knutson with consultation from Klaas.

[2] Author for correspondence. Address after 1 September 1995: National Biological Service, Upper Mississippi Science Center, P.O. Box 2226, LaCrosse, WI 54601.

processes linked to the hydrology of the floodplain. Some mature forests should be located at appropriate elevations so that a diversity of tree species become established. Restoration of higher-elevation terrace forests could provide habitat for nearly the full complement of tree species present prior to largescale forest conversion, including some flood-intolerant species.

Introduction

Large floodplain forests are confined to relatively narrow bands of land bordering large river systems (Sparks 1995). In places where the river channel meanders across a broad floodplain, forests are interspersed with marshes and oxbow sloughs. Along the Upper Mississippi River (UMR), large complexes of floodplain forest are found adjacent to the confluence of major tributaries such as the Black, Root, Upper Iowa and Wisconsin rivers. Elsewhere, forests are found along channel edges and on mid-channel islands or wherever the land is above water most of the growing season.

About 88% of northern botton-land elm-ash forests in the United States have been lost to agriculture or urban development (Mitsch and Gosselink 1986). Lock and dam construction, agriculture, and urban development on the Mississippi River since the 1930s have directly or indirectly caused the conversion of floodplain forests to non-forested habitats (Peck and Smart 1986). Early European settlers continuously harvested floodplain forests for firewood, railroad ties, and fuel for steamboats (Lapham 1854, Telford 1926). Later, large areas of floodplain forest were cut prior to impoundment (Palas 1938, Fremling and Claflin 1984). UMR floodplain forests were also cut to meet forest management objectives and to maintain wildlife habitat (Feavel 1986). About 71% of the Mississippi floodplain in southern Illinois was forested in 1809 but only 23% was forested in 1989 (Yin and Nelson 1995) (Y. Yin and J. Nelson, unpublished data). In Navigation Pool 8, 64% of the floodplain forests was lost between 1894 and 1989 (National Biological Service, unpublished data). Extrapolating from Peck and Smart (1986), Laustrup and Lowenberg (1994), and Yin and Nelson (1995), we estimate that before European settlement, floodplain forests of the entire UMR system (Pools 1-26) occupied about 50-70% of the floodplain, whereas present forests occupy about 22-25%. The remaining remnant forests have changed (Moore 1988, Nelson et al. 1994, Yin and Nelson 1995). Species richness is lower and tree density has declined. *Acer saccharinum* now strongly dominates most floodplain communities and Populus *deltoides* has declined in importance along with some hardwood species. These changes are attributed to hydrologic changes that affect tree seedling establishment, and both juvenile and adult tree survival (Yeager 1949, Hosner 1958, Hosner 1960). Studies on the Upper Missouri River have also demonstrated major changes in forest composition associated with human-induced hydrologic changes (Johnson 1992, Johnson 1994).

The uplands surrounding the floodplain are part of the Driftless section of the larger Maple-Basswood Forest Region, dominated by *Acer saccharum, Quercus rubra* and *Carya* spp. (Braun 1950). The floodplain differs greatly in species composition from the adjacent upland forests due to periodic flooding, primarily in the spring. Tree species composition varies predictably with elevation above the river channel, because of species differences in flood tolerance and germination requirements (Dunn 1985, Galatowitsch and McAdams 1994). Flood frequency and height have been shown to affect the herbaceous species composition of floodplain forests as well (Menges 1986). Because floodplain forests occupy a unique position within the landscape and differ in plant species composition from the surrounding uplands, they provide habitat for some bird species unique to the floodplain or uncommon in upland forests (See Chapters 3 and 6 for a description of the bird community and bird-habitat relationships.) Adverse changes in the structure or composition of these forests could compromise habitat for such species. Our objective was to document the floristic and structural characteristics, and current successional patterns of UMR floodplain forests as part of a larger project aimed at assessing the value of these forests as wildlife habitat.

Study area

The study area consisted of forested habitat in river navigation Pools 6-10 of the UMR floodplain (NW Universal Transverse Mercator (UTM) E602000, N4883000; SE UTM E660000, N4738000). The area extends from near Winona, MN in the north to Guttenburg, IA in the south, a distance of about 177 km, following the main channel of the river. We randomly selected 51 plots from forested (> 70% tree canopy cover) land within Pools 6-9 using a 600 m X 600 m sampling grid overlaid on classified geographic information systems (GIS) land cover maps obtained from the Environmental Management Technical Center, National Biological Service, Onalaska, WI (Appendix A). In addition, 5 large forested plots selected from the largest contiguous tracts of forest identified in Pools 6-10 were included to ensure that large tracts were represented.

Methods

Vegetation was measured from 20 May through 10 July 1992 on the 56 plots. Plots contained between 3 and 10 sampling points (mean = 5.4). We designed sampling points to accommodate both bird censuses and vegetation measurement. Thus, the number of points depended upon the size of a plot; points were spaced at least 200 m apart and at least 50 m from an edge. Distances were determined by pacing. We collected data on trees, snags, and saplings at each point using the point-centered quarter method (Cottam and Curtis 1956, Mueller-Dombois and Ellenberg 1974). We collected shrub, herb, tree canopy cover, and tree canopy height measurements from 4 locations at each sampling point: the center and three additional points at a radius of 35 m from the sampling point, 120 degrees apart. Herb and shrub cover were estimated using releve classes (Mueller-Dombois and Ellenberg 1974). Means of herb and shrub cover were obtained by assigning the midpoint of the releve class to each observation (Bonham 1989). Cover estimates overlapped; total cover could be > 100%. Trees were woody plants with diameter at breast height (dbh) > 8 cm. Saplings were singlesternmed woody plants z 1.5 m in height with a dbh 5 8 cm. Snags included dead standing wood ~t 12 cm dbh and 1.5 m in height. Shrubs were woody plants > 0.5 m and < 1.4 m in height. We calculated canopy cover from the mean of 4 Type A densiometer readings each taken while facing in the cardinal directions. We measured canopy height of the tallest tree at each location with a clinometer.

We tested for overall differences between the 5 large plots and the randomly selected plots using t-tests. We compared mean tree dbh and mean distance to the nearest tree in each quadrant (density), the same measures for saplings and snags, and mean cover of herbs and shrubs. The 5 large plots were compared with 5 plots drawn randomly from the rest of the data set; 5 sets of randomly drawn plots were tested.

We calculated relative and absolute density, frequency and dominance for trees and saplings (Cottam and Curtis 1956, Mueller-Dombois and Ellenberg 1974). Importance values for each species are the sum of relative density, dominance and frequency. To determine tree and sapling size distributions, we grouped trees into 8-cm size classes, labeled with the midpoint of each class (8-16 cm = 12 cm class, 16-24 cm = 20 cm class, etc.). Because we measured saplings and trees separately, we were unable to compare the number of saplings and trees directly. Therefore, to develop a size distribution curve, sapling numbers were reduced to correspond to tree numbers based on the overall ratio of sapling to tree density (Yin et al. 1994). Each sapling species was reduced. by the same ratio, so the relative densities among species are unchanged. The number of saplings (4-cm size class) for each species was estimated using equation 1.

$$(1) \quad N_{si} = n_{si} \left(d_s / d_t\right)$$

N_{si} = estimated number of saplings of species *i* reduced to correspond to tree data, *nsi = raw* count of saplings of species *i* from point-centered quarter method, *ds = total* absolute density of saplings, and dt = total absolute density of trees. We calculated means of vegetative cover and height measurements across all plots. We also calculated the frequency (proportion of points in which a species was identified) and mean cover estimates for the most dominant shrubs and herbs. Species names follow Gleason and Cronquist (1991).

Results

Out of 40 comparisons of large plots with randomly drawn plots (8 variables X 5 sets of plots), we found 3 significant ($P < 0.05$) differences; 2 are expected by chance. This is an indication that the large plots are similar to the randomly selected plots. Therefore, all plots were used in the analysis.

We identified 139 common plant taxa (species or genus) from the floodplain forests (see Appendix B), measuring a total of 1,257 trees, 1,187 saplings, and 1,149 snags at 314 sampling points on 56 plots. *A. saccharinum* was the dominant tree species, followed by *Ulmus* spp., *Fraxinus pennsylvanica,* and *Quercus bicolor* (Table 1). The sapling layer was dominated by Ulmus spp. and *F. pennsylvanica,* followed by *A. saccharinum, Celtis occidentalis* and *Q. bicolor* (Table 2). According to the size distribution curve, *Ulmus* spp. and *F. pennsylvanica* had a large cohort of saplings, whereas *A. saccharinum* had fewer saplings (Figure 1). No *P. deltoides* trees smaller than the 28 cm dbh size class were identified during sampling. Nut-bearing trees, including all *Quercus* and *Carya spp.,* were a minor component of the floodplain forests and had few young trees (Figure 2). (No *Juglans* spp. were identified during sampling, but some were identified during field work.)

Snag density was 0.35 snags / 100 m^2 and mean basal area per snag was 804..7 cm^2. The mean canopy cover was 93.3%, mean shrub cover was 13.9%, and mean herb cover was 68.3% (Table 3). Herbs and shrubs were measured at 305 sampling points. The shrub layer was dominated by *F. pennsylvanica* seedlings (frequency = 43.3%, mean cover = 1.5% [S.E. = 0.2]), followed by *Toxicodendron radicans* (frequency = 26.6%, mean cover = 5.1% [S.E. = 0.8]), *A. saccharinum* seedlings (frequency = 12.1%, mean cover = 0.1% [S. E. = 0.0]), *Zanthoxylum americanum* (frequency = 11.8%, mean cover = 1.0% [S.E. = 0.2]), *Cornus* spp. (frequency = 11.1%, mean cover = 0.8% [S.E. = 0.2]), *Q. bicolor* seedlings (frequency = 9.5%, mean cover = 0.1% [S.E. = 0.0]), and *C. occidentalis* seedlings (frequency = 6.6%, mean cover = 0.3% [S.E. = 0.1]). *Urtica dioica is* the most dominant herb (frequency = 80.3%, mean cover = 32.5% [S.E. = 1.8]). *Phalaris arundinaceae* (frequency = 69.8%, mean cover = 11.7% [S.E. = 1.0]), *Impatiens* spp. (frequency = 23.3%, mean cover = 3.2% [S.E. _ 0.6]), and *T. radicans* (frequency = 17.7%, mean cover = 3.4% [S. E. = 0.7]) follow in herbaceous dominance.

Discussion

We focused our attention on woody vegetation rather than herbs, so we did not comprehensively survey the herbaceous vegetation. Swanson and Sohmer (1978) comprehensively studied vascular plants of Pool 8 and found 482 species. Galatowitsch and McAdams (1994) list 591 species compiled from published reports on UMR vegetation. These lists include plants of all habitat types, not just forested habitats.

Historic species composition and patterns of UMR floodplain forest succession were dependent upon pre-lock and dam hydrology and fluvial dynamics (Peck and Smart 1986, Yin and Nelson 1995). Under natural conditions, a river channel migrates laterally back and forth over time within its floodplain (Everitt 1968). New mud flats and sandbars would give rise to *Salix* spp., *P. deltoides,* and *A. saccharinum* forests and be succeeded by *Q. bicolor, U. americana,* and *Carya cordiformis* on the upper terraces (Galatowitsch and McAdams 1994). Present river hydrology is constrained to the main channel and the river is not allowed to meander laterally, restricting new mud flat development. Consequently, mean water levels and the height and duration of flooding have increased (Grubaugh and Anderson 1988, Grubaugh and Anderson 1989, Lubinski et al. 1991, Sparks 1995, Yin and Nelson 1995). Tree species richness has been negatively affected by these changes (Moore 1988, Nelson et al. 1994),

Moore (1988) studied the floodplain forest at Effigy Mounds National Monument (bottomland forest near the mouth of the Sny-Magill River, Clayton County, IA) and compared his findings with 1837-1854 General Land Office Survey records of bottomland forest from Houston County, MN, Allamakee County and Clayton County, IA. He found that the average size of floodplain forest trees had fallen nearly 40% and total basal area was 50% lower than presettlement forests. He attributed these changes to the negative effects of impoundment on tree growth. He also predicted that frequent inundation would favor *Fraxinus* spp. seedlings, which are more tolerant of flooding than *A. saccharinum* or Ulmus spp. In our study, *Fraxinus* spp. did dominate both the sapling and shrub layer in density and frequency. Our estimates of tree density in Pools 6-10 (Table 4) were even lower than Moore (1988) found in the Sny-Magill tract, but basal areas were similar. Tree sizes are similar to the presettlement forests, but present forests have fewer trees (Table 4). This may be due to hydrologic changes or to continued effects of the Ulmus spp. die-off from Dutch elm disease *(Ophiostoma ulmi* [Buism.] Nannf.) (Sticklen and Sherald 1993). It is likely that the forests are still responding to death of a large proportion of Ulmus spp. canopy trees in the last 20 years. According to our data, A. *saccharinum* continues to increase in dominance in UMR floodplain forests. We hypothesize that A. *saccharinum* may be filling canopy gaps left by *U. americana* by increasing in size but is not producing many seedlings. Although *A. saccharinum, F. pennsylvanica* and *Ulmus* spp. have changed in relative dominance, their combined dominance in UMR Iloodplain forests has changed little in the last 150 years. Historically they comprised about 63%; today they make up about 77% of these forests (Table 4).

Celtis occidentalis ranked fourth in sapling importance value in our study, however, this species does not tolerate flooding well and Yin et al. (1994.) observed substantial mortality following the 1993 flood. It is unlikely that this species will ever attain dominance in the floodplain under current hydrologic conditions. With few seedlings or trees, P. *deltoides* and *Salix nigra* are virtually disappearing as components of mature floodplain forests. The seedlings of these species germinate on open mud flats, which we did not census. However, young or mid-successional stands of cottonwood-willow were noticeably absent in our study. If these species were regenerating, we should have identified more of this forest type. The 1993 flood provided new mud flats with conditions favorable for establishment of stands of *Salix* spp., *P. deltoides,* and *A. saccharinum* (Galatowitsch and McAdams 1994, Yin et al. 1994). Time will tell whether these seedlings will survive to create new forest stands.

When the mature *A. saccharinum* canopy trees begin to die, what species will replace them? How will the floodplain respond to large-scale disturbance, such as the 1993 flood that caused substantial mortality for both seedlings and mature canopy trees in some areas (Yin et al. 1994)? The changes in tree species dominance and sapling composition that are occurring may signal a change in forest structure. Assuming hydrologic and climatic conditions prevailing at the time of our study continue, the present tall, closed-canopy forests could be replaced by forests with smaller trees and more grass and shrub habitats. Judging by flood tolerances and the saplings and small trees present, *F. pennsylvanica* and Ulmus spp. are likely to increase in importance. *F. pennsylvanica is* a small to medium-sized tree with a height at maturity of 10 - 17 m (Harlow et al. *1986). U. americana,* crippled by Dutch elm disease, achieves similar stature and has a short life span. In contrast, several species, common in historic floodplain forests, attain much taller stature than this; *A. saccharinwn* grows to 20 - 27 m*, P. deltoides* to *27 - 33* m, and *Q. bicolor* to 20 - 23 m (Harlow et al. 1986, Preston 1989*).* Prior to Dutch elm disease, *U. americana* grew to heights of *25 - 34* m.

Biotic competitive factors also affect floodplain forest successional patterns and species composition. *P. arundinaceae is* aggressive as a low-elevation terrestrial herb in the study area (Swanson and Sohmer 1978, Peck and Smart 1986*,* Galatowitsch and McAdams 1994). This grass invades the understory when the canopy opens, out-competes tree and shrub seedlings, and retards forest succession in these openings.

Changes in forest canopy height and structure could have corresponding effects on floodplain forest birds. Vertical vegetation structure and heterogeneity are important to some bird species, especially warblers (MacArthur 1958, 1964). Many members of the UMR bird community are heavily dependent on the presence of tall-canopied forests for breeding and feeding and will be adversely affected if a large-scale change toward a more open canopy and small-statured forest occurs. (See Chapter 3 for a description of the floodplain bird community.) Birds nesting in the upper canopy of the forest include herons and egrets (family *Ardeidae),* bald eagles *(Haliaeetus leucocephalus),* red-shouldered hawks *(Buteo lineatus),* great horned owls *(Bubo virginianus),* flycatchers (family *Tyrannidae*), blue-gray gnatcatchers *(Polioptila caerulea),* yellow-throated vireos *(Vireo flavifrons),* warbling vireos (*V. gilvis*), red-eyed vireos (*V. olivaceus),* yellow-throated warblers *(Dendroica dominica),* cerulean warblers *(D. cerulea),* and northern orioles *(Icterus galbula)*. The cerulean warbler, a species of management concern for the U.S. Fish and Wildlife Service (Office of Migratory Bird Management 1987), i*s* experiencing steep population declines continentally and regionally. One hypothesis explaining their decline on the UMR is the loss of mature U. *americana* trees, which were taller and had stronger structure (larger limbs) at high canopy levels than *A. saccharinum* trees. We observed that cerulean warblers do tend to perch in the tallest trees available in a forest patch. Detailed habitat studies elsewhere confirm their preference for tall, old-growth trees. They also prefer a well-developed sub-canopy and understory (Robbins et al. 1992).

Late-successional forests with many large snags are also important to cavity-nesting birds, including wood ducks *(Aix sponsa),* and hooded mergansers *(Lophodytes cucullatus),* barred owls, pileated woodpeckers (*Dryocopus pileatus),* great crested flycatchers *(Myiarchus crinitus),* and prothonotary warblers *(Protonotaria citrea)*. Altogether, there are 23 species of cavity-nesters breeding in the UMR forests we studied. Understory shrubs and vines abundant in mature forests also provide important wildlife habitat. We found that American redstarts *(Setophaga ruticilla)* frequently nested in *T. radicans* and *Vitis riparia* entwined in mature trees, and yellow warblers *(Dendroica petechia)* and indigo buntings *(Passerina cyanea)* nested in *Salix* spp. thickets and other shrub habitats.

Research and planning should focus on improved understanding of how altered floodplain hydrology affects establishment and growth of different tree species. Predictive models of forest succession have been developed for upland forests and could be modified to predict changes in species composition and structure for UMR forests as well as associated changes in the bird community (Gustafson and Crow 1994, Johnson 1994). Techniques should be developed to restore and maintain forest successional processes that favor a mix of tree species composition, structure, and age.

Acknowledgements

Funding was provided by the National Biological Service (Patuxent Environmental Science Center, Branch of Migratory Birds Research), Iowa State University, U.S. Fish and Wildlife Service (Region 3 Nongame Program), and the Minnesota Department of Natural Resources Nongame Program. Special thanks to Ms. Knutson's doctoral committee members Louis Best, Brent Danielson, Kirk Moloney, and Thomas Jurik. Deborah Lewis assisted with identification of herbarium specimens. Field, office, and data management assistance were provided by Ingrid Moore, Brian Collins, Tom Pehowski, Vance Polton, Holly Dick, Pam Heidenreich, and Brenda VanBeek.

Literature cited

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, New York, NY. 338 pp.

Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Pub., New York, NY. 596 pp.

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451-460.

Dunn, C. P. 1985. Description and dynamics of lowland hardwood forests of southeastern Wisconsin. Doctoral diss. Univ. of Wisconsin, Milwaukee. 215 pp.

Everitt, B. L. 1968. Use of cottonwood in an investigation of the recent history of a floodplain. Am. J. Sci. 226: 417-439.

Feavel, T. 1986. Forest management on the Mississippi. *Iowa Conserv.* 45(10): 29-31.

Fremling, C. R. and T. O. Claflin. 1984. Ecological history of the Upper Mississippi River. Pages 5-24 *In* J. G. Wiener, R. V. Anderson and D. R. McConville, Eds. Contaminants in the Upper Mississippi River: Proc. of the 15th Annual Meeting of the Mississippi River Research Consortium. Butterworth Publishers. Boston, MA.

Galatowitsch, S. M. and T. V. McAdams. 1994. Distribution and requirements of plants on the Upper Mississippi River: literature review. Unpub. project report to U.S. Fish and Wildlife Service. June, 1994. Iowa Coop. Fish and Wildlife Res. Unit, Ames, IA. 175 pp.

Gleason, H. A. and A. Cronquist. 1991. Manual of vascular plants of northeastern United States and adjacent Canada, 2nd ed. New York Botanical Garden, Bronx, NY. 910 pp.

Grubaugh, J. W. and R. V. Anderson. 1988. Spatial and temporal availability of floodplain habitat: Long-term changes at Pool 19, Mississippi River. Am. *Midl. Nat.* 119: 402411.

Grubaugh, J. W. and R. V. Anderson. 1989. Long-term effects of navigation dams on a segment of the Upper Mississippi River. *Reg. Riv. Res. Manage.* 4: 97-104.

Gustafson, E. J. and T. R. Crow. 1994. Modeling the effects of forest harvesting on landscape structure and the spatial distribution of cowbird brood parasitism. *Landsc.* Ecol. 9: 237-248.

Harlow, W. M., E. S. Harrar and F. M. White. 1986. Textbook of dendrology, 6th ed. McGraw-Hill, New York, NY. 510 pp.

Hosner, J. F. 1958. The effects of complete inundation upon seedlings of six bottomland tree species. Ecology 39: 371-373.

Hosner, J. F. 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. *For. Sci.* 6: 246-251.

Johnson, W. C. 1992. Dams and riparian forests: case study from the Upper Missouri River. *Rivers* 3: 229-242.

Johnson, W. C. 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. Ecol. *Monogr.* 64: 45-84.

Lapham, I. A. 1854. The forest trees of Wisconsin. *Trans. Wisc. St. Agric. Soc.* 4: 195-251.

Laustrup, M. S. and C. D. Lowenberg. 1994. Development of a systematic land cover/land use database for the Upper Mississippi River System derived from Landsat thematic mapper satellite data. National Biological Survey, Environmental Management Technical Center, Onalaska WI. 90 pp.

Lubinski, K. S., G. Carmody, D. Wilcox and B. Drazkowski. 1991. Development of water level regulation strategies for fish and wildlife, Upper Mississippi River system. *Reg. Riv. Res. Manage.* 6: 117-124.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. Am. Nat. 98: 387-397.

Menges, E. S. 1986. Environmental correlates of herb species composition in five southern Wisconsin floodplain forests. Am. *Midl. Nat.* 115: 106-117.

Mitsch, W. J. and J. G. Gosselink. 1986. Wetlands. Van Nostrand Reinhold, New York. 537 pp.

Moore, G. F. 1988. Plant communities of Effigy Mounds National Monument and their relationship to presettlement regional vegetation. Master's thesis. Univ. of Wisconsin, Madison. 148 pp.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. Eds. John Wiley and Sons, New York. 54.7 pp.

Nelson, J. C., A. Redmond and R. E. Sparks. 1994. Impacts of settlement on floodplain vegetation at the confluence of the Illinois and Mississippi Rivers. *Trans. Ill. St. Acad. Sci.* 87: 117-133.

Office of Migratory Bird Management. 1987. Migratory nongame birds of management concern in the United States: the 1987 list. Washington, D.C. 27 pp.

Palas, A. J. 1938. Extreme northeastern Iowa for bird observation. Iowa *Bird Life* 8: 34-36.

Peck, J. H. and M. M. Smart. 1986. An assessment of the aquatic and wetland vegetation of the Upper Mississippi River. *Hydrobiologia* 136: 57-76.

Preston, R. J., Jr. 1989. North American Trees, 4th ed. Iowa State Univ. Press, Ames, IA. 407 pp.

Robbins, C. S., J. W. Fitzpatrick and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea.* Pages 549-562 *In* J. M. Hagan III and D. W. Johnston, Eds. Ecology and conservation of neotropical migrant landbirds. Manomet Bird Observatory, Woods Hole, MA.

Sparks, R. E. 1995. Need for ecosystem management of large floodplain rivers and their floodplains. *BioScience 45:* 168-182

Sticklen, M. B. and J. L. Sherald. 1993. Dutch elm disease research: cellular and molecular approaches. Springer-Verlag, New York, NY. 344 pp.

Swanson, S. D. and S. H. Sohmer. 1978. The vascular flora. of Navigation Pool 8 of the Upper Mississippi River. Proc. Iowa *Acad. Sci.* 85: 45-61.

Telford, C. J. 1926. Third report on a forest survey of Illinois. *Bull. 111. Nat. Hist. Surv.* 16: 1-102.

Yeager, L. E. 1949. Effect of permanent flooding in a river timber area. *Bull. Ill. Nat. Hist. Surv.* 25: 33-65.

Yin, Y. and J. C. Nelson. 1995. Modifications to the Upper Mississippi River and their effects on floodplain forests. Long-Term Resource Monitoring Program technical report 95-T003. National Biological Service, Environmental Management Technical Center, Onalaska, WI. 17 pp.

Yin, Y., J. C. Nelson, G. V. Swenson, H. A. Langrehr and T. A. Blackburn. 1994. Tree mortality in the Upper Mississippi River and floodplain following an extreme flood in 1993. Pages 39-60 In J. W. Barko and M. M. Wise, Eds. Long-Term Resource Monitoring Program, 1993 flood observation report. National Biological Service, Illinois Natural History Survey, and Wisconsin Department of Natural Resources. Onalaska, WI.

Table 1. Tree species absolute and relative density, dominance, frequency, and importance value.

Scientific name	#Trees	Mean BA (a)	Abs. dens (b)	Rel. dens.	Abs. dom.	Rel. dom.	Abs. freq.	Rel. freq.	IV (c)	IV rank
Acer saccharinum	620	1383.38	1.4670	49.32	2029.39	74.06	0.7744	37.46	160.84	1
Ulmus spp.	213	211.71	0.5040	16.95	106.70	3.89	0.4276	20.68	41.52	2
Fraxinus pennsylvanica	130	486.47	0.3076	10.34	149.64	5.46	0.2828	13.68	29.48	3
Quercus bicolor	79	603.62	0.1869	6.28	112.83	4.12	0.1216	6.03	16.43	4
Populus deltoides	28	2409.89	0.0663	2.23	159.66	5.83	0.0741	3.58	11.64	5
Celtis occidentalis	34	224.86	0.0804	2.70	18.09	0.66	0.0842	4.07	7.44	6
Betula nigra	28	681.18	0.0663	2.23	45.13	1.65	0.0606	2.93	6.81	7
Quercus rubm	32	470.71	0.0757	2.55	35.64	1.30	0.0539	2.61	6.45	8
Tilia americana	25	346.10	0.0592	1.99	20.47	0.75	0.0438	2.12	4.85	9
Carya cordiformis	24	245.94	0.0568	1.91	13.97	0.51	0.0471	2.28	4.70	10
Prunus serotina	14	437.97	0.0331	1.11	14.51	0.53	0.0269	1.30	2.95	11
Robinia pseudo-acacia	14	302.60	0.0331	1.11	10.02	0.37	0.0202	0.98	2.46	12
Acer negundo	7	443.81	0.0166	0.56	7.35	0.27	0.0202	0.98	1.80	13
Salix nigra	2	2307.22	0.0047	0.16	10.92	0.40	0.0067	0.33	0.88	14
Trees, unidentified	2	80.91	0.0047	0.16	0.38	0.01	0.0067	0.33	0.50	15
Mortis spp.	2	76.98	0.0047	0.16	0.36	0.01	0.0034	0.16	0.34	16
Quercus alba	1	962.11	0.0024	0.08	2.28	0.08	0.0034	0.16	0.33	17
Pinus strobus	1	881.41	0.0024	0.08	2:09	408	0.0034	0.16	0.32	18
Betula papyrifera	1	475.29	0.0024	0.08	1.12	0.04	0.0034	0.16	0.28	19
Total	1,257	921.44	2.9742	100.00	2,740.54	100.0	12.0673	100.00	300.01	

(a) Mean basal area per tree (sq. cm).
(b) Density in trees/100 sq. m.
(c) Importance value = sum of relative density, relative dominance and relative frequency.

Table 2. Sapling species absolute and relative density, dominance, frequency, and importance value.

Scientific name	#Saplings	Mean BA (a)	Abs. dens. (b)	Rel. dens.	Abs. dom.	Rel. door.	Abs. freq.	Rel. freq.	IV (c)	IV rank
Ulmus spp.	271	23.73	0.1742	22.83	4.1333	46.80	0.4710	22.96	92.59	1
Fraxinus pennsylvanica	387	5.30	0.2487	32.60	1.3173	14.92	0.5836	28.45	75.97	2
Acer saccharinum	176	15.91	0.1131	14.83	1.7994	20.37	0.2969	14.48	49.68	3
Celtis occidentalis	81	7.69	0.0521	6.82	0.4001	4.53	0.1433	6.99	18.34	4
Quercus bicolor	46	11.45	0.0296	3.88	0.3383	3.83	0.0956	4.66	12.37	5
Carya cordiformis	32	8.12	0.0206	2.70	0.1670	1.89	0.0580	2.83	7.42	6
Robiiua pseudo-acacia	32	9.50	0.0206	2.70	0.1954	2.21	0.0444	2.16	7.07	7
Zanthoxylum americanum	32	1.26	0.0206	2.70	0.0259	0.29	0.0614	3.00	5.98	8
Cornis spp.	18	2.92	0.0116	1.52	0.0338	0.38	0.0410	2.00	3.90	9
Acer negundo	14	2.94	0.0090	1.18	0.0265	0.30	0.0341	1.66	3.14	10
Tilia americana	11	10.28	0.0071	0.93	0.0727	0.82	0.0273	1.33	3.08	11
Quercus rubra	11	8.46	0.0071	0.93	0.0598	0.68	0.0273	1.33	2.93	12
Primus serotina	14	3.83	0.0090	1.18	0.0344	0.39	0.0239	1.16	2.73	13
Morus spp.	11	5.42	0.0071	0.93	0.0383	0.43	0.0239	1.16	2.53	14
Trees, unidentified	14	3.35	0.0090	1.18	0.0301	0.34	0.0205	1.00	2.52	15
Toxicodendron radicans	8	1.98	0.0051	0.67	0.0102	0.12	0.0239	1.16	1.95	16
Vibimum lentago	8	2.58	0.0051	0.67	0.0133	0.15	0.0205	1.00	1.82	17
Betula nigra	5	13.72	0.0032	0.42	0.0441	0.50	0.0102	0.50	1.42	18
Rhamnus cathartica	5	11.95	0.0032	0.42	0.0384	0.43	0.0102	0.50	1.36	19
Vibirnum nudum	3	11.34	0.0019	0.25	0.0219	0.25	0.0102	0.50	1.00	20
Sbrubs, unidentified	2	14.86	0.0013	0.17	0.0191	0.22	0.0068	0.33	0.72	21
Salix nigra	3	4.15	0.0019	0.25	0.0080	0.09	0.0068	0.33	0.68	22
Sambucus canadensis	1	5.31	0.0006	0.08	0.0034	0.04	0.0034	0.17	0.29	23
Amelanchier canadensis	1	2.01	0.0006	0.08	0.0013	0.01	0.0034	0.17	0.27	24
Alnus serrulata	1	0.20	0.0006	0.08	0.0001	0.00	0.0034	0.17	0.25	25
Total	1187	11.58	0.7628	100.00	8.8321	100.00	2.0512	100.00	300.00	

(a) Mean basal area per sapling (sq. cm).
(b) Density in saplings/ 100 sq. m.
(c) Importance value = sum of relative density, relative dominance, and relative frequency.

Table 3. Mean vegetation variables measured on census plots (N = 56).

Variable	Mean	Std. dev.
Distance to trees (m)	5.7	1.5
Distance to saplings (m)	11.8	7.4
Distance to snags (m)	16.8	3.9
Tree dbh (cm)	31.6	9.2
Sapling dbh (cm)	3.6	1.1
Snag dbh (cm)	31.4	9.0
Tree height (m)	27.5	5.5
Canopy cover (%)	93.3	5.3
Shrub cover (%)	13.9	19.1
Herb cover (%)	68.3	24.0

Table 4. Comparison of presettlement and current floodplain forests.

Forest characteristics	1840's (a)	1983 (b)	1992 (c)
Number of species	26	11	19
Trees per ha	511.9	400.0	297.4
Mean tree dbh	34.5	-	31.6
Mean basal area per tree (square dm)	9.3	5.8	9.2
Basal area per ha (square dm)	4760.3	2333.3	2740.5
IV Acer saccharinum (scale of 100)	20.4	38.9	53.6
IV Fraxinus spp. (scale of 100)	26.8	11.2	9.8
IV Ulmus americana (scale of 100)	16.2	20.7	13.8
Sum IV of above species	63.4	70.8	77.3

(a) Analysis by Moore (1988). Presettlement data from surveyors' notes circa 1840's.
(b) Data from Moore (1988) for floodplain forest at the mouth of the Sny-Magill River, Clayton Co., IA.
(c) Present study.

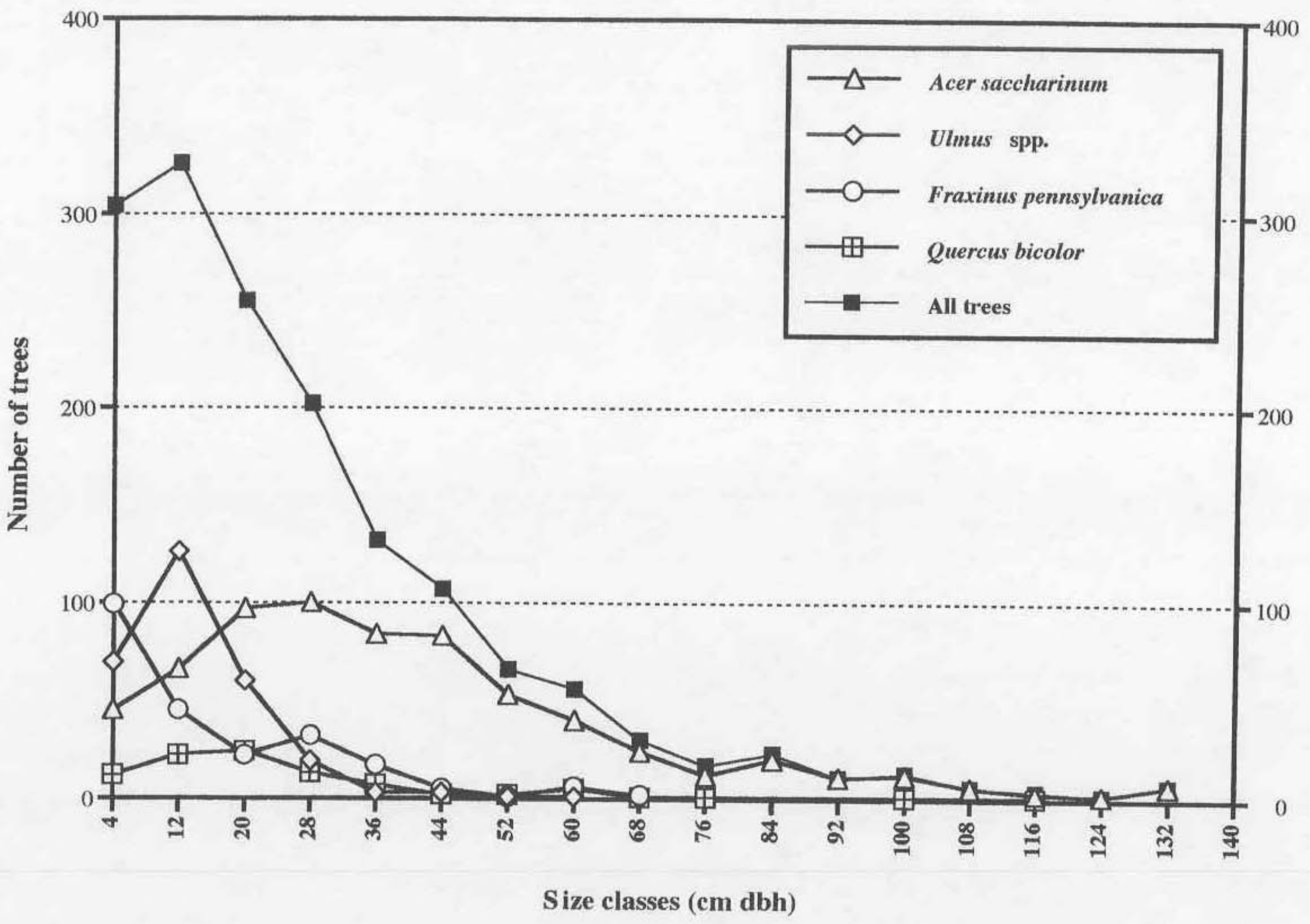

Figure 1. Tree and sapling size distribution of the most dominant floodplain forest trees.

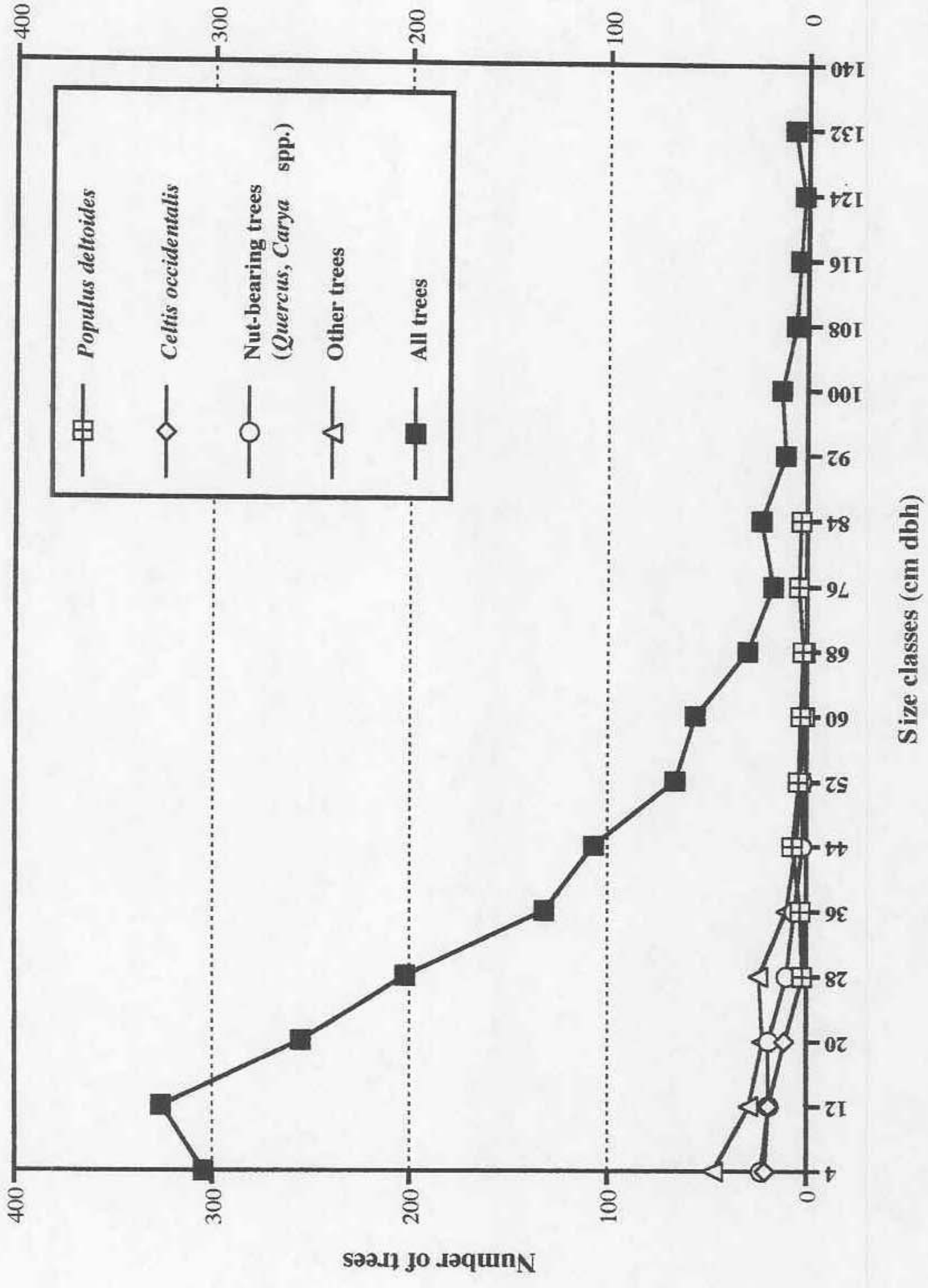

Figure 2. Tree and sapling size distribution of less dominant floodplain forest trees. Nut-bearing trees include all *Quercus* and *Carya* spp. Other category includes trees and saplings not shown elsewhere.

Appendix A. Locations of vegetation study plots, Pools 6-10 of the Upper Mississippi River.

Plot	UTM Coordinates		Plot	UTM Coordinates	
601	E623400	N4873487	812	E640469	N4826985
602	E620979	N4874321	813	E642215	N4824941
603	E616411	N4879532	814	E641342	N4827092
604	E618127	N4877173	850	E639155	N4846642
605	E619338	N4876796	851	E639988	N4846642
606	E619195	N4877495	903	E643407	N4818022
701	E629420	N4869324	904.	E643142	N4814950
702	E629252	N4868700	905	E642077	N4813761
703	E632882	N4863545	906	E641755	N4814083
704	E633398	N4862771	907	E646196	N4806089
705	E631628	N4868901	908	E645673	N4806015
706	E633230	N4869152	909	E646196	N4806962
707	E628563	N4869687	911	E641960	N4818490
708	E626698	N4870292	913	E656884	N4792564
709	E627212	N4871038	914	E657036	N4791869
710	E633140	N4869755	915	E639575	N4821514
711	E633983	N4869062	916	E639596	N4819938
712	E634043	N4861954	917	E642194	N4820087
714	E636968	N4860449	918	E642215	N4821216
801	E639051	N4849443	919	E643106	N4811547
802	E639854	N4848925	920	E644402	N4809877
803	E642056	N4846309	922	E642683	N4817788
804	E637367	N4856438	923	E643109	N4816383
805	E637911	N4855453	924	E640415	N4811497
808	E640022	N4828625	925	E640863	N4809777
809	E639894	N4828284	950	E641414	N4821908
810	E639802	N4847345	951	E640781	N4810471
811	E640512	N4827773	1050	E649284	N4755042

Appendix B. Plants identified from Upper Mississippi River forests in 1992.

(a) Names follow Gleason and Cronquist, 1991; * = species not indigenous to North America;
@ = voucher specimen deposited in the Ada Hayden Herbarium (ISC), Department of Botany, Iowa State University.

Life form	Common name	Scientific name (a)	Family
Tree	Box-elder	Acer negundo L.	Aceraceae
Tree	Silver maple	Acer saccharinum L	Aceraceae
Tree	Sugar maple	Acer saccharum Marsh.	Aceraceae
Herb	Common yarrow	Achillea millefolium L. Q	Asteraceae
Herb	Red baneberry	Actea rubra (Aiton) Willd	Ranunculaceae
Herb	Purple giant hyssop	Agastache scrophulariaefolia (Willd.) Kuntze	Lamiaceae
Shrub/vine	Alder	Alnus serrulata (Ait.) Willd.	Betulaceae
Shrub/vine	Eastern serviceberry	Amelanchier canadensis (L.) Medikus	Rosaceae
Herb	False indigo	Amorpha fruticosa L	Fabaceae
Herb	Hog peanut	Amphicarpa bracteata (L.) Fern. @	Fabaceae
Herb	Canadian anemone	Anemone canadensis L. @	Ranunculaceae
Herb	Rock-cress	Arabis lyrata L. @	Brassicaceae
Herb	Green dragon	Arisaema dracontium (L.) Schott. @	Araceae
Herb	Swamp milkweed	Asclepias incarnata L.	Asclepiadaceae
Herb	Aster	Aster fam.	Asteraceae
Herb	Hoary alyssum	Berteroa incana (L.) DC @	Brassicaceae
Tree	River birch	Betula nigra L.	Betulaceae
Tree	Paper birch	Betula papyrifera var. papyrifera Marshall	Betulaceae
Tree	Birch	Betula spp.	Betulaceae
Herb	Beggar's tick	Bidens spp.	Asteraceae
Herb	Bog-hemp (false nettle)	Boehmerica cylindrica (L.) Sw.	Urticaceae
Herb	Chinese mustard	Brassica juncea (L.) Czernj. @	Brassicaceae
Herb	Black mustard	Brassica nigra L.	Brassicaceae
Herb	Pennsylvania bitter-cress	Cardamine pensylvanica Muhl. @	Brassicaceae
Herb	Sedge	Carex intumescens Rudge. @	Cyperaceae
Tree	Bitternut hickory	Carya cordiformis (Wang.) KKoch.	Jugulandaceae
Tree	Pecan	Carya illinoensis (Wang.) K Koch.	Jugulandaceae
Tree	Shellbark hickory	Carya laciniosa (Michx.) Loud.	Jugulandaceae
Tree	Shagbark hickory	Carya ovata (Mill.) KKoch.	Jugulandaceae
Tree	Northern catalpa	Catalpa speciosa Warder * @	Bignoniaceae
Tree	Hackberry	Celtis occidentalis L. @	Ulmaceae
Shrub/vine	Buttonbush	Cephalanthus occidentalis L. @	Rubiaceae
Herb	Goosefoot (lambsquarter)	Chenopodium album L. *	Chenopodiaceae
Herb	Spotted cowbane (water hemlock)	Cicuta maculata L. @	Apiaceae
Shrub/vine	Knob-styled (silky) dogwood	Cornus amomum Mill. @	Cornaceae
Shrub/vine	Flowering dogwood	Corpus florida L.	Cornaceae
Shrub/vine	Northern swamp (gray) dogwood	Cornus racemosa Lam. @	Cornaceae
Shrub/vine	Round-leaved dogwood	Cornus rugosa Lam.	Cornaceae
Shrub/vine	Red osier dogwood	Cornus sericea L.	Cornaceae
Herb	Honewort	Cryptotaenia canadensis (L.) DC. @	Apiaceae
Herb	Common dodder	Cuscuta gronovii Willd.	Cuscutaceae
Herb	Sedge	Cyperus spp.	Cyperaceae
Herb	Tick-trefoil	Desmodium spp.	Fabaceae
Herb	Prickly cucumber	Echinocystis lobata (Michx.) T. & G.	Curcurbitaceae
Herb	Common horsetail	Fquisetum arvense L. @	Equisataceae
Herb	Common horsetail	Eqnisetum hyemale L. @	Equisetaceae
Herb	Fleabane	Erigeron philadelphicus L.	Asteraceae
Shrub/vine	Wahoo	Euonymous atropurpureus Jacq.	Celastraceae
Herb	Leafy spurge	Euphorbia esula L. *@	Euphorbiaceae
Herb	Wild strawberry	Fragaria virginiana Duchn.	Rosaceae
Tree	Green ash	Fraxinus pennsylvanica Marsh. @	Oleaceae
Herb	Blunt-leaf bedstraw	Galium obtusum Bigelow. @	Rubiaceae
Herb	Wild geranium	Geranium maculatum L.	Geraniaceae
Herb	Ground ivy	Glechoma hederacea L. *	Lamiaceae
Tree	Honey locust	Gleditsia triacanthos L.	Fabaceae
Herb	Hedege-hyssop	Gratiola virginiana L @	Scrophulariaceae
Tree	Kentucky coffee tree	Gymnocladus dioica (L.) K.Koch.	Fabaceae
Herb	Sunflower-everlasting	Heliopsis helianthoides (L) Sweet @	Asteraceae
Herb	Virginia water leaf	Hydrophyllum virginianum L	Hydrophyllaceae
Shrub/vine	Winterberry	Ilex verticillata var. padifolia (Willd.) T.&G. @	Aquifroliacea
Herb	Touch-me-not (jewelweed)	Impatiens spp.	Balsaminaceae
Herb	Northern blue flag	Iris virginica L. var. shrevei (Small) E Anderson @	Iridaceae
Tree	Butternut	Juglans cinerea L.	Juglandaceae
Tree	Black walnut	Juglans nigra L.	Juglandaceae
Shrub/vine	Juniper	Juniper spp.	Cupressaceae
Herb	Wood nettle	Laportea canadensis (L.) Wedd.	Urticaceae
Herb	Mothenvort	Leonurus cardiaca L @	Lamiaceae
Herb	Annual toadflax	Linaria canadensis (L) Dum.-Cours. @	Scrophulariaceae
Shrub/vine	Honeysuckle	Lonicera spp.	Caprifoliaceae

Appendix B. continued.

Life form	Common name	Scientific name (a)	Family
Herb	Bugleweed (horehound)	Lycopus spp.	Lamiaceae
Herb	Fringed loosestrife	Lysimachia ciliata L. @	Primulaceae
Herb	Moneywort	Lysimachia nummularia L. *@	Primulaceae
Herb	Swamp loosestrife	Lysimachia thyrsiflora L.	Primulaceae
Herb	Field mint	Mentha arvensis L.	Lamiaceae
Herb	Allegheny monkey-flower	Mimulus ringens L @	Scrophulariaceae
Herb	Heart-leaved umbrella-wort	Mirabilis nyctaginea (Michx.) MacMillan @	Nyctaginaceae
Tree	White mulberry	Moms alba L. @	Moraceae
Herb	Water scorpion-grass (forget-me-not)	Myosotis scorpioides L. @	Boraginaceae
Herb	Sensitive fern	Onoclea sensibilis L.	Polypodiacxae
Herb	Royal fern	Osmunda regalis L. @	Osmundaceae
Herb	Wood-sorrel	Oxalis stricta L.	Oxalaceae
Herb	Pellitory	Parietaria pensylvanica Muhl. @	Urticaceae
Shrub/vine	Grape-woodbine	Parthenocissus vitacea (Knerr) A. Hitchc. @	Vitaceae
Herb	Reed canary grass	Phalaris arundinacea L.	Poaceae
Herb	Phlox	Phlox spp.	Polemoniaceae
Tree	Sycamore	Platanus occidentalis L.	Plantanaceae
Herb	Lady's thumb	Polygonum persicaria L.	Polygonaceae
Herb	Smartweed	Polygonum spp.	Polygonaceae
Tree	Cottonwood	Populus deltoides Marsh.	Salicaceae
Herb	Old-field five-fingers	Potentilla simplex Michx. @	Rosaceae
Tree	Black cherry	Primus serotina Ehrh. @	Rosaceae
Tree	White oak	Quercus alba L:	Fagaceae
Tree	Swamp white oak	Quercus bicolor Willd.	Fagaceae
Tree	Pin oak	Quercus palustris Muench.	Fagaceae
Tree	Northern red oak	Quercus rubra L.	Fagaceae
Tree	Black oak	Quercus velutina Lam.	Fagaceae
Shrub/vine	Common buckthorn	Rhamnus cathartica L *@	Rhamnaceae
Shrub/vine	European alder-buckthom	Rhamnus frangula L. @	Rhamnaceae
Shrub/vine	Sumac	Rhus spp.	Anacardiaceae
Shrub/vine	Gooseberry	Ribes spp.	Saxifragaceae
Tree	Black locust	Robinia pseudo-acacia L. *	Fabaceae
Herb	Smooth rose	Rosa blanda Aiton. @	Rosaceae
Shrub/vine	Raspberry	Rubus spp.	Rosaceae
Herb	Cutleaf coneflower	Rudbeckia laciniata L. @	Asteraceae
Herb	Red sorrel	Rumex acetosella L. @	Polygonaceae
Herb	Swamp-dock	Rumex verticillatus L @	Polygonaceae
Herb	Arrowhead	Sagittaria spp.	Alismataceae
Shrub/vine	Sandbar willow	Salix exigua Nutt @	Salicaceae
Tree	Black willow	Satix nigra Marsh.	Salicaceae
Shrub/vine	Elderberry	Sambucus canadensis L. @	Caprifoliaceae
Herb	Heart-leaved groundsel	Senecio aureas L. @	Asteraceae
Herb	Single-stemmed groundsel	Senecio integerrimus Nuts. @	Asteraceae
Herb	White campion	Silene latifolia Poiret. @	Caryophyllaceae
Shrub/vine	Catbrier	Smilax herbaceae L. var. lasioneura (Small) Rydb. @	Smilacaceae
Shrub/vine	Bristly greenbrier	Smilax hispida Muhl.	Smilacaceae
Herb	Bittersweet (nightshade)	Solarium dulcamara L.	Solanaceae
Herb	Goldenrod	Solidago spp.	Asteraceae
Herb	Hedge-nettle	Stachys palustris L. @	Lamiaceae
Herb	Smooth hedge-nettle	Stachys tenuifolia Willd. @	Lamiaceae
Herb	Chickweed	Stellaria spp.	Caryophyllaceae
Herb	Dandelion	Taraxacum officinale Weber.	Asteraceae
Herb	Purple meadow-rue	Thalictrum dasycarpura Fischer & Ave'-Lall. @	Ranunculaceae
Tree	Basswood	Tilia americana L.	Tiliaceae
Shrub/vine	Common poison ivy	Toxicodendron radicans var. negundo (Greene) Reveal	Anacardiaceae
Herb	Smooth spiderwort	Tradescantia ohiensis Raf. @	Commelinaceae
Herb	Spiderwort	Tradescantia virginiana *L*	Commelinaceae
Herb	Fistulus goat's beard	Tragopogon dubius Scop. @	Asteraceae
Herb	Trillium	Trillium spp.	Liliaceae
Herb	Cattail	Typha spp.	Typhaceae
Tree	Elm	Ulmus spp.	Ulmacae
Herb	Tall nettle	Urtica dioica L. var procera (Muhl.) Wedd. @	Urticaceae
Herb	Bellwort	Uvularia grandifloraJ. E. Smith	Liliaceae
Herb	Hoary vervain	Verbena stricta Vent @	Verbenaceae

Appendix B. continued.

Life form	Common name	Scientific name (a)	Family
Shrub/vine	Nannyberry	Viburnum lentago L. @	Caprifoliaceae
Shrub/vine	Withe-rod (wild raisin)	Viburnum nudum L. var. cassinoides *(L) T.&G.*	Caprifoliaceae
Shrub/vine	Viburnum, other	Viburnum spp.	Caprifoliaceae
Herb	Dooryard violet	Viola sororia Willd. @	Violaceae
Shrub/vine	Riverbank grape	Vitis riparia Michx.	Vitaceae
Shrub/vine	Common prickly ash	Zanthoxylum americanum Mill. @	Rutaceae

CHAPTER 3. THE BREEDING BIRD COMMUNITY OF UPPER MISSISSIPPI RIVER FLOODPLAIN FORESTS

A paper to be submitted to the Condor

Melinda G. Knutson[1,2] and Erwin E. Klaas[1]

Abstract

We studied year-to-year changes in breeding bird relative abundance, frequency of occurrence and species richness in floodplain forests of the Upper Mississippi River (UMR) from 1992-1994. We found that about 35% of the species changed in abundance or frequency of occurrence over the study period. Species richness overall and relative abundances of several groups of birds classified by management risk categories and guild associations declined in 1994. Lowered abundance and species richness in 1994 may have resulted from effects of the 1993 flood. A few groups of birds increased over the period, including birds preferring habitats near water and piscivores. The UMR floodplain provides forest habitat for birds restricted to large floodplains and may be important for birds declining in other available habitats. Our study of large UMR floodplain forests provides baseline information on species abundances and frequencies of occurrence, along with information on year-to-year variation in this bird community.

Introduction

Riparian forests axe important habitats for breeding birds in many locations (Dobkin and Wilcox 1986, Decamps et al. 1987, Darveau et al. 1995, Murray and Stauffer 1995). Many neotropical migrants prefer forest-water riparian edges over other habitats (Stauffer and Best 1980, Gates and Giffen 1991). Upper Mississippi River (UMR) floodplain forests also provide breeding habitat for many different species of songbirds (Emlen et al. 1986, Grettenberger 1991). Some of these songbirds, especially neotropical migrants, have declined in abundance on a continental or regional basis over the last 10-20 years based on Breeding Bird Survey (BBS) data (Robbins et al. 1989, Sauer and Droege 1992).

---

[1] Graduate student and Professor, respectively, Iowa State University, Department of Animal Ecology and National Biological Service, Iowa Cooperative Fish and Wildlife Research Unit, Ames, IA. Research conducted and manuscript written by Knutson with consultation from Klaas.

[2] Author for correspondence. Address after 1 September 1995: National Biological Service, Upper Mississippi Science Center, P.O. Box 2226, LaCrosse, WI 54601.

Emlen et al. (1986) studied latitudinal effects on the composition of forest bird communities of the UMR floodplain during one breeding season. We studied the floodplain forest bird community over 3 breeding seasons, including 1 year of major flooding. Our objectives were to (1) document the abundance and composition of bird species using UMR floodplain forests during the breeding season, (2) identify species of management concern that are dependent upon large floodplain forest habitat, and (3) assess changes in distribution and relative abundance of bird species among years. This study of the floodplain forest bird community will serve as a benchmark for future monitoring efforts on the UMR.

Methods

The study area consisted of forested habitat in river navigation Pools 6-10 of the UMR floodplain (NW Universal Transverse Mercator (UTM) E602000, N4883000; SE UTM E660000, N4738000) (Appendix A). The area extends from near Winona, MN in the north to Guttenburg, IA in the south, a distance of about 177 km, following the main channel of the river. We randomly selected 62 plots from forested (> 70°lo tree canopy cover) land within Pools 6-9 using a 600 m X 600 m sampling grid overlaid on classified geographic information systems (GIS) land cover maps obtained from the Environmental Management Technical Center, National Biological Service, Onalaska, WI. In addition, 5 large forested plots selected from the largest contiguous tracts of forest identified in Pools 6-10 were included to ensure that large tracts were represented. If a selected plot proved inaccessible, we substituted the nearest accessible forested plot. With the exception of 5 plots censused 2 years and 1 plot censused 1 year, plots were censused for 3 years. We censused 63 plots in 1992, 65 in 1993, and 67 in 1994. High rainfall resulted in a major flood on the UMR during 1993. Rainfall amounts were 1.5 to 2 times normal over the study area during spring and summer 1993 (Wahl et al. 1993) and river water levels were above normal throughout the breeding season (Parrett et al. 1993). (See Chapter 5 for our analysis of the effect of the flood on the bird community.)

Within each plot, we counted birds from a point at the center of 50 m radius circles separated by at least 200 m (Ralph et al. 1993, Smith et al. 1993). Plots contained between 3 and 10 points (mean = 5.4), depending upon their size. We sampled each plot once during each breeding season (May 20 - July 10). To avoid seasonal and latitudinal biases, we sampled plots from several pools each week. This ordering was constrained somewhat during the 1993 flooding. We confined sampling to calm, non-rainy days between 0530 and 1030 hours. We identified to species all birds seen or heard during 10 minutes at each point. We recorded the minimum number of individual birds as determined by concurrent singing, counter-singing, and location. The distance of the bird from the observer was recorded as 025, 26-50, or > 50 m. Observers were experienced in bird identification and had 1 week of field training immediately prior to the field season to verify and improve identification skills.

We classified birds into groups based on guild associations and management risk categories to examine year-to-year variation for groups of species with common attributes. We classified species into several guild, habitat association, and risk categories based on previous research and field observations in our study area (for scientific names and classifications see Appendix B). Species names follow the American Ornithologist's Union (1983). We grouped birds into foraging guilds based on De Graaf et al. (1985) and assigned nesting guild, territory size, and habitat preference categories according to published information (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, Poole and Gill 1992-5). When no data on territory size for a species were available, data for closely-related taxa and body mass were used to estimate territory size (Schoener 1968, Dunning 1993). We grouped birds into categories based on migration distances. Resident birds were defined as wintering in the study area; temperate migrants as wintering in the southern latitudes of the U.S. We divided neotropical migrants into groups based on wintering distributions given in Bellrose (1976), American Ornithologists' Union (1983), Hunter et al. (1993), and Thompson et al. (1993). Species with widespread neotropical winter distributions are considered at lower risk than those with very local distributions (Hunter et al. 1993, Thompson et al. 1993). We based population status on Breeding Bird Survey (BBS) trends in U.S. Fish and Wildlife Service Region 3 (includes MN, IA, MO, IL, WI, MI, IN, and OH) for 1966-1994 and 1980-1994 (BBS, unpublished data). Species with no significant population trend or increasing population trends were classified as stable or increasing (criterion 1 or 2: Thompson et al. 1993). Species that showed both an increase and a decrease for either long or short term trends (criterion 3 or 4: Thompson et al. 1993) were classified as having a mixed trend. Species that showed significant decreases both long and short-term (criterion 5: Thompson et al. 1993) were classified as decreasing. Species were classified into categories of management concern based on scores assigned by Thompson et al. (1993). Species with a mean overall score of 11.99 were classified as low, species with a score of 2 - 2.99 were classified as medium, species with a score of 3 - 5 were classified as high, and species not scored (resident or short distance migrants and water birds) were classified as low unless they are listed as threatened, endangered, or of management concern by the U.S. Fish and Wildlife Service (Office of Migratory Bird Management 1987). The bald eagle and red-shouldered hawk were classified as high, according to this criterion. We assigned birds to categories of habitat preference based on published information and our own field observations (Whitcomb et al. 1981, Freemark and Merriam 1986, Thompson et al. 1993).

We created species-cumulative point curves using the cumulative number of new species identified over all distances from 20 sets of 40 points selected randomly. The data set included the first 4 points in each plot, to reduce any bias associated with larger plots having more points. Each set of 40 points was selected without replacement. The total number of new species increases as additional points are added. Confidence limits, calculated around each point, were plotted to allow comparison among years.

Differences among years were tested for several bird variables: species richness of each plot, species frequency of occurrence, and the relative abundance of species at each plot. Differences among years for relative abundance within management risk and guild association categories were also tested. We used the total number of species identified by the observer on the plot as our estimate of species richness, even though we expect large plots to have higher richness than small plots (Karr et al. 1990, Palmer 1995). Since we are comparing all the plots among years, any biases are similar from year-to-year.

We measured the frequency of occurrence of a bird species as the proportion of plots a species occurred on each year. A species was present on a plot if it was identified from at least one point within 50 m of the observer. We measured the relative abundance of each species as the number of individuals of that species identified within 50 m of the observer and summed over all points in the plot. These totals were divided by the number of points in the plot to derive the mean number of birds per point.

We tested differences among years for species richness and relative abundance using the General Linear Models (GLM) procedure (SAS Institute Inc. 1989). We used the Bonferroni method to control the experiment-wise error (alpha s 0.05) in the GLM analysis of relative abundance for each species. We used the non-parametric Kruskal-Wallis test (Zar 1984, SAS Institute Inc. 1989) as an adjunct to GLM; the large number of zeros in the data set for uncommon species potentially violates the normal distribution assumption of GLM. However, this test did not detect more differences than GLM for rare species in our data set, so the results of the GLM analysis are reported. We tested differences in the proportion of plots species occurred on among years using chi-squared tests (SAS FREQ procedure) ($P < 0.05$). We used the sign test (Zar 1984) to detect year-to-year differences for all species. We show statistical differences at the 5% level of significance, however, we tested a large number of species, increasing the probability of observing spurious significant differences. No clear guidelines are available for adjusting significance for a large number of comparisons without substantial loss of power to detect differences.

Results

We identified a total of 84 bird species over the 3 census years (see Appendix B for scientific and common names of bird species and frequency of occurrence on plots). Censusing 5 random points in the UMR floodplain forest yields about 27 species. Ten points yield about 35 species, 20 points about 40 species, 30 points about 45 species and 40 points about 47 species (Figure 1). Species richness was different among years ($F = 7.02$; 192 df; $P < 0.001$), based on the GLM analysis. Species richness per plot was higher in 1992 (mean = 28.2 [S.E. = 0.5]) than 1993 (mean = 26.4 [SE = 0.5];$P < 0.02$) and 1994 (mean = 25.3 [SE _ 0.5]; $P < 0.003$). No difference was found between 1993 and 1994 ($P < 0.16$).

According to chi-square tests, 33 species had significant increases or decreases in their frequency of occurrence among years (Table 1). The sign test did not indicate that significantly more species declined than increased between 1992 and1993 (+ = 32, - = 48; $P < 0.10$). However, more species declined in frequency of occurrence than increased from 1993-1994 (+ = 25, - = 51, $P < 0.005$) and from 1992-1994 (+ = 18, - = 61, $P < 0.001$).

Mean total abundance (# birds/point) was lower in 1994 than in 1992 or 1993 (Table 2). Abundances in 1992 and 1993 were similar. Thirty-two species experienced significant differences in relative abundance among years (Table 2). Several groups of birds within management risk categories and guild associations also decreased in relative abundance in 1994 (Table 2). Birds preferring habitats near water and piscivores increased their abundance in 1994.

Discussion

Year-to-year differences in distribution or abundance of birds can affect analysis and interpretation of ecological data (Schooley 1994). Therefore, it is important to assess how data from the same study area change from year-to-year. Also, future monitoring efforts depend upon comprehensive baseline information, as well as some measure of variability. Our study provides baseline data on the floodplain forest bird community and includes measures of variance, wherever possible.

The declines in species richness, frequency of occurrence, and relative abundance in 1994 may have resulted from lowered productivity due to bad weather or habitat changes associated with the 1993 flood. However, there was no multi-species exodus from the floodplain during the flood, despite inundation of roughly half the plots. Only about 35% of all species showed some year-to-year changes in either frequency of occurrence or relative abundance; the majority of species showed no changes. Significant overall reduction in frequency of occurrence was not evident until 1994. It is likely that some of the observed changes resulted from effects of the 1993 flood; some represent normal annual variation in a floodplain bird community. (See Chapter 5 for further examination of flood effects on the bird community).

A large group of species that we found to be common in the floodplain forests is experiencing population declines regionally or continentally and is therefore of management concern (BBS, unpublished data, Sauer and Droege 1992, Thompson et al. 1993). These species include the Red-headed Woodpecker, Northern Flicker, Downy Woodpecker, Eastern Wood-pewee, Great Crested Flycatcher, Tree Swallow, Black-capped Chickadee, Whitebreasted Nuthatch, Blue-gray Gnatcatcher, Gray Catbird, Warbling Vireo, Yellow-throated Vireo, Red-eyed Vireo, American Redstart, Prothonotary Warbler, Common Yellowthroat, Rose-breasted Grosbeak, and Northern Oriole. A smaller group of species that we found in small numbers in the floodplain and is also of management concern because of general population declines includes the Acadian Flycatcher, Least Flycatcher, Willow Flycatcher, Veery, Cerulean Warbler, and Ovenbird. The Cerulean Warbler, a species of management concern for the U.S. Fish and Wildlife Service (Office of Migratory Bird Management 1987), prefers large trees within large bottomland forests as nesting habitat (Robbins et al. 1989, Robbins et al. 1992).

A diverse group of cavity-nesting species were abundant in the floodplain forests probably because of the abundance of large snags and mature trees with large dead limbs. This was particularly true for species that require large cavities, such as the Pileated Woodpecker (Renken and Wiggers 1993). On the UMR, 23 species used cavities for nesting, including 7 woodpecker species, the House Wren, Great Crested Flycatcher, White-breasted Nuthatch, Prothonotary Warbler, Black-capped Chickadee, Tree Swallow, Brown Creeper, Wood Duck, Barred Owl, Chimney Swift, European Starling, Carolina Wren, Hooded Merganser, Eastern Bluebird, and Purple Martin. Most of the species in this group depend upon woodpeckers to excavate their nesting cavities. The abundance and size of snags is probably higher in the floodplain than in the adjacent upland forests because of differences in timber harvesting intensity (Feavel 1986, Iowa Department of Natural Resources and North Central Forest Experiment Station 1991).

Some ground-nesters were largely absent from the floodplain. The Ovenbird and Louisiana Waterthrush (Seiurus motacilla) are more common in adjacent uplands (unpublished data). Low nesters such as Wood Thrushes were uncommon in floodplain habitats. However, other low shrub or ground nesters such as the Common Yellowthroat, Yellow Warbler, and Song Sparrow were very common in the floodplain.

A few species can be considered floodplain forest specialist species on the UMR; these include the Prothonotary Warbler, Red-shouldered Hawk, and Bald Eagle. The Prothonotary Warbler and Red-shouldered Hawk use large floodplain forests almost exclusively during the breeding season (Petit 1989, Crocoll 1994). The Bald Eagle is dependent upon large trees for nesting and resting. The UMR also provides important winter habitat for Bald Eagles. For these species, no alternate regional habitat exists, therefore, floodplain forests provide critical habitat.

The management of floodplain forest habitat should consider the conservation of birds using this habitat. In a historical study of bottomland hardwood forests in Louisiana, declines in abundance of bird species were linked to cumulative forest loss (Burdick et al. 1989). Intensive human use of the UMR has resulted in forest loss and changes in tree species composition (Yin and Nelson 1995). The UMR floodplain provides forest habitat for birds restricted to large floodplains and may be important for birds declining in other available habitats. Because the Breeding Bird Survey is conducted from roadside counts, floodplain and wetland habitats, in general, are under-represented (Peterjohn 1994). Our study of large floodplain forests helps to fill this gap for UMR floodplain forests by providing baseline information on species abundances and frequency of occurrence. Periodic monitoring of UMR bird populations should continue. Intensive demographic studies are needed to test the hypothesis that the floodplain serves as a source habitat for species of management concern.

Acknowledgements

Funding was provided by the National Biological Service (Patuxent Environmental Science Center, Branch of Migratory Birds Research), Iowa State University, U.S. Fish and Wildlife Service (Region 3 Nongame Program), and the Minnesota Department of Natural Resources Nongame Program. Ms. Knutson also was supported by a Cooperative Education Agreement with the Patuxent Center. Special thanks to Ms. Knutson's doctoral committee members Louis Best, Brent Danielson, Kirk Moloney, and Thomas Jurik. Field, office, and data management assistance were provided by Ingrid Moore, Brian Collins, Tom Pehowski, Vance Polton, Holly Dick, Pam Heidenreich, Mark Krom, Rebecca Peak, Julie Schreiber, Fredrick Keith, Jesse Audette, Brenda VanBeek, and Sara Handrick.

Literature Cited

American Ornithologists' Union. 1983. Check-list of North American Birds, 6th ed. Allen Press, Lawrence, KS. 877 pp.

Bellrose, F. C. 1976. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg, PA. 540 pp.

Blake, J. G. and J. R. Karr. 1984. Species composition of bird communities and the conservation benefit of large versus small forests. Biol. Conserv. 30: 173-187.

Burdick, D. M., D. Cushman, R. Hamilton and J. G. Gosselink. 1989. Faunal changes and bottomland hardwood forest loss in the Tensas watershed, Louisiana. Conserv. Biol. 3: 282-292.

Crocoll, S. T. 1994. Red-shouldered hawk *(Buteo lineatus).* The birds of North America, No. 107. A. Poole and F. Gill. The Academy of Natural Sciences and The American Ornithologists' Union, Philadelphia, PA and Washington D.C. 20 pp.

Darveau, M., P. Beauchesne, L. Belanger, J. Huot and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. J. Wildl. Manage. 59: 67-78.

De Graaf, R. M., N. G. Tilghman and S. H. Anderson. 1985. Foraging guilds of North American birds. Environ. Manage. 9: 493-536.

Decamps, H., J. Joachim and J. Lauga. 1987. The importance for birds of the riparian woodlands within the alluvial corridor of the River Garonne, S. W. France. Reg. Riv. Res. Manage. 1: 301-316.

Dobkin, D. S. and B. A. Wilcox. 1986. Analysis of natural forest fragments: riparian birds in the Toiyabe Mountains, Nevada.. Pages 293-299 In J. Verner, M. L. Morrison and C. J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. of Wisconsin Press, Madison, WI.

Dunning, J. B., Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL. 371 pp.

Ehrlich, P. R., D. S. Dobkin and D. Wheye. 1988. The birder's handbook. Simon & Schuster, Inc., New York. 785 pp.

Emlen, J. T., M. J. DeJong, M. J. Jaeger, T. C. Moermond, K. A. Rusterholtz and R. P. White. 1986. Density trends and range boundary constraints of forest birds along a latitudinal gradient. Auk 103: 791-803.

Feavel, T. 1986. Forest management on the Mississippi. Iowa Conserv. 45(10): 29-31.

Freemark, K. E. and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Conserv. 36: 115-141.

Gates, J. E. and N. R. Giffen. 1991. Neotropical migrant birds and edge effects at a foreststream ecotone. Wilson Bull. 103: 204-217.

Grettenberger, J. 1991. Habitat fragmentation and forested wetlands on the Upper Mississippi River: Potential impacts on forest interior birds. Passenger Pigeon 53: 227-241.

Hayden, T. J. and J. Faaborg. 1985. Estimates of minimum area requirements for Missouri forest birds. Trans. of the Missouri Acad. of Sc. 19: 11-22.

Hunter, W. C., M. F. Carter, D. N. Pashley and K. Barker. 1993. The Partners in Flight species prioritization scheme. Pages 422 *In* D. M. Finch and P. W. Stangel, eds. Status and management of neotropical migratory birds. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-229, Fort Collins, CO.

Iowa Department of Natural Resources and North Central Forest Experiment Station. 1991. An overview of Iowa's forest resources, 1990. Des Moines, IA. 3 pp.

Karr, J. R., S. K. Robinson, J. G. Blake and R. O. Bierregaard Jr. 1990. Birds of four neotropical forests. Pages 237-269 *In* A. H. Gentry, eds. Four Neotropical Rainforests. Yale Univ. Press, New Haven, CT.

Murray, N. L. and D. F. Stauffer. 1995. Nongame bird use of habitat in central Appalachian riparian forests. J. Wildl. Manage. 59: 78-88.

Office of Migratory Bird Management. 1987. Migratory nongame birds of management concern in the United States: the 1987 list. Wash., D.C. 27 pp.

Palmer, M. W. 1995. How should one count species? Nat. Areas J. 15: 124-135.

Parrett, C., N. B. Melcher and R. W. James Jr. 1993. Flood discharges in the Upper Mississippi River basin, 1993. U.S. Geol. Surv. Circ., 14 pp.

Peterjohn, B. G. 1994. The North American Breeding Bird Survey. Birding 26: 386-398.

Petit, L. J. 1989. Breeding biology of prothonotary warblers in riverine habitat in Tennessee. Wilson Bull. 101: 51-61.

Poole, A. and F. Gill. 1992-5. The birds of North America: life histories for the 21st century. The American Ornithologists' Union and the Academy of Natural Sciences, Washington, DC and Philadelphia, PA. pp.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. Pacific Southwest Research Station, Albany, CA. 41 pp.

Renken, R. B. and E. P. Wiggers. 1993. Habitat characteristics related to Pileated Woodpecker densities in Missouri. Wilson Bull. 105: 77-83.

Robbins, C. S., D. K. Dawson and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildl. Monogr. 103: 1-34.

Robbins, C. S., J. W. Fitzpatrick and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea.* Pages 549-562 *In* J. M. Hagan III and D. W. Johnston, eds. Ecology and conservation of neotropical migrant landbirds. Manomet Bird Observatory, Woods Hole, MA.

Robbins, C. S., J. R. Sauer, R. S. Greenberg and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86: 76587662.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, 4th ed., vol. 2 SAS Institute, Inc. Cary, NC. 846 pp.

Sauer, J. R. and S. Droege. 1992. Geographic pattemrs in population trends of neotropical migrants in North America. Pages 26-4.2 *In* J. M. Hagan III and D. W. Johnston, Eds. Ecology and conservation of neotropical migrant landbirds. Manomet Bird Observatory, Woods Hole, MA.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123-141.

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. J. Wildl. Manage. 58: 367-374.

Smith, P. W., D. J. Twedt, D. A. Wiedenfeld, P. B. Hamel, R. P. Ford and R. J. Cooper. 1993. Point counts of birds in bottomland hardwood forests of the Mississippi Alluvial Valley: duration, minimum sample size, and points versus visits. Res. Paper SO-274. USDA Forest Service, Southern Forest Exp. Station, New Orleans, LA. 21 PP.

Stauffer, D. F. and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alteration. J. Wildl. Manage. 44: 1-15.

Thompson, F. R., S. J. Lewis, J. Green and D. Ewert. 1993. Status of neotropical migrant landbirds in the Midwest: identifying species of management concern. Pages 422 In D. M. Finch and P. W. Stangel, eds. Status and management of neotropical migratory birds. USDA Forest Service, Rocky Mountain Forest and Range Exp. Station, Gen. Tech. Rep. RM-229, Fort Collins, CO.

Wahl, K. L., K. C. Vining and G. J. Wiche. 1993. Precipitation in the Upper Mississippi River Basin, January 1 - July 31, 1993. U.S. Geol. Surv. Circ., 13 pp.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-201 In B. R. L. and D. M. Sharpe, eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY.

Yin, Y. and J. C. Nelson. 1995. Modifications to the Upper Mississippi River and their effects on floodplain forests. Long-Term Resource Monitoring Program technical report 95-T003. National Biological Service, Environmental Management Technical Center, Onalaska, Wl. 17 pp.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice Hall, Englewood Cliffs, NJ. 718 PP.

Table 1. Bird species with significant differences in the proportion of plots they occurred on among years. (Chi-square, P < 0.05).

	Percentage of plots			Prob > chi-square		
Common name	1992	1993	1994	92-93	93-94	92-94
Great Blue Heron	19.05	53.85	41.79	0.000	0.166	0.005
Wood Duck	9.52	36.92	31.34	0.000	0.499	0.002
Mallard	3.17	23.08	11.94	0.001	0.092	0.061
Mourning Dove	25.40	21.54	5.97	0.606	0.009	0.002
Yellow-billed Cuckoo	39.68	29.23	23.88	0.213	0.486	0.053
Ruby-throated Hummingbird	19.05	0.00	4.48	0.000	0.084	0.009
Red-headed Woodpecker	44.44	15.38	17.91	0.000	0.697	0.001
Red-bellied Woodpecker	74.60	81.54	61.19	0.343	0.010	0.102
Downy Woodpecker	80.95	61.54	65.67	0.015	0.622	0.050
Hairy Woodpecker	61.90	29.23	28.36	0.000	0.912	0.000
Northern Flicker	61.90	69.23	17.91	0.383	0.000	0.000
Pileated Woodpecker	14.29	3.08	16.42	0.024	0.100	0.736
Least Flycatcher	4.76	12.31	2.99	0.128	0.043	0.599
Tree Swallow	57.14	15.38	43.28	0.000	0.000	0.114
Blue Jay	63.49	67.69	40.30	0.617	0.002	0.008
American Crow	46.03	60.00	32.84	0.113	0.002	0.124
Black-capped Chickadee	66.67	61.54	37.31	0.545	0.005	0.001
White-breasted Nuthatch	88.89	83.08	52.24	0.344	0.000	0.000
Brown Creeper	47.62	26.15	14.93	0.012	0.110	0.000
American Robin	98.41	93.85	86.57	0.182	0.161	0.011
Cedar Waxwing	14.29	1.54	4.48	0.007	0.325	0.054
European Starling	11.11	1.54.	4.48	0.025	0.325	0.156
Warbling Vireo	61.90	81.54	73.13	0.014	0.249	0.171
Cerulean Warbler	9.52	15.38	1.49	0.316	0.004	0.043
Prothonotary Warbler	84.13	67.69	68.66	0.030	0.905	0.039
Ovenbird	4.76	10.77	1.49	0.205	0.026	0.281
Common Yellowthroat	71.43	67.69	40.30	0.646	0.002	0.000
Scarlet Tanager	7.94	4.62	0.00	0.438	0.075	0.019
Rose-breasted Grosbeak	34.92	44.62	20.90	0.263	0.004	0.074
Indigo Bunting	28.57	4.62	2.99	0.000	0.624	0.000
Song Sparrow	88.89	95.38	82.09	0.171	0.016	0.273
Brown-headed Cowbird	5.71	60.00	77.61	0.001	0.029	0.234
American Goldfinch	53.97	43.08	10.45	0.218	0.000	0.000

Table 2. Significant (P < 0.05) differences in relative abundance (# of individuals per point) for species, management risk categories, and guild associations among years.

Species and categories (a)	1992 (b)			1993			1994		
Total abundance, all species ***	17.19	(0.55)	A	17 .22	(0.55)	A	14.31	(0.54)	B
Great Blue Heron ***	0.04	(0.03)	B	0.17	(0.03)	A	0.19	(0.03)	A
Wood Duck **	0.03	(0.03)	B	0.11	(0.03)	AB	0.17	(0.03)	A
Mallard ***	0.01	(0.02)	B	0.11	(0.02)	A	0.05	(0.02)	AB
Mourning Dove***	0.10	(0.02)	A	0.05	(0.02)	AB	0.01	(0.02)	B
Ruby-throated Hummingbird ***	0.04	(0.01)	A	0.00	(0.01)	B	0.01	(0.01)	B
Red-headed Woodpecker***	0.12	(0.01)	A	0.03	(0.01)	B	0.04	(0.01)	B
Red-bellied Woodpecker***	0.29	(0.04)	B	0.43	(0.04)	A	0.25	(0.04)	B
Downy Woodpecker***	0.37	(0.03)	A	0.18	(0.03)	B	0.25	(0.03)	B
Hairy Woodpecker***	0.19	(0.02)	A	0.07	(0.02)	B	0.09	(0.02)	B
Northern Flicker ***	0.29	(0.03)	A	0.30	(0.03)	A	0.05	(0.03)	B
Pileated Woodpecker *	0.03	(0. of)	AB	0.01	(0.01)	B	0.04	(0.01)	A
Eastern Wood-Pewee ***	0.75	(0.05)	A	0.72	(0.05)	A	0.46	(0.05)	B
Great Crested Flycatcher**	0.89	(0.07)	AB	0.94	(0.07)	A	0.67	(0.06)	B
Tree Swallow ***	0.27	(0.04)	A	0.09	(0.04)	B	0.24	(0.04)	A
Blue Jay **	0.27	(0.04)	AB	0.32	(0.04)	A	0.16	(0.04)	B
American Crow***	0.18	(0.04)	AB	0.32	(0.04)	A	0.12	(0.04)	B
Black-capped Chickadee***	0.26	(0.03)	A	0.29	(0.03)	A	0.11	(0.03)	B
White-breasted Nuthatch***	0.46	(0.04)	A	0.53	(0.04)	A	0.23	(0.04)	B
Brown Creeper***	0.17	(0.02)	A	0.07	(0.02)	B	0.03	(0.02)	B
Gray Catbird **	0.55	(0.06)	A	0.34	(0.06)	B	0.32	(0.06)	B
Cerulean Warbler	0.02	(0.01)	AB	0.04	(0.01)	A	0.00	(0.01)	B
Common Yellowthroat***	0.31	(0.06)	AB	0.46	(0.05)	A	0.18	(0.05)	B
Northern Cardinal *	0.40	(0.05)	AB	0.51	(0.05)	A	0.33	(0.05)	B
Rose-breasted Grosbeak	0.11	(0.03)	AB	0.18	(0.03)	A	0.09	(0.03)	B
Indigo Bunting***	0.10	(0.01)	A	0.01	(0.01)	B	0.00	(0.01)	B
Song Sparrow ***	0.57	(0.07)	B	1.05	(0.07)	A	0.67	(0.07)	B
Red-winged Blackbird *	0.47	(0.08)	B	0.75	(0.08)	A	0.48	(0.08)	AB
American Goldfinch ***	0.25	(0.04)	A	0.14	(0.03)	AB	0.03	(0.03)	B
Winter distribution, neotropical local***	0.31	(0 .02)	A	0.31	(0.02)	A	0.21	(0.02)	B
Winter distribution, resident***	0.20	(0.01)	A	0.18	(0.01)	A	0.13	(0.01)	B
Population status, stable**	0 .19	(0.01)	AB	0.21	(0 01)	A	0.17	(0.01)	B
Management status, high***	0.19	(0.01)	A	0.19	(0.01)	A	0.13	(0.01)	B
Management status, low***	0.20	(0.01)	A	0.20	(0.01)	A	0.16	(0.01)	B
Habitat preference, interior-edge***	0.26	(0.01)	A	0.27	(0.01)	A	0.19	(0.01)	B
Habitat preference, near water***	0.01	(0.01)	B	0.04	(0.01)	A	0.05	(0.01)	A
Territory size, > 5 ha*	0.09	(0.01)	AB	0.11	(0.01)	A	0.09	(0.01)	B
Territory size, 2-5 ha***	0.22	(0.01)	A	0.21	(0.01)	A	0.15	(0.01)	B
Nesting location, ground***	0.09	(0.01)	B	0.15	(0.01)	A	0.09	(0 01)	B
Nesting location, hole***	0.28	(0.01)	A	0.26	(0.01)	A	0.19	(0.01)	B
Foraging guild, air*	0.20	(0.02)	A	0.18	(0.01)	AB	0.14	(0.01)	B
Foraging guild, bark***	0.28	(0.01)	A	0.24	(0.01)	A	0.17	(0.01)	B
Foraging guild, piscivore* * *	0.01	(0.01)	B	0.04	(0.01)	A	0.04	(0.01)	A

(a) Significance level of overall general linear model (*P < 0.05; **P < 0.01; ***P < 0.005).
See Methods and Appendix B for a description of the management risk categories and guild associations.
(b) Relative abundances (S. E.) with different letters are statistically different (P < 0.05).

<Figure 1 not included>

Appendix A. Locations of study plots, Pools 6-10 of the Upper Mississippi River.

Plot	UTM Coordinates		Plot	UTM Coordinates	
601	E623400	N4873487	813	E642215	N4824941
602	E620979	N4874321	814	E641342	N4827092
603	E616411	N4879532	815	E638896	N4852397
604	E618127	N4877173	850	E639155	N4846642
605	E619338	N4876796	851	E639988	N4846642
606	E619195	N4877495	901	E641385	N4823004
701	E629420	N4869324	902	E642385	N4822067
702	E629252	N4868700	903	E643407	N4818022
703	E632882	N4863545	904	E643142	N4814950
704	E633398	N4862771	905	E642077	N4813761
705	E631628	N4868901	906	E641755	N4814083
706	E633230	N4869152	907	E646196	N4806089
707	E628563	N4869687	908	E645673	N4806015
708	E626698	N4870292	909	E646196	N4806962
709	E627212	N4871038	910	E642492	N4818129
710	E633140	N4869755	911	E641960	N4818490
711	E633983	N4869062	912	E650282	N4802925
712	E634043	N4861954	913	E656884	N4792564
713	E638989	N4863201	914	E657036	N4791868
714	E636968	N4860449	915	E639575	N4821514
715	E628019	N4869223	916	E639596	N4819938
716	E628251	N4870675	917	E642194	N4820087
801	E639051	N4849443	918	E642215	N4821216
802	E639854	N4848925	919	E643106	N4811547
803	E642056	N4846309	920	E644402	N4809877
804	E637367	N4856438	921	E641853	N4815552
805	E637911	N4855453	922	E642683	N4817788
806	E643740	N4842319	923	E643109	N4816383
807	E642989	N4840972	924.	E640415	N4811497
808	E640022	N4828625	925	E640863	N4809777
809	E639894	N4828284	926	E642087	N4816149
810	E639802	N4847345	950	E641414	N4821908
811	E640512	N4827773	951	E640781	N4810471
812	E640469	N4826985	1050	E649284	N4755042

Appendix B. Number and proportion of plots species occurred on in 1992 (N=63), 1993 (N=65), and 1994 (N=67), management risk categories, and guild associations. Species names follow American Ornithologists' Union (1983).

Family	Common name	Scientific name	Number of plots			Percent of plots			winter (a)	pop.(b)	status (c)	habitat (d)	territory (e)	nesting (f)	foraging (g)
			1992	1993	1994	1992	1993	1994							
Podicipedidae	Pied-billed Grebe	Podilymbus podiceps	0	4	0	0.00	6.15	0.00	T	M	L	W	M	O	O
Ardeidae	Great Blue Heron	Ardea herodias	12	35	28	19.05	53.85	41.79	T	S	L	W	L	UC	P
	Great Egret	Casmerodius albus	0	0	1	0.00	0.00	1.49	T	S	L	W	L	UC	P
	Green-backed Heron	Butorides striatus	0	1	1	0.00	1.54	1.49	T	M	L	W	L	UC	P
Anatidae	Canada Goose	Branta canadensis	0	0	3	0.00	0.00	4.48	T	S	L	W	L	G	G
	Wood Duck	Aix sponsa	6	24	21	9.52	36.92	31.34	T	S	L	W	L	H	G
	Mallard	Anas platyrhynchos	2	15	8	3.17	23.08	11.94	T	S	L	W	L	G	G
	Hooded Merganser	Lophodytes cucullatus	1	1	0	1.59	1.54	0.00	T	ND	L	W	L	H	P
Pelicanidae	American White Pelican	Pelecanus erythrorhynchos	0	2	0	0.00	3.08	0.00	T	ND	L	W	L	O	P
Laridae	Black Tern	Chlidonias niger	0	1	0	0.00	1.54	0.00	NI	ND	H	W	L	O	A
Gruidae	-Sandhill Crane	Grua canadensis	1	0	4	1.59	0.00	5.97	NW	ND	L	W	L	O	G
Meleagrididae	Wild Turkey	***Meleagris gallopavo***	1	0	1	1.59	0.00	1.49	R	S	L	IE	L	G	G
Accipitridae	Bald Eagle	Haliaeetus leucocephalus	2	1	3	3.17	1.54	4.48	R	M	H	W	L	UC	P
	Red-tailed Hawk	Buteo jamaicensis	0	0	1	0.00	0.00	1.49	R	S	L	E	L	UC	C
	Red-shouldered Hawk	Buteo lineatus	2	1	2	3.17	1.54	2.99	R	M	H	I	L	UC	C
Rallidae	Sora	Porzana carolina	0	2	0	0.00	3.08	0.00	T	M	L	W	S	O	G
Charaddidae	Killdeer	Charadrius vociferus	0	1	2	0.00	1.54	2.99	T	S	L	E	S	G	G
Scolopacidae	American Woodcock	Scolopax minor	2	0	0	3.17	0.00	0.00	T	D	L	E	M	G	G
Columbidae	Mourning Dove	Zenaida macroura	16	14	4	25.40	21.54	5.97	R	M	L	E	M	UC	G
Cltculidae	Black-billed Cuckoo	Coccyzus erythropthalmus	1	1	2	1.59	1.54	2.99	NL	M	H	IE	M	LC	LC
	Yellow-billed Cuckoo	Coccyzus americanus	25	19	16	39.68	29.23	23.88	NI	D	H	IE	M	LC	LC
Strigidae	Great Homed Owl	Bubo virginianus	1	0	0	1.59	0.00	0.00	R	S	L	IE	L	UC	C
	Barred Owl	Strix vatfa	5	2	1	7.94	3.08	1.49	R	S	L	I	L	H	C
Apodidae	Chimney Swift	Chaetura pelagica	7	5	2	11.11	7.69	2.99	NI	D	M	E	S	H	A
Trochilidae	Ruby-throated Hummingbird	Archilochus colubris	12	0	3	19.05	0.00	4.48	NI	S	M	IE	M	UC	LC
Alcedinidae	Belted ICrngfisher	Ceryle alcyon	4	5	1	6.35	7.69	1.49	T	M	L	W	L	O	P
Picidae	Red-headed Woodpecker	Melanerpes erythrocephalus	28	10	12	44.44	15.38	17.91	R	D	L	IE	L	H	B
	Red-bellied Woodpecker	Melanerpes carolinus	47	53	41	74.60	81.54	61.19	R	S	L	IE	L	H	B

(a) Wintering distribution: R= resident; T = temperant migrant; NW = neotropical, widespread; NI = neotropical, intermediate; NL = neotropical, local.
(b) Population status: S = stable, increasing (Thompson et al. 1993, categories 1 or 2); M = mixed (categories 3 or 4); D = decreasing (category 5); ND = no data.
(c) Management status: L = low (Thompson et al. 1993, rank 1 - 1.99); M = medium (rank 2 - 2.99); H = high (rank 3 - 5.00).
(d) Habitat preference: I = interior forest; IE = interior-edge; E = edge; W = near water.
(e) Territory size: S = < 2 ba; M = 2-5 ha; L = > 5 ha.
(f) Nesting location: G = ground; LC = lower canopy; UC = upper canopy; H = hole; O = other.
(g) 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, 0 = other.

Appendix B continued.

Family	Common name	Scientific name	Number of plots			Percent of plots			winter (a)	pop. (b)	status (c)	habitat (d)	territory (e)	nesting (f)	fora ing (g)
			1992	1993	1994	1992	1993	1994							
	Yellow-bellied Sapsucker	Sphyrapicus varius	58	57	56	92.06	87.69	83.58	T	ND	L	IE	M	H	B
	Downy Woodpecker	Picoides pubescens	51	40	44	80.95	61.54	65.67	R	M	L	IE	M	H	B
	Hairy Woodpecker	Picoides villosus	39	19	19	61.90	29.23	28.36	R	S	L	I	L	H	B
	Northern Flicker	Colaptes auratus	39	45	12	61.90	69.23	17.91	R	D	L	IE	M	H	B
	Pileated Woodpecker	Dryocopus pileatus	9	2	11	14.29	3.08	16.42	R	S	L	I	L	H	B
Tyrannidae	Eastern Wood-Pewee	Contopus virens	59	59	60	93.65	90.77	89.55	NL	D	H	IE	M	UC	A
	-Acadian Flycatcher	Empidonax virescens	4	2	2	6.35	3.08	2.99	NL	D	H	I	S	UC	A
	Least Flycatcher	Empidonax minimus	3	8	2	4.76	12.31	2.99	NI	D	M	E	S	UC	A
	Willow Flycatcher	Empidonax traillti	2	1	0	3.17	1.54	0.00	NI	ND	M	E	S	LC	A
	Eastern Phoebe	Sayornis phoebe	0	2	2	0.00	3.08	2.99	T	S	L	IE	S	O	A
	Great Crested Flycatcher	Myiarchus crinitus	60	63	61	95.24	96.92	91.04	NL	M	H	IE	M	H	A
	Eastern Kingbird	Ty- tyrannus	2	1	0	3.17	1.54	0.00	NI	D	M	E	*M*	LC	A
Hirundinidae	Purple Martin	Progne subis	2	0	0	3.17	0.00	0.00	NI	D	H	E	S	H	A
	Tree Swallow	Tachycineta bicolor	36	10	29	57.14	15.38	43.28	T	*M*	L	E	S	H	A
Corvidae	Blue Jay	Cyanocitta cristata	40	44	27	63.49	67.69	40.30	R	D	L	IE	*M*	*UC*	*UC*
	American Crow	Corvus brachyrhynchos	29	39	22	46.03	60.00	32.84	R	S	L	E	L	UC	G
Paridae	Black-capped Chickadee	Parts atricapillus	42	40	25	66.67	61.54	37.31	R	M	L	IE	M	H	LC
	Tufted Titmouse	Paris bicolor	1	0	1	1.59	0.00	1.49	R	S	L	IE	M	Ii	LC
Sittidae	White-breasted Nuthatch	Sins carolinensis	56	54	35	88.89	83.08	52.24	R	M	L	1E	L	H	B
Certhiidae	Brown Creeper	Certhia americans	30	17	10	47.62	26.15	14.93	R	S	L	I	M	H	B
Troglodytidae	Carolina Wren	Thryothorus ludovicianus	2	5	2	3.17	7.69	2.99	R	S	L	IE	S	LC	LC
	House Wren	Troglodytes aedon	61	63	66	96.83	96.92	98.51	NW	S	L	E	S	H	LC
	Winter Wren	Troglodytes troglodytes	0	0	1	0.00	0.00	1.49	T	S	L	I	M	G	G
Muscicapidae	Blue-gray Gnatcatcher	Polioptila caerulea	46	50	54	73.02	76.92	80.60	NI	S	M	IE	S	UC	UC
	EasternBluebird	Sialiasialis	2	0	0	3.17	0.00	0.00	T	S	L	E	S	H	G
	Veery	Catharusfuscescens	9	7	4	14.29	10.77	5.97	NI	D	H	I	S	G	G
	WoodThrush	Hylocichlamustelina	2	4	2	3.17	6.15	2.99	NL	M	H	IE	S	LC	G
	American Robin	Turdus migratorius	62	61	8	98.41	93.85	86.57	T	S	L	E	S	UC	G
Mimidae	Gray Catbird	Dumetella carolinensis	47	40	41	74.60	61.54	61.19	NI	S	M	E	S	LC	G
	Brown Thrasher	Toxostoma nrfum	2	0	0	3.17	0.00	0.00	T	D	L	E	M	G	G
Bombycillidae	Cedar Waxwing	Bombycilla cedrorum	9	1	3	14.29	1.54	4.48	R	S	L	E	M	UC	A
Sturnidae	European Starling	Stumus vulgaris	7	1	3	11.11	1.54	4.48	R	D	L	E	S	H	G
Vireonidae	Yellow-throated Vireo	Vireo flavifrons	33	39	33	52.38	60.00	49.25	NI	S	H	IE	S	UC	UC
	Warbling Vireo	vireo gilvus	39	53	49	61.90	81.54	73.13	NI	D	M	IE	M	UC	UC
	Red-eyed Vireo	Vireo olivaceus	31	36	30	49.21	55.38	44.78	NI	S	M	IE	S	UC	UC
Emberizidae	Yellow Warbler	Dendroicapetechia	27	21	21	42.86	32.31	31.34	NW	S	L	E	S	LC	LC
	Yellow-throated Warbler	Dendroica dominica	2	0	0	3.1	0.00	0.00	NI	S	M	IE	S	UC	UC
	Cerulean Warbler	Dendroica cerulea	6	10	1	9.52	15.38	1.49	NL	D	H	I	S	UC	UC
	American Redstart	Setophaga ru6cilla	59	59	61	93.65	90.77	91.04	NW	M	M	I	S	LC	LC

Appendix B continued.

Family	Common name	Scientific name	Number of plots			Percent of plots			winter (a)	pop. (b)	status (c)	habitat (d)	territory (e)	nesting (f)	foraging (g)
			1992	1993	1994	1992	1993	1994							
	Prothonotary Warbler	Protonotaria citrea	53	44	46	84.13	67.69	68.66	NL	S	H	IE	S	H	LC
	Ovenbird	Seimus aurocapillus	3	7	1	4.76	10.77	1.49	NI	S	H	I	S	G	G
	Common Yellowthroat	Geothlypis trichas	45	44	27	71.43	67.69	40.30	NW	M	M	E	S	G	LC
	Scarlet Tanager	Piranga olivacea	5	3	0	7.94	4.62	0.00	NL	S	H	I	M	UC	UC
	Northern Cardinal	Cardinalis cardinalis	50	53	46	79.37	81.54	68.66	R	S	L	IE	S	LC	G
	Rose-breasted Grosbeak	Pheucticus ludovicianus	22	29	14	34.92	44.62	20.90	NI	M	H	IE	M	UC	UC
	Indigo Bunting	Passerina cyanea	18	3	2	28.57	4.62	2.99	NI	D	M	E	M	LC	LC
	Rufous-sided Towhee	Pipilo erythrophthalmus	1	0	0	1.59	0.00	0.00	T	D	L	IE	M	LC	G
	Chipping Sparrow	Spizella passerina	1	0	0	1.59	0.00	0.00	NW	S	L	E	S	LC	G
	Field Sparrow	Spizella pusilla	1	2	0	1.59	3.08	0.00	T	D	L	E	S	G	G
	Song Sparrow	Melospiza melodia	56	62	55	88.89	95.38	82.09	T	S	L	E	S	G	LC
	Swamp Sparrow	Melospiza georgiana	0	2	0	0.00	3.08	0.00	T	S	L	W	S	O	G
	Red-winged Blackbird	Agelaius phoeniceus	45	52	41	71.43	80.00	61.19	T	D	L	E	S	LC	G
	Common Grackle	Quiscalus quiscula	51	47	56	80.95	72.31	83.58	R	D	L	E	S	UC	G
	Brown-headed Cowbird	Molothrus ater	54	39	52	85.71	60.00	77.61	R	M	L	E	L	O	G
	Northern Oriole	Icterus galbula	59	56	59	93.65	86.15	88.06	NI	D	M	E	M	UC	UC
Fringillidae	American Goldfinch	Carduelis trfstis	34	28	7	53.97	43.08	10.45	R	M	L	E	S	LC	LC

CHAPTER 4. LOCAL AND REGIONAL HABITAT ASSOCIATIONS AND AREA-SENSITIVITY OF BIRDS IN FLOODPLAIN FORESTS OF THE UPPER MISSISSIPPI RIVER

A paper to be submitted to Ecological Applications

Melinda G. Knutson [1,2], Erwin E. Klaas[1], and R. Michael Erwin[3]

Abstract

Our study of Upper Mississippi River (UMR) floodplain forests identifies patterns in bird species richness and relative abundance associated with floodplain habitat features at two scales, the plot and the region surrounding the plot. We examined relationships between the bird community and specific habitat features and identified area-sensitive species and area-sensitive bird classifications based on guild membership or management risk. We compared the influence of vegetation (plot) or landscape matrix (region surrounding the plot) variables on bird species distribution and identified floodplain forest habitat sub-types important for conservation and management. UMR floodplain bird species richness, and the abundance and richness of hole-nesting and bark-gleaning bird guilds, are associated with a landscape matrix dominated by mature forests. Within the floodplain, vegetation (small scale) variables had a larger influence on bird abundance than landscape matrix (large scale) factors. The yellow-billed cuckoo, ruby-throated hummingbird, red-bellied woodpecker, hairy woodpecker, white-breasted nuthatch, brown creeper, yellow-bellied sapsucker and chimney swift were area-sensitive. Many species, identified by others as area-sensitive in uplands, do not show these patterns in the floodplain. If density and species richness are reliable indicators of habitat quality, the UMR floodplain may provide important habitat for area-sensitive species, including some neotropical migrants.

---

[1] Graduate student and Professor, respectively, Iowa State University, Department of Animal Ecology and National Biological Service, Iowa Cooperative Fish and Wildlife Research Unit, Ames, IA. Research conducted and manuscript written by Knutson with consultation from Klaas and Erwin.

[2] Author for correspondence. Address after 1 September 1995: National Biological Service, Upper Mississippi Science Center, P.O. Box 2226, LaCrosse, WI 54601.

[3] National Biological Service, Patuxent Environmental Science Center, Laurel, MD.

Introduction

Several studies have focused on habitat relationships of riparian birds (Best and Stauffer 1980, Stauffer and Best 1980, Bull and Skovlin 1982, Finch 1989, Darveau et al. 1995, Murray and Stauffer 1995), but few have examined large floodplain forests of northern latitudes (Emlen et al. 1986, Decamps et al. 1987). Because of differences in latitude, composition of the dominant vegetation, and floodplain dynamics, bird species composition and habitat associations of large northern U.S. river systems are likely to be very different from those of large southern floodplains (Emlen et al. 1986, Mitsch and Gosselink 1986, Burdick et al. 1989, Rudis 1993, Smith et al. 1993, Jones et al. 1994, Sparks 1995).

Extensive loss of midwestem forests due to agriculture has led to a preponderance of small, isolated, remnant forests with a substantially different physical environment and landscape matrix than the original forests (Saunders et al. 1991). In the Upper Mississippi River (UMR) floodplain, much forest has also been lost to agriculture and to hydrologic changes caused by lock and dam construction in the 1930s (Peck and Smart 1986, Yin and Nelson 1995). Little is known about the effects of forest fragmentation on northern floodplain forest birds (Best and Stauffer 1980, Stauffer and Best 1980, Grettenberger 1991).

Stauffer and Best (1980) found that riparian woodlands had higher densities of breeding birds than upland forest or herbaceous habitats. In addition, wide riparian strips have more species than narrow strips (Stauffer and Best 1980, Darveau et al. 1995). In a study of river corridor birds (dominated by waterbirds rather than forest birds) Rushton et al. (1994) found a close link between bird abundance and water quality. Decamps et al. (1987), in study of the River Garonne in France, found that riparian woodlands had high species richness and bird abundances. In addition, area effects on the bird community were important in the higher-elevation terraces but not in the riparian woodlands.

Studies of upland birds have repeatedly found that some species are sensitive to habitat fragmentation (e.g. Whitcomb et al. 1981, Ambuel and Temple 1983, Robbins et al. 1989b). Thompson (1993) attributed this phenomenon to population dynamics within forest patches. Small patches of upland forest and nests closer to forest edges experience higher predation rates (Gates and Gysel 1978, Wilcove 1985, Yahner and Scott 1988, BohningGaese et al. 1993). In addition, cowbird parasitism is greater along edges and within small forest patches (Norman and Robertson 1975, Brittingham and Temple 1983, Robinson et al. 1995). The combination of high predation and parasitism reduces reproductive success in small patches relative to large patches and species disappear from the smallest patches if colonization is low (Ambuel and Temple 1983, Temple 1986, Temple and Cary 1988). Even when colonization rates are not affected by forest size, stochastic processes lead to losses of uncommon or poorly reproducing species from small fragments (Urban and Shugart 1986, Hinsley et al. 1995). It is believed that these factors partially explain large-scale population declines of forest-interior neotropical migrant birds in the continental United States (Robbins et al. 1989b, Askins et al. 1990, Bohning-Gaese et al. 1993, Askins 1995). Adverse factors on the wintering grounds may also be contributing to these trends (Rappole and McDonald 1994).

Predator or parasite dynamics in the adjacent matrix may be more important in determining the rates of forest predation or parasitism than the dynamics of the forest patch itself (Angelstam 1986, Askins 1995). If this is true, different patterns of species richness or abundance might be observed when the matrix differs. Upland forests usually occur within a matrix of agriculture or urban development. Forest patches in large river floodplains occur within a matrix of water and marsh, and the spatial pattern of floodplain forests is more sinuous and interconnected than upland forests.

Gustafson et al, (1994) correlated proximity to other suitable habitat with habitat quality for the wild turkey *(Meleagris gallopavo).* Upland forests tend to form discrete patches separated by agriculture, urban development, and roads. Within the patches, forest cover tends to be internally consistent, without large canopy openings, except in the most extensive, pristine forests where natural successional processes continue (Mladenhoff et al. 1993). Given these differences between upland and lowland forests, different patterns in species abundance and richness are expected.

Bird communities are affected by processes at many spatial scales because individual birds respond to habitat features at more than one scale and because different birds have different home ranges and integrate habitat variables over different scales (Wiens 1981, Urban and Shugart 1986, Allen and Hoekstra 1992). In a study of birds wintering in Georgia, Pearson (1993) found that species richness, diversity, and bird abundance were highly influenced by landscape matrix (large spatial scale) factors. Examining habitat at more than one scale should improve our ability to explain bird distributions and abundance.

Our study identifies patterns in bird species richness and relative abundance associated with floodplain habitat features at two scales, the plot (20 - 40 ha) and the region surrounding the plot (150 - 250 ha) in UMR forests. We examined relationships between the bird community and specific habitat features, identified area-sensitive species and classifications of birds based on guild membership or management risk, compared the influence of vegetation (plot) or landscape matrix (region surrounding the plot) variables on bird species distribution, and identified floodplain forest habitat sub-types important for conservation and management.

Study area

The study area consisted of forested habitat in River Navigation Pools 6-10 of the UMR floodplain (NW Universal Transverse Mercator (UTM) E602000, N4883000; SE UTM E660000, N4738000). The area extends from near Winona, MN in the north to Guttenburg, IA in the south, a distance of about 177 km, following the main channel of the river. We randomly selected 50 plots from forested (> 70% tree canopy cover) land within Pools 6-9 using a 600 m X 600 m sampling grid overlaid on classified geographic information systems (GIS) land cover maps provided by the Environmental Management Technical Center, National Biological Service, Onalaska, WI. In addition, 5 large forested plots selected from the largest contiguous tracts of forest identified in Pools 6-10 were included to ensure that large tracts were represented.

Methods

Bird relative, abundance variables

We censused birds in 1992, 1993 and 1994 on 55 plots and in each plot we counted birds at 3 to 10 points (details of the census methodology are given in Chapter 3). The number of points depended upon the size of a plot; points were spaced at least 200 m apart and at least 50 m from an edge. We calculated the relative abundance of each species for each plot using the number of individuals of each species identified within 50 m of the observer over a 10-minute period and summed 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. Since the goal of this paper was to examine persistent trends and relationships for the entire bird community, we used the mean relative abundance over the three years in our analysis.

We estimated species richness for each plot with a jackknife estimate from the program CAPTURE (White et al. 1978). The jackknife estimator has been shown to perform as well or better than other methods of estimation of species richness (Palmer 1990, Palmer 1991, Baltanas 1992, Bunge and Fitzpatrick 1993, Nichols and Conroy in press). The jackknife estimator has been used to estimate species richness in other studies (Derleth et al. 1989, Karr et al. 1990). Details of the method and equations are given in Swensen (1994) and Burnham and Overton (1979). We calculated an estimate of species richness rather relying only on raw counts (the total number of species identified by the observer on the plot) because all plots do not have the same number of point-counts. Plots with more point-counts are expected to have greater raw species richness (Karr et al. 1990, Palmer 1995). The model we used takes into account new species identified as additional points are censused and calculates an estimate of the total number of species present, including those not seen. We report raw species richness as well, although those results may be biased, for the reasons described above.

We classified birds into groups based on guild associations and management risk categories to examine relationships between groups of species sharing common attributes and the habitat variables. We classified species into several guild, habitat association, and risk categories based on previous research and field observations in our study area (for scientific names and classifications see the Appendix). Species names follow the American Ornithologist's Union (1983). We grouped birds into foraging guilds based on De Graaf et al. (1985) and assigned nesting guild, territory size, and habitat preference categories according to published information (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. 1989a, Poole and Gill 1992-5). When no data on territory size for a species were available, data for closely-related taxa or body mass were used to estimate territory size (Schoener 1968, Dunning 1993). We assigned birds to categories of habitat preference based on published information and our own field observations (Whitcomb et al. 1981, Freemark and Merriam 1986, Thompson et al. 1993). Habitat preferences include birds found primarily within interiors of large forests, birds found both in forests and near edges (interior-edge), birds found primarily near edges, and birds found associated with water. We grouped birds into categories based on migration distances. Resident birds were defined as wintering in the study area; temperate migrants as wintering in the southern latitudes of the U.S. We divided neotropical migrants into groups based on wintering distributions given in Bellrose (1976), American Ornithologists' Union (1983), Hunter et al. (1993), and Thompson et al. (1993). Species with widespread neotropical winter distributions are considered at lower risk than those with very local distributions (Hunter et al. 1993, Thompson et al. 1993). We based population status on Breeding Bird Survey (BBS) trends in U.S. Fish and Wildlife Service Region 3 (includes MN, IA, MO, IL, WI, MI, IN, and OH) for 1966-1994. and 1980-1994 (BBS, unpublished data). Species with no significant population trend or increasing population trends were classified as stable or increasing (criterion 1 or 2: Thompson et al. 1993). Species that showed both an increase and a decrease for either long or short term trends (criterion 3 or 4: Thompson et al. 1993) were classified as having a mixed trend. Species that showed significant decreases both long and short-term (criterion 5: Thompson et al. 1993) were classified as decreasing. Species were classified into categories of management concern based on scores assigned by Thompson et al. (1993). Species with a mean overall score of 1-1.99 were classified as low, species with a score of 2 - 2.99 were classified as medium, species with a score of 3 - 5 were classified as high, and species not scored (resident or short-distance migrants and water birds) were classified as low unless they are listed as threatened, endangered, or of management concern by the U.S. Fish and Wildlife Service (Office of Migratory Bird Management 1987). The bald eagle and red-shouldered hawk were classified as high, according to this criterion.

Relative abundances for species within each classification served as the dependent variable in our analyses. Species richness for each classification is the total number of species observed within those groups. We did not calculate jackknife estimates for sub-sets of the bird community, as this would violate assumptions of the method. Therefore, we expected to find a positive relationship with area for species richness within bird classifications.

Vegetation variables

We calculated 12 vegetation variables for each plot based on measurements taken from 20 May through 10 July 1992 on 55 plots where bird census data were collected. We collected data on trees, snags, and saplings at each point using the point-centered quarter method (Cottam and Curtis 1956, Mueller-Dornbois and Ellenberg 1974). We collected shrub, herb, tree canopy cover, and tree canopy height measurements from 4 locations at each sampling point: the center and three additional points at a radius of 35 m from the sampling point, 120 degrees apart. Herb and shrub cover were estimated using releve classes (MuellerDombois and Ellenberg 1974). Means of herb and shrub cover were obtained by assigning the midpoint of the releve class to each observation (Bonham 1989). Cover estimates overlapped; total cover could be > 100%. Trees were woody plants with diameter at breast height (dbh) > 8 cm. Saplings were single-stemmed woody plants z 1.5 m in height with a dbh s 8 cm. Snags included dead standing wood z 12 cm dbh and z 1.5 m in height. Shrubs were woody plants > 0.5 m and < 1.4 m in height. We calculated canopy cover from the mean of 4 Type A densiometer readings each taken while facing in the cardinal directions. We measured canopy height of the tallest tree at each location with a clinometer.

Point-centered quarter measures for trees, saplings, and snags yielded six variables. DISTANCE TO TREES is the mean distance (m) from the central point (bird census point) to the nearest tree in each quarter averaged over the entire plot. DISTANCE TO SAPLINGS and DISTANCE TO SNAGS are similar distances for saplings and snags. TREE DBH is the mean dbh (cm) of the tree nearest the central point in each quarter averaged over the plot. SAPLING DBH and SNAG DBH are similar measures for saplings and snags. TREE HEIGHT is the mean height (m) of the tallest trees in each 50 m census circle averaged over the plot. CANOPY COVER is the mean of canopy cover estimates (%) averaged over the plot. HERB COVER is the mean herbaceous cover estimate (% of all grasses and forbs) averaged over the plot and SHRUB COVER is a similar estimate for shrubs. NETTLE COVER and GRASS COVER represent the percent cover of the two dominant herbs, nettles (Laportea and Boehmerica spp.) and grasses, (primarily Phalaris arundinaceae).

Landscape matrix variable

Landscape matrix metrics for each plot were determined based on geographic information system (GIS) analysis using ARC/INFO (ARC/INFO 1992) and the raster version of the FRAGSTATS analysis program (McGarigal and Marks 1994.). Classified Landsat Thematic Mapper data with a 30-m grid cell resolution from 1989 were used. The overall classification accuracy associated with the forest (trees/brush) cover category is 80.7% (Laustrup and Lowenberg 1994). Study locations were transferred to the GIS maps from locations identified on U.S.G.S. topographic maps. A patch is defined as 1 or more cells of the same classification (cover type) surrounded by cells of unlike classification. Eight measures of landscape matrix composition and patch shape were used, calculated from the region within 800 m of the central axis of the plot. This area is large enough to encompass an entire home range for all but the largest and most wide-ranging birds in the study. We excluded land outside the boundaries of the floodplain from the analysis because upland forests have different tree species than the floodplain and constitute a different habitat type. The area of forested land within the 800-m zone around each plot ranged from 16-286 ha.

The variable FOREST is the percentage of the 800-m radius region surrounding each plot classified as forest (Laustrup and Lowenberg 1994). The variable SHAPE INDEX (areaweighted mean shape index) is the average shape index of forest patches, weighted by patch area, so that larger patches have a greater influence on the metric than smaller patches (McGarigal and Marks

1994). This variable was chosen as a measure of how square or irregularly shaped the forest patches were. SHAPE INDEX = 1 ,when all forest patches are square; the metric increases as the patch shapes become more irregular. The variable CORE AREA is an index of the total core area of forest, i.e. the percentage of the region surrounding each plot that is classified as forest and is > 50 m from another cover type (edge). Paton (1994), in a review of edge effects on birds, concluded that the strongest evidence for edge effects was limited to within 50 m of an edge. CORE AREA = 0 when none of the forest patches contain any core area and approaches 1,00 when the forest patches contain mostly core area. The variable DIVERSITY INDEX is the Shannon diversity index applied to patches within the landscape matrix (McGarigal and Marks 1994). DIVERSITY INDEX = 0 when the landscape contains only one patch and increases as the number of different patch types and/or the proportional distribution of area among patch types becomes more equitably. Shannon's index, a commonly used diversity metric, is reasonably good at discriminating between sites (Magurran 1988), and has been previously used in landscape studies (Rom a 1982). WATER, AQUATIC VEGETATION, HERBACEOUS VEGETATION , and DISTURBED LAND are the percentages o$ the 800 m radius region surrounding etch plot classified as open water, aquatic vegetation, grasses/forbs, and disturbed land I (urban/developed and agriculture) (Laustrup and Lowenberg 1994).

Results

Principal components rents / regression analyses

We us d Principal Components (PC) analysis to reduce the number of vegetation and landscape matrix variables to two sets of factors - a set of matrix factors and a set of vegetation factors (SAS PRINCOMP) (SAS Institute Inc. 1989). This reduced intercorrelation of variables and allowed us to compare the effects of vegetation vs. landscape factors on the bird community. An interpretation of each PC was made, based on loadings on the eigenvectors (Tabachnick and Fidel] 1989). We identified 4 landscape matrix and 5 vegetation PCs, (Table 1). The 4 matrix PCs (M1-4.) each had eigenvalues > 0.90 and together explained 87% of the variance of the original variables. The 5 vegetation PCs (V1-5) each had eigenvalues > 1 and together explained 79% of the variance of the original variables. Pearson correlation coefficients between the sets of PCs were low except for M1 and V1 (r = 0.) and Ml and V2 (r = 0.39). The first matrix PC (Ml) represents a continuum wit) high positive loadings on FOREST COVER, CORE AREA and negative loadings on WATER (Tables 1 and 2). The first vegetation PC (V1) represents a continuum with high positive loadings on TREE DBH, DISTANCE TO SAPLINGS, DISTANCE

TO TREES, SNAG DBH, and TREE HEIGHT and negative loadings on SHRUB COVER and CANOPY COVER. Using step-wise regression, habitat models for species abundances (Table 3) and abundance within bird classifications (Table 4) were obtained. Habitat models were obtained for species richness overall and species richness within ecological and management classifications (Table 5). Regression models for all species are given, but may be unreliable for species identified on few plots.

The ratio of r^2 for the matrix variable over r^2 for the entire model is the proportion of total explained variance accounted for by the matrix variables. Matrix variables account for an average of 42.3% of the variance explained by the entire regression model for species with at least one variable significant (Table 3). For abundance within bird classifications, matrix variables account for an average of 28.8% of the variance explained by the entire regression model (Table 4) and for species richness, matrix variables account for an average of 50.3% of the variance explained by the entire regression model (Table 5).

Relative abundances of neotropical migrants with local winter distributions are positively associated with mature, open-canopy forests (V1), as is abundance of species with stable populations, interior-edge habitat preferences, large territory sizes, hole nesters, piscivores, lower canopy and bark gleaners and species of management concern (Table 4). Abundances of great blue herons, hooded mergansers, ruby-throated hummingbirds, redheaded woodpeckers, red-bellied woodpeckers, white-breasted nuthatches, brown creepers, blue-gray gnatcatchers, yellow-throated vireos, and prothonotary warblers are all positively associated with V1 (Table 3). Raw species richness and richness for resident birds, neotropical migrants with local winter distributions, birds with decreasing population trends, low and high management status, interior forest and interior-edge habitat preferences, large territory sizes, upper canopy and hole nesters, and air and bark feeding guilds are all positively associated with mature, open-canopy forests (Table 5).

Species with abundances associated with early or mid-successional forests (V2 and V3) include water birds, ground nesters, air hawkers and bark gleaners (Table 4). Species include the mourning dove, ruby-throated hummingbird, downy woodpecker, pileated woodpecker, eastern wood-pewee, great crested flycatcher, American crow, gray catbird, brown thrasher, yellow warbler, common yellowthroat, northern cardinal, and chipping sparrow (Table 3). Species richness of resident birds, neotropical migrants with widespread winter distributions, lower canopy nesters, ground gleaners, and bark gleaners is also positively associated with early or mid-successional forests (Table 5).

Species abundances associated with forests with a well developed shrub understory (V4) include neotropical migrants with intermediate winter distribution, birds with mixed population trends, medium management status, lower canopy nesters, and upper canopy gleaners (Table 4). Species include the pileated woodpecker, eastern wood-pewee, yellowthroated vireo, American redstart, and ovenbird (Table 3). Species richness of neotropical migrants with local winter distributions and interior forest habitat preferences is also positively associated with V4 (Table 5).

The relative abundance of bark gleaners is positively associated with a high percentage of the landscape matrix in forest cover (Ml). Individual species positively associated with M1 include yellow-billed cuckoos, chimney swifts, yellow-bellied sapsuckers, hairy woodpeckers, and indigo buntings (Table 3). Other bird classifications positively associated with Ml include birds with stable and mixed population trends, medium and high management status, interior and interior-edge habitat preferences, small and intermediate territory sizes, lower canopy nesters, and lower and upper canopy gleaners (Table 4). Species richness overall is positively associated with Ml along with richness of neotropical migrants with widespread and intermediate winter distributions (Table 5).

Bird abundances associated with landscape matrix diversity (M2) include neotropical migrants with local winter distributions, hole nesters, bald eagles, and great crested flycatchers (Table 3 and 4). Species richness overall, richness of birds with mixed population trends, edge species, and species with a small territory size are also associated with M2 (Table 5).

Bird abundances associated with landscape matrices containing disturbed patches (M3 or M4) include species with stable or mixed population trends, water birds, ground nesters, and lower canopy nesters (Table 4). Species include the wood duck, Acadian flycatcher, least flycatcher, red-eyed vireo, indigo bunting, field sparrow, song sparrow, and American goldfinch (Table 3). Species richness of birds with stable populations, edge species, and small territory size were also associated with M3 or M4 (Table 5).

Cluster / diacriminant analyses

We used SAS CLUSTER procedure (SAS Institute Inc. 1989) with Ward's minimum variance method to separate plots into groups based on vegetation and landscape matrix habitat features. This method tends to equalize the numbers of observations in each cluster. Variables were standardized to mean = 0 and standard deviation = 1 before analysis because cluster analysis is sensitive to differences in scale among the variables. Based on a tree diagram of the results and considerations of sample size, three clusters were selected. We interpreted the clusters using the

SAS CANDISC (SAS Institute Inc. 1989) procedure. Total canonical correlations with the original variables describe the axes along which the clusters vary and provide an interpretation of the clusters.

We tested differences among clusters for species richness and relative abundance using the General Linear Models (GLM) procedure (SAS Institute Inc. 1989). We used the Bonferroni method to control the experiment-wise error (alpha < 0.05) in the GLM analysis of relative abundance for each species. We used the non-parametric Kruskal-Wallis test (Zar 1984, SAS Institute Inc. 1989) as an adjunct to GLM; the large number of zeros in the data set for uncommon species potentially violates the normal distribution assumption of GLM. However, this test did not detect more differences than GLM for rare species in our data set, so the results of the GLM analysis are reported. We show statistical differences at the 5% level of significance, however, we tested a large number of species, increasing the probability of observing spurious significant differences. No clear guidelines are available for adjusting significance for a large number of comparisons without substantial loss of power to detect differences.

The cluster analysis classified vegetation and landscape variables into 3 clusters with 16, 29, and 10 plots, respectively. Means for the variables within each cluster were significantly different ($P < 0.05$) for 14 of the 20 variables (Table 6). Variation in FOREST, CORE AREA, WATER, DIVERSITY INDEX, DISTANCE TO SAPLINGS, and SHRUB COVER had the most influence on the results, based on univariate r^2 and F statistics. The first canonical variable (CAN1) had a high correlation with FOREST and CORE AREA, followed by DISTANCE TO SAPLINGS, NETTLE COVER, SAPLING DBH, TREE DBH, and SNAG DBH in decreasing importance (Table 7). The first canonical variable had an eigenvalue of 5.85 and accounts for 60.9% of the variability in the data set. The second canonical variable (CAN2) had an eigenvalue of 3.75 and accounts for the remaining 39.1 of the variability. CAN2 had a high correlation with CORE AREA, SHRUB COVER, and WATER.

A graph of the plots based on their locations within canonical variable space provides a visual interpretation of the clusters (Figure 1). Interpretation of the meaning of the clusters was based on the canonical correlations with the original variables (Table 7). Cluster 1 (LARGE FOREST) had high values for CANT and CAN2. These plots represent mature forests within a landscape matrix dominated by forest with a high core area. Cluster 2 (DIVERSE FOREST) represents forests with high grass cover and less core area (more fragmented) within a diverse patch matrix of aquatic and herbaceous vegetation and water. Cluster 3 (SHRUB FOREST) has low values for CAN1 and high values for CAN2. These plots are forests with high core area and shrub cover within a water matrix (often islands).

Fifteen individual species differed ($P < 0.05$) in their relative abundances among clusters (Table 8). The brown creeper, chimney swift, red-bellied woodpecker, ruby-throated hummingbird, white-breasted nuthatch, yellow-billed cuckoo, and yellow-bellied sapsucker had higher relative abundance in LARGE FOREST plots. The American goldfinch, brown thrasher, cedar waxwing, green-backed heron, gray catbird, red-winged blackbird, and wood thrush had higher relative abundance in SHRUB FOREST plots. Mallards had higher relative abundance in DIVERSE FOREST plots, whereas 6 species had intermediate relative abundances in these plots. Differences for species identified from more than I plot are presented, but caution should be used in interpreting the results for species such as the brown thrasher, green-backed heron, and wood thrush, which were identified on few plots.

We found few differences in relative abundances within management and ecological classifications among clusters (Table 9). Species experiencing population declines had higher relative abundances in SHRUB FOREST and DIVERSE FOREST plots. Hole nesters and bark gleaners (dominated by the woodpeckers) have higher relative abundances in LARGE FOREST plots and intermediate abundances in DIVERSE FOREST plots. Ground gleaners have higher relative abundances in SHRUB FOREST and DIVERSE FOREST plots.

We identified greater differences in species richness among clusters, as expected since species richness within classifications is not adjusted for plot size (Table 10). Both raw richness and the jackknife estimate of species richness were higher in LARGE FOREST and DIVERSE FOREST plots. Most management and ecological classifications showed declining trends in species richness, with DIVERSE FOREST plots having intermediate richness between LARGE FOREST (highest) and SHRUB FOREST (lowest) plots. All the significant differences were in this direction. A few groups (species with declining population trends, edge and water species, lower canopy nesters, and ground gleaners) had the highest species richness in DIVERSE FOREST plots, but the differences were not significant ($P < 0.05$).

Discussion

Area-sensitivity follows a different pattern in the floodplain than has been reported in uplands (Table 11). Some species showing area-sensitivity in the floodplain have also been identified as area-sensitive in upland studies conducted in the Eastern or Midwestern U. S., including the yellow-billed cuckoo, ruby-throated hummingbird, red-bellied woodpecker, hairy woodpecker, white-breasted nuthatch and brown creeper (Whitcomb et al. 1981, Blake and Karr 1984, Blake and Karr 1987, Robbins et al. 1989a). However, a large number of species, especially neotropical migrants, identified as area-sensitive from upland studies (Ambuel and Temple 1983, Blake and Karr 1984, Lynch and Whigham 1984, Hayden and Faaborg 1985, Temple 1986, Blake and Karr 1987, Robbins et al. 1989a), show no areasensitivity here. Emlen et al. (1986) list only one species, the yellow-throated vireo, in which large forest extent was the principal constraint on its density. However, they sampled primarily from large stands. Stauffer and Best (1980) list species of riparian forests that do not tolerate breeding habitat alteration. Some of these species (blue-gray gnatcatcher, warbling vireo, American redstart, common yellowthroat, rose-breasted grosbeak, and redeyed vireo) are common in UMR floodplain forests. High abundances for these species are an indication that UMR forests provide high-quality floodplain habitat.

Other studies have identified clear trends in area-sensitivity within bird classifications (Ambuel and Temple 1983, Blake and Karr 1984, Lynch and Whigham 1984, Hayden and Faaborg 1985, Freemark and Merriam 1986, Robbins et al. 1989a). Long-distance migrants and interior and interior-edge species show the highest sensitivity. In our study, bark gleaner relative abundance was the only bird classification positively associated with large forests (Ml) in the step-wise regression (Table 4). In the cluster analysis, interior-edge species showed a trend toward higher relative abundance in LARGE FOREST plots, but it was not significant (Table 9). Hole nesters and bark gleaners also are more numerous in LARGE FOREST and DIVERSE FOREST plots. These groups of birds are dominated by resident woodpeckers rather than long-distance migrants. In the floodplain, the woodpeckers and other hole-nesters are most dependent upon large, unfragmented tracts of forest. These forests tend to have high densities of large standing snags interspersed with mature forest trees, ideal habitat for these species.

Why would contrasting patterns of area-sensitivity be found in uplands vs. floodplains? One major factor may be the landscape matrix in which the forest occurs. In uplands, croplands, pastures, and urban areas are adjacent to forests. These forest edges support high predator and cowbird populations that can negatively affect reproductive success of songbirds (Brittingham and Temple 1983, Paton 1994, Askins 1995). In addition, upland forest patches are often separated by long distances (several km). When a species is lost from a patch, re-colonization may not occur, depending upon reproductive success in adjacent habitats and the distance between patches. Island biogeography theory predicts small patches, long distances from source patches, have low colonization rates (MacArthur and Wilson 1967). In the floodplain, the distances between patches is not great in some cases only 50 - 100 m. Floodplain forests tend to be sinuous and interconnected, and adjacent to open water or marsh, quite different habitats from those that support predators and cowbirds in upland habitats. We know little about nest predator distribution and abundance in large fioodplains (but see Chapter 3, Best and Stauffer 1980). Cowbirds were common in the floodplain, but it is unclear what effect they have on the reproductive success of songbirds there. It may be that the relative negative effects on some host species of predators and cowbirds in the floodplain are less than in upland habitats. In addition, if some locations in or near the floodplain act as source habitats (sensu Pulliam (1988), colonization may be rapid.

The uplands surrounding the study area are typical of the Driftless Section of the Maple-Basswood Forest Region (Braun 1950), with rolling hills dominated by maple, oak, and hickory. The forests are highly fragmented by agriculture, both in the valleys and on the ridges. Almost all of these forests are heavily managed for timber production (Iowa Department of Natural Resources and North Central Forest Experiment Station 1991); there are no large, unfragmented old-growth forests in the region. It is unlikely that these upland forests represent a significant source area for birds identified as area-sensitive. It is more likely that the floodplain represents the source area, if one exists in the region. This is probably especially true for area-sensitive species common in the floodplain, such as American redstarts, rose-breasted grosbeaks, blue-gray gnatcatchers, yellow-throated vireos, red-eyed vireos, yellow-billed cuckoos, red-bellied woodpeckers, yellow-bellied sapsuckers, downy and hairy woodpeckers, eastern wood-pewees, great crested flycatchers, white-breasted nuthatches, and brown creepers. The American redstart, a very common species in the floodplain, has experienced population declines in upland forests in the Midwest since the 1930's (Schorger 1931, Temple and Cary 1988). Recent Midwestern studies of nest succes in neotropical migrants indicate that large regions of the Midwest may be population sinks for birds requiring unfragmented forest habitat for successful reproduction (Robinson 1992, Robinson et al. 1995). Intensive study of population parameters, such as reproductive success and/or survival of selected species, would help clarify whether the floodplain is a source or sink for area-sensitive species declining in adjacent upland habitats (Van Horne 1983).

Our observations of floodplain forests are similar in some respects to those of DeCamps et al. (1987), who also noted a weak relationship between forest area and bird density in riparian forests in France. They found that riparian forests had higher richness and abundance of birds than higher elevation terrace forests. They attributed their findings to the shape and connectivity of the riparian forests, which may buffer the effects of isolation on patch dynamics. In contrast, McGarigal and McComb (1992), working in riparian coniferous forests in the Pacific Northwest, found higher species diversity, richness, and abundance away from streams than adjacent to them.

Presence-absence and relative abundance data have long been used as indicators of favorable habitat for species (Fretwell and Lucas 1970, Fish and Wildlife Service 1980). Under certain conditions, high relative abundance may not indicate favorable habitat (Van Home 1983, Hobbs and Hanley 1990). This is a problem when a species experiences high population levels, forcing some individuals to fill less suitable habitats (O'Connor 1986). How reliable are census data as an indicators of habitat quality on the UMR? There has been no recent, large-scale habitat loss in the UMR region that would lead to abnormally high packing of individuals into a smaller available space. Since regional upland source areas for area-sensitive species have been scarce for decades (Temple and Cary 1988), it is unlikely that birds are dispersing from adjacent uplands to the floodplain in any large numbers (rescue effect of Brown and Kodric-Brown 1977). Rainfall over the last 7 years has been highly variable, including a record-setting drought year (1988) and flood year (1993). This climatic variability is more likely to depress populations levels than increase them. For some species, territorial social interactions may lead to high relative abundance in poor habitats (Van Home 1983). However, area-sensitive bird species declining or disappearing from poor upland habitats should similarly decline in poor floodplain habitats.

Gibbs and Faaborg (1990) found that high densities of ovenbirds coincided with a high proportion of paired males on large forest tracts whereas Kentucky warbler densities and proportions of paired males were similar between habitats. However, Vickery et al. (1992) did not find a correlation between high density and high reproductive success for emberizine sparrows. Given these considerations, it seems prudent to test whether density is an indicator of reproductive success in the floodplain.

Island biogeography theory predicts that species richness will increase as area increases (MacArthur and Wilson 1967). Species richness for birds at all levels of management concern and for interior forest and interior-edge birds was highest in LGFOR plots (Table 10). Because mature, open-canopy forests (Ml) and LARGE FOREST plots are associated with large tracts of forest, it is not surprising that this PC was frequently positively related to species richness. Whereas richness was correlated with large forests in our study, relative abundance usually was not. In the floodplain, both the landscape matrix and site vegetation influence the number of species, but the vegetation has more effect on bird abundance. This indicates that smaller scale variation (measured on the plot rather than the region surrounding the plot) has greater influence on the relative abundance of floodplain forest birds.

We found no clear trends in habitat associations for birds of management concern. The different categories of neotropical migrants were not influenced by forest size, except for birds with intermediate winter distributions. Too few data were collected on red-shouldered hawks and cerulean warblers to asses clearly their habitat associations, and no significant relationships were identified. Bald eagles were associated with landscape matrix diversity (M2). The prothonotary warbler, a specialist on large floodplain forests, was associated with mature forests (V1), a finding similar to other studies (Petit 1989, Brush 1994). It is unclear why yellow-bellied sapsuckers are so clearly associated with LARGE FOREST sites, since the tree species composition across the floodplain is heavily dominated by silver maple, a favorite sap tree. Dobkin and Wilcox (1986) also found evidence for area-sensitivity in yellow-bellied sapsuckers in the mountains of the western U.S. Two species, the indigo bunting and chimney swift, have not previously been identified as area-sensitive (Table 11) and their association in this study with large forests may be coincidental with other habitat features found within these forests. We observed indigo buntings in small grassy openings and shrub edges within the large forests and chimney swifts nesting in large, standing snags. Caution should be used in interpreting habitat associations for species with large territories and home ranges like the eagle, pileated woodpecker, barred owl and red-shouldered hawk. They nest in large forest tracts (Renken and Wiggers 1993), but may be observed in other places. Forests with a well developed shrub layer may be important habitats in the floodplain; we associated species with declining population status and ground-gleaning birds (wood thrush) with them. In an overall management ranking of neotropical migrant birds in the Midwest, Thompson et al. (1993) found that more high-priority species were found in lowland deciduous forests than any of the other habitats considered.

Principal components (PC) analysis is an accepted method of reducing the dimensionality of ecological habitat data and deriving uncorrelated variables to use in regression analyses (Moloney 1989, Tabachnick and Fidell 1989, Dunning and Watts 1990) . Pearson (1993) used PC analysis to examine the relative contribution of vegetation and landscape matrix factors on a bird community. Cluster analysis followed by discriminant analysis has an advantage over PC analysis in that independent variables are not required to be linearly related to dependent variables. Once sampling plots are classified into clusters, hypothesis tests of differences among clusters for a dependent variable are possible.

The PC analysis and the cluster analysis provide complementary perspectives on bird habitat relations in the floodplain. The PC/regression analysis provides more information on relations between specific habitat features and individual bird species than the cluster analysis, which only looks at differences among clusters. The PC analysis separates vegetation (small-scale) variables from landscape matrix (large scale) variables and allows examination of their relative influence on the bird community. The cluster analysis is useful in describing how vegetation and landscape features are related for purposes of conservation and management. The plots integrate the measured variables into actual locations within the floodplain. It is likely that additional plot samples would share both regional and local characteristics in a pattern similar to our sampled plots. For example, forests with higher shrub cover tend to be located within a context dominated by water (island forests) and have smaller trees. We observed that these island forests tended to be of higher elevation than some of the larger forested tracts and probably flood less frequently. Shrubs may be favored in these more open, infrequently flooded locations. SHRUB FOREST plots had higher relative abundances for 7 species and 2 categories of birds, as previously noted. Conservation of plots with common features and their attendant bird species is more clearly defined by the cluster analysis.

Acknowledgements

Funding was provided by the National Biological Service (Patuxent Environmental Science Center, Branch of Migratory Birds Research), Iowa State University, U.S. Fish and Wildlife Service (Region 3 Nongame Program), and the Minnesota Department of Natural Resources Nongame Program. Classified Thematic Mapper databases were provided by NBS, Upper Mississippi Science Center, Environmental Management Technical Center. Ms. Knutson also was supported by a Cooperative Education Agreement with the Patuxent Center. Special thanks to Ms. Knutson's doctoral committee members Louis Best, Brent Danielson, Kirk Moloney, and Thomas Jurik. Kari Jovaag and Kenneth Koehler provided statistical consultation. James Majure and Todd Bishop provided technical GIS consultation. Field, office, and data management assistance were provided by Ingrid Moore, Brian Collins, Tom Pehowski, Vance Polton, Holly Dick, Pam Heidenreich, Mark Krom, Rebecca. Peak, Julie Schreiber, Fredrick Keith, Jesse Audette, Brenda VanBeek, and Sara Handrick.

Literature Cited

Allen, T. F. H. and T. W. Hoekstra. 1992. Toward a Unified Ecology. Columbia University Press, New York, NY. 384 pp.

Ambuel, B. and S. A. Temple. 1983. Area.-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64: 1057-1068.

American Ornithologists' Union. 1983. Check-list of North American Birds, 6th ed. Allen Press, Lawrence, KS. 877 pp.

Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47: 365-373.

ARC/INFO. 1992. ARC/INFO v6.1. Environmental Systems Research Institute, Inc. Redlands CA 92373-8100.

Askins, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. Science 267: 1956-1957.

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

Baltanas, A. 1992. On the use of some methods for the estimation of species richness. Oikos 65: 484-4.92.

Bellrose, F. C. 1976. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg, PA. 540 pp.

Best, L. B. and D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. Condor 82: 149-158.

Blake, J. G. and J. R. Karr. 1984. Species composition of bird communities and the conservation benefit of large versus small forests. Biological Conservation 30: 173187.

Blake, J. G. and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68: 1724-1734.

Bohning-Gaese, K., M. L. Taper and J. H. Brown. 1993. Are the declines of North American songbirds due to causes on the breeding range? Conservation Biology 7: 76-86.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, New York, NY. 338 pp.

Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Publishing, New York, NY. 596 pp.

Brittingham, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33: 31-35.

Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration and extinction. Ecology 58: 445-449.

Brush, T. 1994. Effects of competition and predation on prothonotary warblers and house wrens nesting in eastern Iowa. Journal of the Iowa Academy of Science 101: 28-30.

Bull, E. L. and J. M. Skovlin. 1982. Relationships between avifauna and streamside vegetation. Transactions of the North American Wildlife Natural Resources Conference 47: 497-506.

Bunge, J. and M. Fitzpatrick. 1993. Estimating the number of species: a review. Journal of the American Statistical Association 88: 364-373.

Burdick, D. M., D. Cushman, R. Hamilton and J. G. Gosselink. 1989. Faunal changes and bottomland hardwood forest loss in the Tensas watershed, Louisiana. Conservation Biology 3: 282-292.

Burnham, K. P. and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60: 927-936.

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451-460.

Darveau, M., P. Beauchesne, L. Belanger, J. Huot and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. Journal of Wildlife Management 59: 6778.

De Graaf, R. M., N. G. Tilghman and S. H. Anderson. 1985. Foraging guilds of North American birds. Environmental Management 9: 493-536.

Decamps, H., J. Joachim and J. Lauga. 1987. The importance for birds of the riparian woodlands within the alluvial corridor of the River Garonne, S. W. France. Regulated Rivers: Research and Management 1: 301-316.

Derleth, E. L., D. G. McAuley and T. J. Dwyer. 1989. Avian community response to smallscale habitat disturbance in Maine. Canadian Journal of Zoology 67: 385-390.

Dobkin, D. S. and B. A. Wilcox. 1986. Analysis of natural forest fragments: riparian birds in the Toiyabe Mountains, Nevada. Pages 293-299 In J. Verner, M. L. Morrison and C. J. Ralph, Eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Dunning, J. B., Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL. 371 pp.

Dunning, J. B., Jr. and B. D. Watts. 1990. Regional differences in habitat occupancy by Bachman's sparrow. Auk 107: 463-4.72.

Ehrlich, P. R., D. S. Dobkin and D. Wheye. 1988. The birder's handbook. Simon & Schuster, Inc., New York. 785 pp.

Emlen, J. T., M. J. DeJong, M. J. Jaeger, T. C. Moermond, K. A. Rusterholtz and R. P. White. 1986. Density trends and range boundary constraints of forest birds along a latitudinal gradient. Auk 103: 791-803.

Finch, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. Ecology 70: 866-880.

Fish and Wildlife Service. 1980. Habitat as a basis for environmental assessment. Ecological Services Manual 101. U.S. Department of the Interior, Fish and Wildlife Service, Division of Ecological Services. Government Printing Office, Washington, D. C. 84 pp.

Freemark, K. E. and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36: 115141.

Fretwell, S. D. and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Part I. Theoretical development. Acta Biotheoretica 19: 16-36.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledgling outcome in fieldforest edges. Ecology 59: 871-883.

Gibbs, J. P. and J. Faaborg. 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. Conservation Biology 4: 193-196.

Grettenberger, J. 1991. Habitat fragmentation and forested wetlands on the Upper Mississippi River: Potential impacts on forest interior birds. Passenger Pigeon 53: 227-241.

Gustafson, E. J., G. R. Parker and S. E. Backs. 1994. Evaluating spatial pattern of wildlife habitat: a case study of the wild turkey *(Meleagris gallopavo).* American Midland Naturalist 131: 24=33.

Hayden, T. J. and J. Faaborg. 1985. Estimates of minimum area requirements for Missouri forest birds. Transactions of the Missouri Academy of Science 19: 11-22.

Hinsley, S. A., P. E. Bellamy and 1. Newton. 1995. Bird species turnover and stochastic extinction in woodland fragments. Ecography 18: 41-50.

Hobbs, N. T. and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? Journal of Wildlife Management 54: 515-522.

Hunter, W. C., M. F. Carter, D. N. Pashley and K. Barker. 1993. The Partners in Flight species prioritization scheme. Pages 422 In D. M. Finch and P. W. Stangel, Eds.

Status and management of neotropical migratory birds. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-229, Fort Collins, CO.

Iowa Department of Natural Resources and North Central Forest Experiment Station. 1991. An overview of Iowa's forest resources, 1990. Des Moines, IA. 3 pp.

Jones, R. H., R. R. Sharitz, P. M. Dixon, D. S. Segal and R. L. Schneider. 1994. Woody plant regeneration in four floodplain forests. Ecological Monographs 64: 345-367.

Karr, J. R., S. K. Robinson, J. G. Blake and R. O. Bierregaard Jr. 1990. Birds of four neotropical forests. Pages 237-269 In A. H. Gentry, Eds. Four Neotropical Rainforests. Yale University Press, New Haven, CT.

Laustrup, M. S. and C. D. Lowenberg. 1994.. Development of a systematic land cover/land use database for the Upper Mississippi River System derived from Landsat thematic mapper satellite data. National Biological Survey, Environmental Management Technical Center, Onalaska WI. 90 pp.

Lynch, J. F. and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation 28: 287 324.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Monographs in population biology. 1. Princeton University Press, Princeton, NJ. 203 pp.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ. 179 pp.

McGarigal, K. and B. J. Marks. 1994. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure v2.0. Kevin McGarigal, P.O. Box 606, Dolores, CO 81323-9998. Corvallis, OR. pp.

McGarigal, K. and W. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon coast range. Journal of Wildlife Management 56: 10-23.

Mitsch, W. J. and J. G. Gosselink. 1986. Wetlands. Van Nostrand Reinhold, New York. 537 pp.

Mladenhoff, D. J., M. A. White, J. Pastor and T. R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3: 294-306.

Moloney, K. A. 1989. The local distribution of a perennial bunchgrass: biotic or abiotic control? Vegetatio 80: 47-61.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.

Murray, N. L. and D. F. Stauffer. 1995. Nongame bird use of habitat in central Appalachian riparian forests. Journal of Wildlife Management 59: 78-88.

Nichols, J. D. and M. J. Conroy. in press. Estimation of species richness. *In* D. S. Wilson, J. D. Nichols, R. Rudran and M. Foster, Eds. Handbook of methods for studying biodiversity of mammals. Smithsonian Institution Press, Washington, D.C.

Norman, R. F. and R. J. Robertson. 1975. Nest-searching behavior in the Brown-Headed Cowbird. Auk 92: 610-611.

O'Connor, R. J. 1986. Dynamical aspects of avian habitat use. Pages 235-240 *In* J. Verner, M. L. Morrison and C. J. Ralph, Eds. Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Office of Migratory Bird Management. 1987. Migratory nongame birds of management concern in the United States: the 1987 list. Washington, D.C. 27 pp.

Palmer, M. W. 1990. The estimation of species richness by extrapolation. Ecology 71: 1195-1198.

Palmer, M. W. 1991. Estimating species richness: the second-order jackknife reconsidered. Ecology 72: 1512-1513.

Palmer, M. W. 1995. How should one count species? Natural Areas Journal 15: 124-135.

Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8: 17-26.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology 8: 3-18.

Peck, J. H. and M. M. Smart. 1986. An assessment of the aquatic and wetland vegetation of the Upper Mississippi River. Hydrobiologia 136: 57-76.

Petit, L. J. 1989. Breeding biology of prothonotary warblers in riverine habitat in Tennessee. Wilson Bulletin 101: 51-61.

Poole, A. and F. Gill. 1992-5. The birds of North America: life histories for the 21st century. The American Ornithologists' Union and the Academy of Natural Sciences, Washington, DC and Philadelphia, PA. pp.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652-661.

Rappole, J. H. and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. Auk 111: 652-660.

Renken, R. B. and E. P. Wiggers. 1993. Habitat characteristics related to Pileated Woodpecker densities in Missouri. Wilson Bulletin 105: 77-83.

Robbins, C. S., D. K. Dawson and B. A. Dowell. 1989a. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildlife Monographs 103: 1-34.

Robbins, C. S., J. R. Sauer, R. S. Greenberg and S. Droege. 1989b. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences 86: 7658-7662.

Robinson, S. K. 1992. Population dynamics of breeding neotropical migrants in a fragmented Illinois landscape. Pages 408-418 In J. M. Hagan III and D. W. Johnston, Eds. Ecology and conservation of neotropical migrant landbirds. Manomet Bird Observatory, Woods Hole, MA.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987-1957.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52: 199-221.

Rudis, V. A. 1993. Forest fragmentation of southern U. S. bottomland hardwoods. General Technical Report SO-93, Southern Forest Experiment Station. Pages 35-46 In J. C. Brissette, Eds. Proceedings of the 7th Biennial Southern Silvicultural Research Conference.

Rushton, S. P., D. Hill and S. P. Carter. 1994. The abundance of river corridor birds in relation to their habitats: a modelling approach. Journal of Applied Ecology 31: 313328.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, 4th ed., vol. 2 SAS Institute, Inc. Cary, NC. 846 pp.

Saunders, D. A., R. J. Hobbs and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5: 18-32.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123-141.

Schorger, A. W. 1931. The birds of Dane County, Wisconsin (Part 2). Transactions of the Wisconsin Academy of Sciences, Arts and Letters 26: 1-60.

Smith, P. W., D. J. Twedt, D. A. Wiedenfeld, P. B. Hamel, R. P. Ford and R. J. Cooper. 1993. Point counts of birds in bottomland hardwood forests of the Mississippi Alluvial Valley: duration, minimum sample size, and points versus visits. Research Paper. SO-274. May, 1993. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA. 21 pp.

Sparks, R. E. 1995. Need for ecosystem management of large floodplain rivers and their floodplains. BioScience 45: 168-182.

Stauffer, D. F. and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alteration. Journal of Wildlife Management 44: 1-15.

Swensen, A. R. 1994. Using capture-recapture methodology to estimate the number of bird species. Creative Component, M.S., Statistics. Iowa State University. 42 pp.

Tabachnick, B. G. and L. S. Fidell. 1989. Using Multivariate Statistics. Harper & Row, New York. 746 pp.

Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: A comparison of two models. Pages 301-304 *In* J. Verner, M. L. Morrison and C. J. Ralph, Eds. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Temple, S. A. and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2: 340-347.

Thompson, F. R., 111. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. Conservation Biology 7: 325-341.

Thompson, F. R., S. J. Lewis, J. Green and D. Ewert. 1993. Status of neotropical migrant landbirds in the Midwest: identifying species of management concern. Pages 422 *In* D. M. Finch and P. W. Stangel, Eds. Status and management of neotropical migratory birds. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-229, Fort Collins, CO.

Urban, D. L. and H. H. Shugart Jr. 1986. Avian demography in mosaic landscapes: modeling paradigm and preliminary results. Pages 273-279 *In* J. Verner, M. L. Morrison and C. J. Ralph, Eds. Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates. Madison, WI.

Van Home, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

Vickery, P. D., M. L. Hunter Jr. and J. V. Wells. 1992. Is density an indicator of breeding success? The Auk 109: 706-710.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-201 *In* B. R. L. and D. M. Sharpe, Eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY.

White, G. C., K. P. Burnham, D. L. Otis and D. R. Anderson. 1978. User's manual for program CAPTURE. Utah State University Press. Logan, UT. 40 pp.

Wiens, J. A. 1981. Scale problems in avian censusing. Pages 513-521 *In C.* J. Ralph and J. M. Scott, Eds. Estimating numbers of terrestrial birds. Cooper Ornithological Society, Lawrence, Kansas.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Yahner, R. H. and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. Journal of Wildlife Management 52: 158-161.

Yin, Y. and J. C. Nelson. 1995. Modifications to the Upper Mississippi River and their effects on floodplain forests. Long Term Resource Monitoring Program technical report 95-TOO3. National Biological Service, Environmental Management Technical Center, Onalaska, Wl. 17 pp.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice Hall, Englewood Cliffs, NJ. 718 pp.

Table 1. Eigenvectors for principal components derived from landscape and vegetation variables. Variables are described in Methods.

	Principal components			
	M1	M2	M3	M4
Landscape variables				
FOREST	0.56	-0.15	0.11	0.08
SHAPE INDEX	0.35	0.21	-0.14	-0.55
CORE AREA	0.48	-0.31	0.09	0.31
WATER	-0.51	-0.24	0.16	-0.32
AQUATIC VEGETATION	-0.08	0.33	-0.65	0.45
HERBACEOUS VEGETATION	0.23	0.46	0.26	-0.29
DISTURBED LAND	-0.12	0.19	0.66	0.45
DIVERSITY INDEX	-0.03	0.65	0.12	0.07
Eigenvalue	2.85	1.85	1.34	0.91
Variance explained (°70)	35.60	23.16	16.75	11.33

	Principal components			
	V1	V2	V3	V4V5
Vegetation variables				
DISTANCE TO TREES	0.34	-0.33	0.18	0.24-0.04
DISTANCE TO SAPLINGS	0.41	-0.04	-0.32	-0.070.28
DISTANCE TO SNAGS	0.12	0.33	0.47	-0.01-0.33
SAPLING DBH	0.12	0.19	-0.51	-0.390.05
TREE DBH	0.48	-0.17	0.07	0.060.01
SNAG DBH	0.32	0.22	0.12	-0.11-0.54.
TREE HEIGHT	0.32	0.02	0.01	0.560.27
CANOPY COVER	-0.25	0.40	-0.14	0.280.06
HERB COVER	0.02	0.48	0.36	-0.060.39
SHRUB COVER	-0.40	-0.22	0.09	0.350.06
NETTLE COVER	0.17	0.47	-0.17	0.290.13
GRASS COVER	0.05	-0.09	0.43	-0.410.52
Eigenvalue	3.13	2.17	1.70	1.411.09
Variance explained (°Io)	26.05	18.07	14.18	11.799.06

Table 2. Interpretation of principal components (PC) derived from landscape and vegetation variables.

PC		Interpretation
Landscape	M 1	High percentage forest cover and core area; little water cover; patches irregular
	M 2	High cover diversity; high percentage herbaceous and aquatic vegetation
	M 3	High percentage disturbed and herbaceous vegetation; little aquatic vegetation
	M 4	High percentage disturbed and aquatic vegetation, patches square with high core area
Vegetation	V 1	Mature, open-canopy forest; large, tall trees and snags; few saplings; few shrubs
	V 2	Early successional, closed-canopy forest; small trees; large saplings; nettles
	V 3	Mid-successional, open-canopy forest; medium trees; frequent, small saplings; grass
	V 4	Closed canopy forest; well-developed shrub understory; sparse herbs
	V 5	Closedly spaced, medium trees; frequent, small snags; few saplings; grass

Table 3. Habitat models generated by stepwise regression analysis. All habitat variables in the models have $P < 0.05$ (*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$). (-) indicates a negative relationship.

Common name	N (a)	Model	Model r-sq. (b)	Matrix r-sq. (c)
Great Blue Heron	40	V1*	0.08	0.08
Green-backed Heron	2	Vl(-)*	0.08	0.00
Canada Goose	2	Nothing significant		
Wood Duck	35	M4**	0.11	0.11
Mallard	16	Ml(-)**	0.11	0.11
Hooded Merganser	2	V2(-)*** + V1*	0.22	0.00
Bald Eagle	6	M2**	0.12	0.12
Red-shouldered Hawk	5	Nothing significant		
Soya	2	V4(-)***	0.15	0.00
Killdeer	3	Nothing significant		
American Woodcock	2	Nothing significant		
Mourning Dove	25	V3***	0.20	0.00
Black-billed Cuckoo	4	Nothing significant		
Yellow-billed Cuckoo	34	Ml*** + V2(-)**	0.28	0.16
Barred Owl	6	Nothing significant		
Chimney Swift	13	Ml*** + M4(-)**	0.24	0.24
Ruby-Hummingbird	13	M2(-)** + V2* + V1*	0.25	0.12
Belted Kingfisher	8	Nothing significant		
Red headed Woodpecker	30	Vl*	0.09	0.00
Redbellied Woodpecker	52	Vl*	0.07	0.00
Yellow-bellied Sapsucker	54	Ml***	0.33	0.33
Downy Woodpecker	54	V2***	0.17	0.00
Hairy Woodpecker	44	Ml***	0.15	0.15
Northern Flicker	48	V4(-)*	0.08	0.00
Pileated Woodpecker	16	V2** + V4*	0.21	0.00
Eastern Wood-Pewee	55	V4** + V3* + V2* + V 1()*	0.33	0.00
Acadian Flycatcher	6	M4*	0.09	0.08
Least Flycatcher	12	M4**	0.13	0.13
Fastem Phoebe	3	Nothing significant		
Great Crested Flycatcher	54	M3(-)** + V3* + M2*	0.28	0.18
Eastern Kingbird	3	Nothing significant		
Purple Martin	2	Nothing significant		
Tree Swallow	44	V2(-)***	0.15	0.00

(a) N = # plots. Only species occur ing on 2 or more plots are shown.
(b) Model r-square is the coefficient of determination for the entire regression model.
(c) Matrix r-square shows the proportion of variation explained by only the landscape variables.

Table 3 continued.

Common name	N (a)	Model	Model r-sq. (b)	Matrix r-sq. (c)
Blue Jay	46	Nothing significant		
American Crow	46	V5(-)** + V2*	0.20	0.00
Black-capped Chickadee	50	Nothing significant		
Tufted Titmouse	2	Nothing significant		
White-breasted Nuthatch	52	Vl***	0.23	0.00
Brown Creeper	33	V1***	0.24	0.00
Carolina Wren	6	Nothing significant		
House Wren	5.5	V4(-)*	0.10	0 00
Blue-gray Gnatcatcher	52	V1* + V2(-)*	0.18	0.00
Veery	16	Nothing significant		
WoodThrush	6	Nothing significant		
American Robin	55	Nothing significant		
Gray Catbird	50	V 1(-)** + V3**	0.25	0.00
Brown Thrasher	2	M2(-)***+Ml(-)*+V3*	0.31	0.23
Cedar Waxwing	10	Ml(-)* + V4(-)*	0.17	0.09
European Starling	11	Ml(-)***	0.15	0.15
Yellow-throated Vireo	45	V4* + V1*	0.15	0.00
Warbling Vireo	50	V2(-)*** +Ml(-)*	0.27	0.07
Red-eyed Vireo	46	M4*	0 08	0 08
Yellow Warbler	37	V3*	0.11	0.00
Cendean Warbler	11	Nothing significant		
American Redstart	52	V4**	0.12	0.00
Prothonotary Warbler	49	V2(-)*** + V1*** + V3(-)**	0.57	0.00
Ovenbird	10	V4*	0.09	0.00
Common Yellowthroat	46	V3** + M3(-)**	0.22	0.11
Scarlet Tanager	5	Nothing significant		
Northern Cardinal	53	V3*** + V2**	0.25	0.00
Rose-breasted Grosbeak	38	Nothing significant		
Indigo Bunting	17	Ml** + M3*	0.18	0.18
Field Sparrow	3	V4(-)** + M3(-)** + M4**	0.33	0.21
Song Sparrow	53	M4** + V2(-)* + V4(-)*	0.26	0.12
Swamp Sparnnv	2	Nothing significant		
Red winged Blackbird	49	Ml(-)*** +M3(-)**	0.33	0.33
Common Grackle	55	M2(-)* + M4(-)* + V2(-)*	0.28	0.14
Brown-headed Cowbird	52	Nothing significant		
Northern Oriole	54	M4(-)*	0.09	0.09
American Goldfinch	44	Ml(-)*** + M4**	0.25	0.25

Table 4. Habitat models for abundance within bird classifications generated by stepwise regression analysis. All habitat variables have $P < 0.05$ (*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$). (-) indicates a negative relationship.

Class	Sub-class	Model	Model r-sq. (a)	Matrix r-sq. (b)
	Total density, all classes	Nothing significant		
Winter distribution	Resident	V5(-)*	0.08	0.00
	Temperate migrant	Nothing significant		
	Neotropical, widespread	Nothing significant		
	Neotropical, intermediate	V4***	0.17	0.00
	Neotropical, local	M2** + V2(-)* + Vl* + M3(-)*	0.37	0.20
Population status	Stable, increasing	V1*** +M4*	0.31	0.06
	Mixed	V4** + M4** + V5(-)*	0.28	0.11
	Decreasing	Ml(-)***	0.21	0.21
Management status	Low	V5(-)*	0.09	0.00
	Medium	V4***	0.14	0.00
	High	V1*** + V2(-)*	0.25	0.00
Habitat preference	Interior forest	V4***	0.17	0.00
	Intetior-edge	V1***	0.22	0.00
	Edge	Ml(-)***	0.15	0.15
	Near water	M4* + V2(-)* + V3*	0.25	0.09
Territory size	< 2 ha	V2(-)***	0.14	0.00
	2-5 ha	Nothing significant		
	>5ha	V1***+V5(-)*	0.29	0.00
Nesting location	Ground	M4** + M3(-)** + V4(-)* + V31	0.34	0.20
	Lower canopy	Ml(-)* + V4* + M4*	0.23	0.16
	Upper canopy	Nothing significant		
	Hole	V1***+M2*	0.45	0.06
	Other	Nothing significant		
Foraging guild	Carnivore	V5(-)*	0.08	0.00
	Piscivore	V1*	0.09	0.00
	Ground gleaner	Ml(-)***	0.24	0.24
	Lower canopy gleaner	V1 * + V2(-)*	0.18	0.00
	Upper canopy gleaner	V4**	0.11	0.00
	Air hawker	V3** + M3(-)**	0.23	0.11
	Bark gleaner	Ml *** + V1** + V2*	0.55	0.45

(a) Model r-square is the coefficient of determination for the entire regression model.
(b) Matrix r-square shows the proportion of variation explained by only the landscape variables, as determined by the regression model.

Table 5. Habitat models for species richness overall and by classification generated by stepwise regression analysis. All habitat variables have P < 0.05 (*P < 0.05; **P < 0.01; ***P < 0.005). (-) indicates a negative relationship.

Class	Sub-class	Model	Model r-sq. (a)	Matrix r-sq. (b)
Species richness	Jackknife estimate	M2*** + Ml***	0.37	0.37
	Raw richness	M1*** + M2** + V 1*	0.55	0.51
Winter distribution	Resident	V1 *** + V2***	0.46	0.00
	Temperate migrant	V4(-)*	0.10	0.00
	Neotropical, widespread	Ml** + V3*	0.19	0.13
	Neotropical, intermediate	Ml***	0.21	0.21
	Neotropical, local	V1*** + V4*	0.24	0.00
Population status	Stable, increasing	Ml*** + M4**	0.32	0.32
	Mixed	Ml*** + M2*	0.33	0.33
	Decreasing	V1 * * *	0.18	0.00
Management status	Low	V1 *** + M4*	0.31	0.07
	Medium	Ml***	0.17	0.17
	High	Ml*** + V1*	0.31	0.26
Habitat preference	Interior forest	V1*** + V4*** + Ml*	0.47	0.05
	Interior-edge	Ml*** + V1*	0.44	0.38
	Edge	M4** + M2*	0.22	0.22
	Near water	M2*	0.08	0.08
Territory size	< 2 ha	Ml** + M4* + M2*	0.26	0.26
	2-5 ha	Ml***	0.27	0.27
	> 5 ha	V1***	0.30	0.00
Nesting location	Ground	Nothing significant		
	Lower canopy	V3*** + Ml*	0.23	0.08
	Upper canopy	V1 * * *	0.22	0.00
	Hole	V1***	0.55	0.00
	Other	Nothing significant		
Foraging guild	Carnivore	Nothing significant		
	Piscivore	Nothing significant		
	Ground gleaner	V3***	0.14	0.00
	Lower canopy gleaner	M1***	0.23	0.23
	Upper canopy gleaner	Ml***	0.14	0.14
	Air hawker	V1 **	0.11	0.00
	Bark gleaner	V1*** + V2***	0.57	0.00

(a) Model r-square is the coefficient of determination for the entire regression model.
(b) Matrix r-square shows the amount o' variation explained by only the landscape variables, as determined from the regression model.

Table 6. R-square values and F statistics for differences in means among clusters. Variables described in Methods.

	r-sqr.	F	P > F
Landscape variables			
FOREST	0.67	54.33	0.0001
SHAPE INDEX	0.13	3.90	0.0263
CORE AREA	0.54	30.83	0.0001
WATER	0.58	36.76	0.0001
AQUATIC VEGETATION	0.13	3.99	0.0244
HERBACEOUS VEGETATION	0.21	7.09	0.0019
DISTURBED LAND	0.10	2.77	0.0715
DIVERSITY INDEX	0.40	17.38	0.0001
Vegetation variables			
DISTANCE TO TREES	0.09	2.47	0.0945
DISTANCE TO SAPLINGS	0.38	16.46	0.0001
DISTANCE TO SNAGS	0.00	0.04	0.9616
SAPLING DBH	0.27	9.65	0.0003
TREE DBH	0.25	8.69	0.0005
SNAG DBH	0.21	7.13	0.0018
TREE HEIGHT	0.11	3.42	0.0402
CANOPY COVER	0.04	1.08	0.3454
HERB COVER	0.08	2.19	0.1217
SHRUB COVER	0.48	24.64	0.0001
NETTLE COVER	0.28	10.13	0.0002
GRASS COVER	0.09	2.67	0.0788

Table 7. Total canonical correlations with vegetation and landscape variables. Variables described in Methods.

	Canl	Cant
Landscape variables		
FOREST	0.87	0.17
SHAPE INDEX	0.37	-0.13
CORE AREA	0.72	0.35
WATER	-0.79	0.24
AQUATIC VEGETATION	-0.05	-0.40
HERBACEOUS VEGETATION	0.19	-0.48
DISTURBED LAND	-0.19	-0.29
DIVERSITY INDEX	-0.07	-0.70
Vegetation variables		
DISTANCE TO TREES	0.23	-0.22
DISTANCE TO SAPLINGS	0.67	0.00
DISTANCE TO SNAGS	-0.03	0.03
SAPLING DBH	0.54	0.14
TREE DBH	0.46	-0.29
SNAG DBH	0.41	-0.30
TREE HEIGHT	0.35	-0.11
CANOPY COVER	-0.09	0.20
HERB COVER	0.25	0.17
SHRUB COVER	-0.64	0.41
NETTLE COVER	0.57	-0.02
GRASS COVER	-0.03	-0.34
Eigenvalue	5.85	3.75
Variance explained (%)	60.90	39.10

Table 8. Differences in relative abundance (individuals per point) among clusters for bird species.

Common name (a)	N (b)	LARGE (c)			DIVERSE		SHRUB	
Green-backed Heron**	2	0.00	(0.00)	B	0.00 (0.00)	B	0.02 (0.01)	A
Mallard*	16	0.00	(0.02)	B	0.06 (0.01)	A	0.05 (0.02)	AB
Yellow-billed Cuckoo*	34	0 .14	(0.03)	A	0 .11 (0.02)	AB	0.02 (0.03)	B
Chimney Swift***	13	0.06	(0.01)	A	0.01 (0.01)	B	0.01 (0.01)	B
Ruby-throated Hummingbird*	13	0.04	(0.01)	A	0.01 (0.01)	B	0.01(0.01)	AB
Red-bellied Woodpecker*	52	0.39	(0.04)	A	0.34 (0.03)	AB	0 .21 (0.05)	B
Yellow-bellied Sapsucker***	54	0.77	(0.07)	A	0.49 (0.05)	B	0.35 (0.08)	B
White-breasted Nuthatch*	52	0.51	(0.06)	A	0.42 (0.04)	AB	0 .26 (0.07)	B
Brown Creeper*	33	0 .14	(0.02)	A	0.07 (0.02)	AB	0.04 (0.03)	B
Wood Thrush*	6	0.01	(0.01)	AB	0.00 (0.01)	B	0.03 (0.01)	A
Gray Catbird**	50	0.29	(0.08)	B	0.41 (0.06)	B	0.73 (0.10)	A
Brown Thrasher**	2	0 . 0 0	(0.01)	B	0 .00 (0.01)	B	0 . 0 3 (0.01)	A
Cedar Waxwing*	10	0.01	(0.01)	B	0.01 (0.01)	AB	0.06 (0.02)	A
Red-winged Blackbird**	49	0 .26	(0.02)	B	0 .62 (0.09)	A	0.79 (0.15)	A
American Goldfinch*	44	0 .07	(0.04)	B	0 .17 (0.03)	AB	0 .22 (0.08)	A

(a) Significance level of overall general linear model (*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$).
(b) Number of plots on which species occurred.
(c) Abundances (S. E.) with different letters within rows are statistically different ($P < 0.05$).
LARGE = LARGE FOREST, DIVERSE = DIVERSE FOREST, SHRUB = SHRUB FOREST.

Table 9. Differences in relative abundance (individuals per point) among clusters for bird classifications.

Class	Sub-class (a)	LARGE (b)		DIVERSE		SHRUB	
Total abundance (all species)		15.75 (0.70)	A	16.59 (0.52)	A	16.18 (0.88)	A
Winter distribution	Resident	3.91 (0.28)	A	4.12 (0.21)	A	4.40 (0.35)	A
	Temperate migrant	3.14 (0.29)	A	3.31 (0.21)	A	3.02 (0.36)	A
	Neotropical, widespread	3.94 (0.30)	A	4.06 (0.22)	A	3.87 (0.37)	A
	Neotropical, intermediate	2.65 (0.19)	A	2.81 (0 .14)	A	2.92 (0.24)	A
	Neotropical, local	2 .10 (0 .15)	A	2 . 2 7 (0.11)	A	1.97(0.19)	A
Population status	Stable, increasing	6.76 (0.31)	A	6.57 (0.23)	A	5.70 (0.39)	A
	Mixed	4.98 (0.30)	A	5.40 (0.22)	A	5.11 (0.38)	A
	Decreasing*	3.24 (0.39)	B	4.11 (0.29)	AB	5.02 (0.49)	A
Management status	Low	8.53 (0.44)	A	8.90 (0.32)	A	8.87 (0.55)	A
	Medium	4.62 (0.38)	A	4.94 (0.28)	A	4.95 (0,48)	A
	High	2.60 (0.16)	A	2.74 (0.12)	A	2.35 (0.21)	A
Habitat preference	Interior forest	2.53 (0.28)	A	2.49 (0.21)	A	2.52 (0.36)	A
	Interior-edge	6.67 (0.28)	A	6.60 (0.21)	A	5.59 (0.35)	A
	Edge	6.27 (0.45)	A	7.12 (0.33)	A	7.82 (0.57)	A
	Near water	0.28 (0.07)	A	0.37 (0.05)	A	0.24(0.09)	A
Territory size	< 2 ha	9 .16 (0.61)	A	10 .10 (0.46)	A	9.96 (0.78)	A
	2-5 ha	4.54 (0.23)	A	4.57 (0.17)	A	4.69 (0.29)	A
	> 5 ha	2.05 (0.14)	A	1.91 (0.10)	A	1.52 (0.18)	A
Nesting location	Ground	1.30 (0.17)	A	1.22 (0.13)	A	1.01 (0.22)	A
	Lower canopy	3.42 (0.36)	A	4.21 (0.27)	A	4.65 (0.45)	A
	Upper canopy	4.79 (0.42)	A	5.16 (0.31)	A	5.64 (0.53)	A
	Hole"	5.87 (0.28)	A	5.54 (0.20)	A	4.43 (0.35)	B
	Other	0.37 (0.07)	A	0.44 (0.05)	A	0.44 (0.09)	A
Foraging guild	Carnivore	0.02 (0.01)	A	0.02 (0.01)	A	0.01 (0.01)	A
	Piscivore	0 .16 (0.04)	A	0 .17 (0.03)	A	0 .10 (0.05)	A
	Ground gleaner***	2.51 (0.29)	B	3.50 (0.22)	A	4.51 (0.37)	A
	Lower canopy gleaner	6.87 (0.41)	A	6.88 (0.31)	A	5.67 (0.52)	A
	Upper canopy gleaner	2.25 (0.19)	A	2.41 (0.14)	A	2.42 (0.24)	A
	Air hawker	1.56 (0.13)	A	1.83 (0.09)	A	1.94 (0.16)	A
	Bark gleaner***	2.30 (0.12)	A	1.76 (0.09)	B	1.21(0.15)	C

(a) Significance level of overall general linear model (*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$).

(b) Abundances (S.E.) with different letters within a row are statistically different ($P < 0.05$).

LARGE = LARGE FOREST, DIVERSE = DIVERSE FOREST, SHRUB = SHRUB FOREST.

79

Table 10. Differences in species richness among clusters for bird classifications.

Class	Sub-class (a)	LARGE (b)	DIVERSE	SHRUB
Total richness	Jackknife estimate***	35.78 (1.27) A	35.06 (0.97) A	29.15 (1.66) B
	Raw richness***	29.16 (0.68) A	27.06 (0.52) A	22.63 (0.89) B
Winter distribution	Resident***	9.19 (0.36) A	8.57 (0.27) A	6.83 (0.45) B
	Temperate migrant	4.79 (0.26) A	4.76 (0.19) A	4.62 (0.33) A
	Neotropical, widespread	3.13 (0.17) A	2.86 (0.13) A	2.60 (0.22) A
	Neotropical, intermediate*	5.71 (0.29) A	5.43 (0 .22) AB	4.50 (0.37) B
	Neotropical,local	3.06 (0.13) A	2.82 (0.10) A	2.55 (0.17) A
Population status	Stable, increasing"	11.25 (0.42) A	10.24 (0.31) AB	9.08 (0.53) B
	Mixed***	7.20 (0.26) A	6.86 (0.19) A	5.65 (0.33) B
	Decreasing	6.44 (0.26) A	6.47 (0.19) A	5.62 (0.33) A
Management status	Low"	15.31 (0.51) A	14.61 (0.38) A	12.75 (0.64) B
	Medium*	5.81 (0.25) A	5.60 (0.19) AB	4.80 (0.32) B
	High"	4.75 (0.24) A	4.24 (0.18) AB	3.55 (0.30) B
Habitat preference	Interior forest***	2.65 (0.18) A	1.98 (0.13) B	1.70 (0.22) B
	Interior-edge***	12.94 (0.43) A	11.79 (0.32) A	9.43 (0.54) B
	Edge	9.40 (0.36) A	9.74 (0.27) A	9.10 (0.45) A
	Near water	0.90 (0.14) A	0.94 (0.10) A	0.87 (0.17) A
Territory size	< 2 ha	12.10 (0.44) A	11.86 (0.32) A	10.47 (0.55) A
	2-5 ha**	8.81 (0.32) A	8.17 (0.24) AB	7.18 (0.41) B
	> 5 ha***	4.96 (0.26) A	4.41 (0.19) A	3.45 (0.33) B
Nesting location	Ground	1.96 (0.17) A	1.85 (0.13) A	1.70 (0.22) A
	Lower canopy	4.29 (0.23) A	4.51 (0.17) A	4.08 (0.29) A
	Upper canopy*	8.94 (0.30) A	8.50 (0.22) AB	7.68 (0.37) B
	Hole***	9.83 (0.35) A	8.73 (0.26) B	6.87 (0.45) C
	Other	0.85 (0.09) A	0.85 (0.06) A	0.77 (0.11) A
Foraging guild	Carnivore	0.13 (0.04) A	0.06 (0.03) A	0.07 (0.05) A
	Piscivore	0.54 (0.10) A	0.48 (0.07) A	0.45 (0.12) A
	Ground gleaner	5.31 (0.30) A	5.71 (0.22) A	5.65 (0.38) A
	Lower canopy gleaner***	7.50 (0.29) A	7.03 (0 .21) A	5.88 (0.36) B
	Upper canopy gleaner*	4.75 (0.23) A	4.50 (0.17) AB	3.78 (0.29) B
	Air hawker	2.75 (0.14) A	2.57 (0.11) A	2.53 (0.18) A
	Bark gleaner***	4.90 (0.22) A	4.09 (0.16) B	2.73 (0.28) C

(a) Significance of overall general linear model (*P < 0.05; **P < 0.01; ***P < 0.005).

(b) Species richness values (S.E.) with different letters within rows are statistically different (P < 0.05). LARGE = LARGE FOREST, DIVERSE = DIVERSE FOREST, SHRUB = SHRUB FOREST.

Table 11. Birds identified as area-sensitive in this and other studies conducted in the Eastern or Midwestern U.S.

Common name	N (a)	This study (b)	Other studies (c)
Yellow-billed Cuckoo	34	M1***, LARGE*	B, W, R
Chimney Swift @	13	M1***, LARGE***	
Ruby-throated Hummingbird	13	LARGE*	B
Red-bellied Woodpecker	52	LARGE*	B, R, S
Yellow-bellied Sapsucker	54	M1***, LARGE***	
Downy Woodpecker	54		B
Hairy Woodpecker	44	M1***	B, W, R
Pileated Woodpecker	16		T, W, R
Eastern Wood-Pewee	55		A
Acadian Flycatcher	6		T, B, W, R
Least Flycatcher	12		T
Great Crested Flycatcher	54.		B, R
Blue Jay	45		R
American Crow	46		R
Black-capped Chickadee	50		B
Tufted Titmouse	2		T, B, R, S
White-breasted Nuthatch	52	LARGE*	W, R
Brown Creeper	33	LARGE*	B
Blue-gray Gnatcatcher	52		T, W, R, B, S
Veery	16		T, R, B
Wood Thrush	6		T, H, B, W, R, S
Yellow-throated Vireo	45		T, W, E
Warbling Vireo	50		S
Red-eyed Vireo	46		B, W, R, L, A
Cerulean Warbler	11		T, R, B
American Redstart	52		T, W, B, S
Prothonotary Warbler	49		W
Ovenbird	10		T, H, W, R, B, S
Scarlet Tanager	5		T, B, W, R, A, S
Northern Cardinal	53		B
Rose-breasted Grosbeak	38		R, A, B
Indigo Bunting Q	17	Ml*	B (-), R(-)
Red-winged Blackbird	49		B
Brown-headed Cowbird	52		B

@ Area-sensitivity may be spurious due to coincidental association with other habitat features.

(a) Number of plots species were identified from in this study.

(b) Area-sensitive as indicated by step-wise regression (M1) or cluster analysis (LARGE FOREST) (*P < 0.05; **P < 0.01; ***P < 0.005).

(c) Area-sensitive as indicated by other studies in the Eastern or Midwestern U.S.: A = Ambuel & Temple 1983; B= Blake & Karr 1984, 1987; E = Emlen, et al. 1986; H = Hayden, et al. 1985; L = Lynch & Whigham 1984, R= Robbins, et a1. 1989; S = Stauffer & Best 1980; T = Temple 1986; W = Whitcomb, et al. 1981.

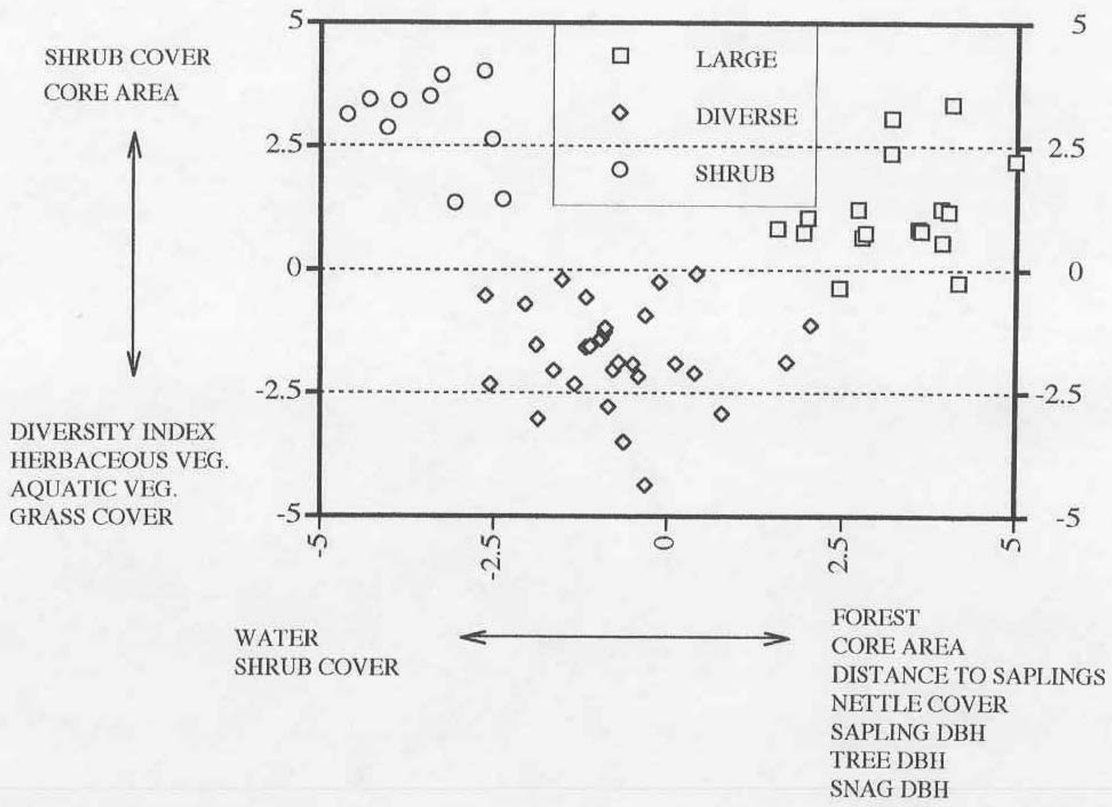

Figure 1. Clusters of plots based on two canonical (Can) variables. Variables described in Methods. LARGE = LARGE FOREST, DIVERSE = DIVERSE FOREST, SHRUB = SHRUB FOREST.

Appendix. Management risk categories and guild associations of Upper Mississippi River birds.

Family	Common name	Scientific name	N (a)	Winter (b)	Pop (c)	Status (d)	Habitat (e)	Territory (f)	Nesting (g)	Foraging (h)
Ardeidae	Great Blue Hers	Ardea herodias	40	T	S	L	W	L	UC	P
	Great Egret	Casmerodius albus	1	T	S	L	W	L	UC	P
	Green-backed Heron	Butaides striates	2	T	M	L	W	L	UC	P
Anatidae	Canada Goose	Branta canadensis	2	T	S	L	W	L	G	G
	Wood Duck	Aix sponsa	35	T	S	L	W	L	H	G
	Mallard	Anus platyrhynchos	16	T	S	L	W	L	G	G
	Hooded Merganser	Lophodytes cucullatus	2	T	ND	L	W	L	H	P
Accipitridae	Bald Eagle	Haliaeetus leucocephalus	6	R	M	H	W	L	UC	P
	Red-shouldered Hawk	Buteo lineatus	5	R	M	H	I	L	UC	C
Rallidae	Sara	Porzana caroling	2	T	M	L	W	S	O	G
Charaddidae	Killdeer	Charadrius vociferus	3	T	S	L	E	S	G	G
Scolopaadae	American Woodcock	Scolopax minor	2	T	D	L	E	M	G	G
Columbidae	Mourning Dove	Zenaida macroura	25	R	M	L	E	M	UC	G
Cuculidae	Black-billed Cuckoo	Coccyzus erythropthalmus	4	NL	M	H	IE	M	LC	LC
	Yellow-billed Cuckoo	Coccyzusamericanus	35	NJ	D	H	IE	M	LC	LC
Strigidw	Great Homed Owl	Bubo virginianus	1	R	S	L	fE	L	UC	C
	Barred Owl	Shix varia	6	R	S	L	I	L	H	C
Apodidae	Chimney Swift	Chaetura pelagica	13	NJ	D	M	E	S	H	A
Trochilidae	Ruby throated Hummingbird	Archilochus colubris	13	NJ	S	M	is	M	UC	LC
Alcedinidae	Belted Kingfisher	Ceryle alcyon	8	T	M	L	W	L	O	P
Picidae	Red-headed Woodpecker	Melanerpes erythrocephalus	31	R	D	L	IE	L	H	B
	Red-bellied Woodpecker	Melanerpescaralinus	52	R	S	L	fE	L	H	B
	Yellow-bellied Sapsucker	Sphyrapicus varies	55	T	ND	L	IE	M	H	B
	Downy Woodpecker	Picoidespubescems	55	R	M	L	IE	M	H	B
	Hairy Woodpecker	Picoides villosus	45	R	S	L	I	L	H	B
	Nortitem Flicker	Colaptes aerates	48	R	D	L	IE	M	H	B
	Pileated Woodpecker	Dryocopus pileatus	16	R	S	L	I	L	H	B
Tyrannidae	Eastern Wood-Pewee	Contopus vireos	56	NL	D	H	IE	M	UC	A
	Acadian Flycatcher	Empidonax virescens	6	NL	D	H	I	S	UC	A
	Least Flycatcher	Empidonax minimus	12	NJ	D	M	E	S	UC	A
	Eastern Phoebe	Sayomis Phoebe	3	T	S	L	IE	S	O	A
	Great Crested Flycatcher	Myiarchus crinitus	SS	NL	M	H	IE	M	H	A
	Eastern IGngbird	Tyrarmus tyrannus	3	NJ	D	M	E	M	LC	A
Hirundinidae	Purple Martin	Progne, subis	2	NJ	D	H	E	S	H	A
	Tree Swallow	Tachyaneta bicolor	44	T	M	L	E	S	H	A
Corvidae	Blue Jay	Cyanocitta cristata	46	R	D	L	IE	M	UC	UC
	American Crow	Corvus bractryrhynchos	46	R	S	L	E	L	UC	G
Paridae	Black-capped Chickadee	Pares atricapillus	Sl	R	M	L	IE	M	H	LC
	Tufted Titmouse	Pxivs bicolor	2	R	S	L	fE	M	H	LC
Sittidae	White-breasted Nuthatch	Sitta carolicunsis	53	R	M	L	IE	L	H	B
CeRhiidae	Brown Creeper	Certhia americana	34	R	S	L	I	M	H	B
Troglodytidae	Carolina Wren	Thryorhorus ludovicianus	8	R	S	L	IE	S	LC	LC
	House Wren	Troglodytes aedon	56	NW	S	L	E	S	H	LC

(a) Number of plots species was identified from
(b) Wintering distribution: R = resident; T = temperant migrant; NW = neotropical, widespread; NI = neotropical, intermediate; NL = neotropical, local.
(c) Population status: S = stable, increasing (Thompson, et al. 1993, categories 1 or 2); M = mixed (categories 3 or 4); D = decreasing (category 5); ND = no data.
(d) Management status: L = low (Thompson, et al. 1993, rank 1 - 1.99); M = medium (rank 2 - 2.99); H = high (rank 3 - 5.00).
(e) Habitat preference: I = interior forest; IE = interior-edge; E = edge; W = near water.
(f) Territory size: S = < 2 ha; M = 2-5 ha; L = > 5 ha.
(g) Nesting location: G = ground; LC = lower canopy; UC = upper canopy; H = hole; O = other.
(h) Foraging guild: C = carnivore (vertebrates other than fish); P = piscivore; G =ground gleaner, grazer, forager; LC =lower canopylshrub gleaner, hawker, forager; UC = upper canopy gleaner, hawker, forager; A = air hawker, saltier, screener; B = bark gleaner, excavator.

Appendix continued.

Family	Common name	Scientific name	N (a)	Winter (b)	Pop (c)	Status (d)	Habitat (e)	Territory (f)	Nesting ( )	Foraging (h)
Troglodytidae	Winter Wren	Troglodytes hrogIodytes	1	T	S	L	I	M	G	G
Muscicapidae	Blue-grey Gnatcatcher	Polioptila caerulea	53	NI	S	M	IE	S	UC	UC
	Eastern Bluebird	Sialia sialis	1	T	S	L	E	S	H	G
	Very	Catharus fuscescens	16	NI	D	H	I	S	G	G
	Wood Thrush	Hylocichla mustelina	6	NL	M	H	IE	S	LC	G
	American Robin	Tvrdus migratorius	56	T	S	L	E	S	UC	G
Mimidae	Gray Catbird	Dumetella carolinensis	50	NI	S	M	E	S	LC	G
	BrownThrasher	Toxostomarufum	2	T	D	L	E	M	G	G
Bombyallidae	Cedar Waxwing	Bombycilla cedronun	10	R	S	L	E	M	UC	A
Sturnidae	European Starling	Sturnus vutgads	11	R	D	L	E	S	H	G
Vireoitidae	Yellow-throated Vireo	Vireo tlavifroms	46	NI	S	H	IE	S	UC	UC
	Warbling Vireo	Vireo gilvus	Si	NI	D	M	IE	M	UC	UC
	Red-eyed Vireo	Vireo olivaceuu	47	NI	S	M	IE	S	UC	UC
Emberizidae	Yellow Warbler	Dendroicapetechia	37	NW	S	L	E	S	LC	LC
	Yellow-throated Warbler	Dendroicadominica	1	NI	S	M	IE	5	UC	UC
	Cerulean Warbler	Dendroica cerulea	11	NL	D	H	I	S	UC	UC
	American Redstart	Setophaga nrticdia	53	NW	M	M	I	S	LC	LC
	Prothonotary Warbler	Protonararia citrea	50	NL	S	H	IE	S	H	LC
	Ovenbird	Seiurus aurocapillus	10	NI	S	H	I	5	G	G
	Common Yellowthroat	Geothiypistrichas	47	NW	M	M	*E*	S	G	LC
	Scarlet Tanager	Pirangaolivacea	5	NL	S	H	1	M	UC	UC
	Northem Cardinal	Cardiimlis cardinatis	54	R	S	L	IE	S	LC	G
	Rose-breasted Grosbeak	Pheucticusludovicianus	38	NI	M	H	IE	M	UC	UC
	Indigo Bunting	Passerina cyanea	18	NI	D	M	E	M	LC	LC
	Rufous-sided Towhee	Pipiloerythnophthalmus	1	T	D	L	IE	M	LC	G
	Chipping Sparrow	Spizellapasserina	1	NW	S	L	*E*	*S*	*LC*	G
	Field Spanrnv	Spizella pusilla	3	T	D	L	E	S	G	G
	Song Sparrow	Melospizametodia	54	T	S	L	E	S	G	LC
	Swamp Sparrow	Melospiza georgiana	2	T	S	L	W	S	O	G
	Red-winged Blackbird	Agelaius phoeniceus	50	T	D	L	E	S	LC	G
	Common Grackle	Quiscalus quiscu)a	56	R	D	L	E	S	UC	G
	Brown-headed Cowbird	Molothrus atcr	53	R	M	L	E	L	O	G
	NoAhemOriole	Ictemsgalbuta	55	NI	D	M	E	M	UC	UC
Fringillidae	American Goldfinch	Carduelis tristis	44	R	M	L	E	S	LC	LC

CHAPTER 5. EFFECTS OF A MAJOR FLOOD ON THE BREEDING BIRD COMMUNITY OF LARGE FLOODPLAIN FORESTS

A paper to be submitted to the Auk

Melinda G. Knutson[1,2] and Erwin E. Klaas[1]

Abstract

We studied the effects of the 1993 flood on the bird community of Upper Mississippi River floodplain forests. We found that species richness did not differ among the plots tested, but abundance was lower in 1994 overall and for several individual species and species groups. Species with the strongest evidence of lowered abundance during flooding include the Blue Jay *(Cyanocitta cristata),* House Wren *(Troglodytes aedon),* Yellow Warbler *(Dendroica petechia),* Common Yellowthroat *(Geothlypis trichas),* Brown-headed Cowbird *(Molothrus ater),* and American Goldfinch *(Carduelis tristis).* For the Blue Jay, House Wren, and Common Yellowthroat, we present evidence that lowered abundance coincident with the flood persists into the following breeding season. These birds constitute a relatively small percentage of the total floodplain bird community. Relative abundances of most floodplain birds were little affected. Abundances of birds within management risk categories or guild associations did not show similar strong evidence of flood sensitivity. Not all flood effects were negative; some species increased in abundance on flooded plots, including the Cerulean Warbler *(Dendroica cerulea)* and White-breasted Nuthatch (*Sitta carolinensis).* Major flooding may maintain appropriate habitat for Prothonotary Warblers *(Protonotaria citrea)* in the face of nest-site competition from House Wrens.

Introduction

Few studies have examined habitat requirements of breeding birds of large floodplain forests (Emlen et al. 1986, Decamps et al. 1987) . Only one other study of Upper Mississippi River (UMR) floodplain forests and the associated bird community has been conducted

---

[1] Graduate student and Professor, respectively, Iowa State University, Department of Animal Ecology and National Biological Service, Iowa Cooperative Fish and Wildlife Research Unit, Ames, IA. Research conducted and manuscript written by Knutson with consultation from Klaas.

[2] Author for correspondence. Address after 1 September 1995: National Biological Service, Upper Mississippi Science Center, P.O. Box 2226, Lacrosse, WI 54601.

(Emlen et al. 1986). To our knowledge, no previous study has examined the effect of a major flood on breeding birds of large northern floodplain forests, although Hunter et al. (1987) showed major effects on the riparian bird community in Arizona from flooding that destroyed the birds' cottonwood-willow habitat.

In 1993, the UMR experienced major flooding, which extended over much of the breeding season. We took advantage of this natural experiment to examine flood effects. We tested the null hypothesis that a major flood does not change the relative abundance and species richness of birds nesting in large floodplain forests of the UMR. One might expect that a large flood would have a dramatic effect on birds nesting in floodplain forests, especially those nesting on or near the ground. Certainly, many species may delay nesting until flood waters recede. If flooding is prolonged, some species might abandon their territories in favor of drier sites in adjacent uplands. One way to examine effects of flooding is to compare counts of birds on flooded and unflooded plots. If the relative abundance of a species or group of species differs either between flooded and unflooded plots in the same year or among years, a likely explanation is the flood. We examined changes in relative abundance for bird species and groups of birds within management risk categories and guild associations and changes in species richness for the years 1992-1994. for plots that flooded in 1993. In addition, we examined similar changes for flooded and unflooded plots in 1993. We eliminated birds that differed on these plots before the flood, by testing for a similar difference in 1992. We looked for persistent changes by testing for differences in flooded and unflooded plots in 1994.

Study Area

The study area included forested habitat in Pools 6-10 of the UMR (NW UTM E602000, N4883000; SE UTM E660000, N4738000). (Chapter 3 gives details of study site location and selection. Chapter 2 describes the floodplain forest plant community.) Rainfall amounts on the UMR were 1.5 to 2 times higher than normal over the study area during spring and summer 1993 (Wahl et al. 1993) and river water levels were above normal throughout the breeding season (Parrett et al. 1993). A few plots were flooded early in the breeding season, however, most study plots remained under water for the rest of the breeding season, after 5 to 18 cm (2 to 7 inches) of rain fell throughout the region on 17-18 June (Wahl et al. 1993). Plots censused after these dates were traversed by boat (primarily canoe or kayak). Strong winds accompanied several storms, which affected the entire study area (Wahl et al. 1993). Thirty-four plots were under water during censuring in 1993 and 31 were above water.

Methods

In each study plot we counted birds at 3 to 10 points. We calculated the relative abundance of each species for each plot using the number of individuals of each species identified within SO m of the observer over a 10-minute period and summed 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.

We estimated species richness for each plot with a jackknife estimate from the program CAPTURE (White et al. 1978). The jackknife estimator has been shown to perform as well or better than other methods of estimation of species richness (Palmer 1990, Palmer 1991, Baltanas 1992, Bunge and Fitzpatrick 1993, Nichols and Conroy in press). The jackknife estimator has been used to estimate species richness in other studies (Derleth et al. 1989, Karr et al. 1990). Details of the method and equations are given in Swensen (1994) and Burnham and Overton (1979). We calculated an estimate of species richness rather than using raw counts (the total number of species identified by the observer on the plot) because all plots do not have the same number of point-counts. Plots with more point-counts are expected to have greater raw species richness (Karr et al. 1990, Palmer 1995). The model we used takes into account new species identified as additional points are censused and calculates an estimate of the total number of species present, including those not seen. A total of 84 bird species were included in the analysis.

We classified birds into groups based on guild associations and management risk categories to examine relationships between groups of species sharing common attributes and the habitat variables. We classified species into several guild, habitat association, and risk categories based on previous research and field observations in our study area (for scientific names and classifications see the Appendix). Species names follow the American Ornithologist's Union (1983). We grouped birds into foraging guilds based on De Graaf et al. (1985) and assigned nesting guild, territory size, and habitat preference categories according to published information (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, Poole and Gill 1992-5). When no data. on territory size for a species were available, data for closely-related taxa or body mass were used to estimate territory size (Schoener 1968, Dunning 1993). We assigned birds to categories of habitat preference based on published information and our own field observations (Whitcomb et al. 1981, Freemark and Merriam 1986, Thompson et al. 1993). Habitat preferences include birds found primarily within interiors of large forests, birds found both in forests and near edges (interior-edge), birds found primarily near edges, and birds found associated with water. We grouped birds into categories based on migration distances. Resident birds were defined as wintering in the study area; temperate migrants as wintering in the southern latitudes of the U.S. We divided neotropical migrants into groups based on wintering distributions given in $ellrose (1976), American Ornithologists' Union (1983), Hunter et al. (1993), and Thompson et al. (1993). Species with widespread neotropical winter distributions are considered at lower risk than those with very local distributions (Hunter et al. 1993, Thompson et al. 1993). We based population status on Breeding Bird Survey (BBS) trends in U.S. Fish and Wildlife Service Region 3 (includes MN, IA, MO, IL, WI, MI, IN, and OH) for 1966-1994 and 1980-1994 (BBS, unpublished data). Species with no significant population trend or increasing population trends were classified as stable or increasing (criterion 1 or 2: Thompson et al. 1993). Species that showed both an increase and a decrease for either long or short term trends (criterion 3 or 4: Thompson et al. 1993) were classified as having a mixed trend. Species that showed significant decreases both long and short-term (criterion 5: Thompson et al. 1993) were classified as decreasing. Species were classified into categories of management concern based on scores assigned by Thompson et al. (1993). Species with a mean overall score of 1-1.99 were classified as low, species with a score of 2 - 2.99 were classified as medium, species with a score of 3 - 5 were classified as high, and species not scored (resident or short-distance migrants and water birds) were classified as low unless they are listed as threatened, endangered, or of management concern by the U.S. Fish and Wildlife Service (Office of Migratory Bird Management 1987). The bald eagle and red-shouldered hawk were classified as high, according to this criterion. The relative abundance of birds within the above categories were used as dependent variables in the analysis.

We first tested for a flood effect by taking the subset of plots that flooded in 1993 and comparing the relative abundance (# of birds /point) of bird species on these plots with the relative abundance on the same plots in 1992 and 1994 (among years comparison, Figure 1). We made the same comparison for species richness and for relative abundance within managment risk categories and guild associations. Next, we made the same comparisons for the subset of plots that were not flooded at the time of censusing in 1993. To test for withinyear differences, we compared the relative abundance of bird species/categories and species richness on flooded and unflooded plots in 1993 (flooded vs. unflooded comparison, Figure 1). For groups that showed significant differences on flooded vs. unflooded plots, we made a similar comparison between these same plots in 1992, to eliminate groups with abundance differences existing prior to the flood. To identify abundance differences persisting into 1994, we compared relative abundances on flooded vs. unflooded plots in 1994.

We tested differences for species richness and relative abundance using the General Linear Models (GLM) procedure (SAS Institute Inc. 1989). We used the Bonferroni method to control the experiment-wise error (alpha:!-, 0.05) in the GLM analysis of relative abundance for each species. We used the non-parametric Kruskal-Wallis test (Za.r 1984, SAS Institute Inc. 1989) as an adjunct to GLM; the large number of zeros in the data set for uncommon species potentially violates the normal distribution assumption of GLM. However, this test did not detect more differences than GLM for rare species in our data set, so the results of the GLM analysis are reported. We show statistical differences at the S% level of significance, however, we tested a large number of species, increasing the probability of observing spurious significant differences. No clear guidelines are available for adjusting significance for a large number of comparisons without substantial loss of power to detect differences.

Results and discussion

Jackknife estimates of species richness did not differ among years (1992 = 33.6 [S.E. = 1.4], 1993 = 35.6 [S.E. = 1.4], 1994 = 34.0 [S.E. = 1.4]; F = 0.57; 2, 96 df; P = 0.57). Jackknife estimates of species richness between flooded and unflooded plots in 1993 also did not differ (flooded = 35.6 [S.E. = 1.6], unflooded = 34.2 [S.E. = 1.6]; F = 0.39; 1, 63 df; P = 0.54).

Total abundance for all species was higher in 1992 than 1994 (Table 1). Twenty species had significant ($P < 0.05$) differences in relative abundance among years for plots that flooded in 1993 (Table 1). Species that declined in abundance over the period, and may have been affected by deteriorating habitat conditions on flooded plots, include the Great Crested Flycatcher, Mourning Dove, Ruby-throated Hummingbird, Hairy Woodpecker, Northern Flicker, Eastern Wood-Pewee, Blue Jay, Black-capped Chickadee, Brown Creeper, House Wren, Yellow Warbler, Common Yellowthroat, Indigo Bunting, and American Goldfinch. The Brown-headed Cowbird had lower abundance in 1993 only. Several bird groups declined in abundance from 1992-1994, but birds that prefer water as a habitat increased (Table 1).

Total abundance for all species was higher in 1993 than 1994 (Table 2). Twentythree species had significant ($P < 0.05$) differences in relative abundance among years for plots that were not flooded at the time of censusing in 1993 (Table 2). Most species that had significant differences in abundance on both flooded and unflooded plots showed declining trends from 1992-94 (Tables 1 and 2), but the Great Blue Heron increased on both sets of plots. The Yellow Warbler and Common Yellowthroat had high abundances in 1993 on unflooded plots and low abundances on flooded plots, indicating they may have been displaced from adjacent flooded habitats onto these plots. For both these species, abundance was lower on both flooded and unflooded plots in 1994, indicating flood effects may have persisted into the following season. For the Song Sparrow, abundance increased on both sets of plots in 1993 and returned to 1992 levels in 1994. Again, this may indicate general displacement into any forested habitat, flooded or not, from adjacent habitats. Most bird groups with significant differences among years for unflooded plots also showed a general decline in relative abundance from 1992-1994, but birds preferring habitats associated with water increased over the period (Table 2). Ground nesters increased on unflooded plots in 1993, returning to 1992 levels in 1994. These birds may have been displaced from adjacent flooded habitats.

Total abundance for all species did not differ between flooded and unflooded plots in 1993 (Table 3). Twenty-two species had significant ($P < 0.05$) differences in relative abundance between flooded and unflooded plots in 1993 (Table 3). Fifteen species had lower relative abundance on flooded plots and 7 species had higher relative abundance on flooded plots. By comparing these differences with differences present in 1992, we can eliminate species that differed in abundance on these two sets of plots prior to the flood (Table 4). By this criterion, the Yellow-billed Cuckoo, Yellow-bellied Sapsucker, Gray Catbird, and Prothonotary Warbler probably differed in abundance due to pre-existing habitat differences in the two sets of plots. The Yellow-billed Cuckoo, Yellow-bellied Sapsucker, and Prothonotary Warbler apparently preferred the habitats that flooded while the Gray Catbird preferred the habitats that did not flood, even prior to the flood. Species with lower abundance on flooded plots only in 1993 and 1994 likely were affected by the flood with effects persisting into the year following the flood (Table 3). The Blue Jay, House Wren, Common Yellowthroat, and Northern Cardinal meet this criterion. The Rose-breasted Grosbeak would be included if an alpha level of 0.10 rather than 0.05 were used. The Common Grackle increased in abundance on flooded plots in both 1993 and 1994. Several bird groups showed declines in abundance on flooded plots in 1993, but these changes did not persist into 1994 (Tables 3 and 4). Bark foraging bird abundance increased on flooded plots in 1993 and this change persisted into 1994.

Sources of year-to-year variation in relative abundance on the same plots include fluctuation in bird populations not related to local habitat features and annual changes in habitat or climate. Sources of variation for a within-year comparison of two sets of plots include habitat variables that differ between the two plots and seasonal differences. Using both sets of criteria, we attempted to eliminate species and group differences that can be explained by these factors. Species with lower relative abundance among years for flooded plots and between flooded vs. unflooded plots in 1993 give the strongest evidence for sensitivity to flooding. These include the Blue Jay, House Wren, Yellow Warbler, Common Yellowthroat, Brown-headed Cowbird, arid American Goldfinch (Tables 1 and 2). For the Blue Jay, House Wren, and Common Yellowthroat we present evidence that lowered abundance coincident with the flood persists into the following breeding season (Table 3). No bird groupings show similar strong evidence of flood effects. For species and bird groups with lower abundance on flooded plots in 1993, based on either among-years or flooded vs. unflooded tests (but not both), we found less compelling evidence of flood sensitivity. The Cerulean Warbler and White-breasted Nuthatch increased in abundance on flooded plots both within 1993 and across years on flooded plots.

Bird species or groups might decline on flooded plots due to disruption of nesting habitat or loss of food resources. If flooding induces long-term habitat change, species or group changes in relative abundance persisting into the year following the flood are expected. We observed that some shrubs on our study plots were killed, probably due to extended inundation by flood waters. Sapling mortality was 7.2% and tree mortality 1.7% in Pool 8 the summer after the flood (Yin et al. 1994). Although flooding was extensive and of long duration over our study area, it was even more severe in southern Iowa, northern Missouri and Illinois. Tests of flood-induced changes in the bird community in these habitats would likely yield more dramatic results than ours. Other flood-sensitive species in our study may have responded to reduction of preferred food resources. Blue Jays and Brown-headed Cowbirds feed on the ground (De Graaf et al. 1985). These species are known nest predators and the Brown-headed Cowbird is a nest parasite; their decline during flooding may benefit other breeding songbirds in the floodplain, at least temporarily.

Other studies have shown that House Wrens and Prothonotary Warblers have different preferences for flooded forest habitat and the wrens frequently destroy prothonotary nests (Petit 1989, Brush 1994). Also, we recorded wren destruction of prothonotary nests with subsequent wren occupation of the cavities on our study plots (unpublished data). House Wren avoidance of the lowest elevation (frequently inundated) sites may allow prothonotaries to coexist when they occupy the same region (Brush 1994). We present evidence that House Wren abundances declined on inundated plots in 1993 and that these declines persisted into 1994. Prothonotary Warblers had higher abundances on the plots that flooded even before flooding, suggesting that these plots may be lower in elevation and subject to minor flooding even in years of normal rainfall. Periodic major flooding may maintain suitable floodplain habitat for Prothonotary Warblers in the face of stiff competition from House Wrens for nest sites.

Conclusion

Floodplains are dynamic habitats where flooding is a natural disturbance that sets back succession in some places while providing new sites for vegetative colonization (Peck and Smart 1986, Kupfer and Malanson 1993, Jones et al. 1994, Sparks 1995, Yin and Nelson 1995). Major floods can constitute a large-scale disturbance to the plant community and dramatically change the vegetative cover (Yin et al. 1994). The bird community must adapt to changes in the plant community, which provides major nesting and food resources. In addition, this regular disturbance regime may maintain habitat for some bird species that would be out-competed in drier, less disturbed habitats. We found that species richness did not differ among the plots tested, but abundance was lower in 1994 overall and for several species and species groups. Species with the strongest evidence of lowered abundance during flooding include the Blue Jay, House Wren, Yellow Warbler, Common Yellowthroat, Brown-headed Cowbird, and American Goldfinch. For the Blue Jay, House Wren, and Common Yellowthroat, we present evidence that lowered abundance coincident with the flood persists into the following breeding season.

Acknowledgements

Funding was provided by the National Biological Service (Patuxent Environmental Science Center, Branch of Migratory Birds Research), Iowa State University, U.S. Fish and Wildlife Service (Region 3 Nongame Program), and the Minnesota Department of Natural Resources Nongame Program. Ms. Knutson also was supported by a Cooperative Education Agreement with the Patuxent Center. Special thanks to Ms. Knutson's doctoral committee members Louis Best, Brent Danielson, Kirk Moloney, and Thomas Jurik. Field, office, and data management assistance were provided by Ingrid Moore, Brian Collins, Tom Pehowski, Vance Polton, Holly Dick, Pam Heidenreich, Mark Krom, Rebecca Peak, Julie Schreiber, Fredrick Keith, Jesse Audette, Brenda VanBeek, and Sara Handrick.

Literature Cited

American Ornithologists' Union. 1983. Check-list of North American Birds, 6th ed. Allen Press, Lawrence, KS. 877 pp.

Baltanas, A. 1992. On the use of some methods for the estimation of species richness. Oikos 65: 484-492.

Bellrose, F. C. 1976. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg, PA. 540 pp.

Blake, J. G. and J. R. Karr. 1984. Species composition of bird communities and the conservation benefit of large versus small forests. Bioi. Conserv. 30: 173-187.

Brush, T. 1994. Effects of competition and predation on prothonotary warblers and house wrens nesting in eastern Iowa. J. Iowa Aca.d. Sci. 101: 28-30.

Bunge, J. and M. Fitzpatrick. 1993. Estimating the number of species: a review. J. Am. Stat. Assoc. 88: 364-373.

Burnham, K. P. and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60: 927-936.

De Graaf, R. M., N. G. Tilghman and S. H. Anderson. 1985. Foraging guilds of North American birds. Environ. Manage. 9: 493-536.

Decamps, H., J. Joachim and J. Lauga. 1987. The importance for birds of the riparian woodlands within the alluvial corridor of the River Garonne, S. W. France. Reg. Riv. Res. Manage. 1: 301-316.

Derleth, E. L., D. G. McAuley and T. J. Dwyer. 1989. Avian community response to smallscale habitat disturbance in Maine. Can. J. Zool. 67: 385-390.

Dunning, J. B., Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL. 371 pp.

Ehrlich, P. R., D. S. Dobkin and D. Wheye. 1988. The birder's handbook. Simon & Schuster, Inc., New York. 785 pp.

Emlen, J. T., M. J. DeJong, M. J. Jaeger, T. C. Moermond, K. A. Rusterholtz and R. P. White. 1986. Density trends and range boundary constraints of forest birds along a latitudinal gradient. Auk 103: 791-803.

Freemark, K E. and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Conserv. 36: 115-141.

Hayden, T. J. and J. Faaborg. 1985. Estimates of minimum area requirements for Missouri forest birds. Trans. Missouri Acad. Sc. 19: 11-22.

Hunter, W. C., B. W. Anderson and R. D. Ohmart. 1987. Avian community structure changes in a mature floodplain forest after extensive flooding. J. Wildl. Manage. 51: 495-502.

Hunter, W. C., M. F. Carter, D. N. Pashley and K. Barker. 1993. The Partners in Flight species prioritization scheme. Pages 422 In D. M. Finch and P. W. Stangel, Eds. Status and management of neotropical migratory birds. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-229, Fort Collins, CO.

Jones, R. H., R. R. Sharitz, P. M. Dixon, D. S. Segal and R. L. Schneider. 1994. Woody plant regeneration in four floodplain forests. Ecol. Monogr. 64: 345-367.

Karr, J. R., S. K. Robinson, J. G. Blake and R. O. Bierregaard Jr. 1990. Birds of four neotropical forests. Pages 237-269 *In* A. H. Gentry, Eds. Four Neotropical Rainforests. Yale Univ. Press, New Haven, CT.

Kupfer, J. A. and G. P. Malanson. 1993. Observed and modeled directional change in riparian forest composition at a cutbank edge. Landsc. Ecol. 8: 185-200.

Nichols, J. D. and M. J. Conroy. in press. Estimation of species richness. Pages *In* D. S. Wilson, J. D. Nichols, R. Rudran and M. Foster, Eds. Handbook of methods for studying biodiversity of mammals. Smithsonian Inst. Press, Washington, D.C.

Office of Migratory Bird Management. 1987. Migratory nongame birds of management concern in the United States: the 1987 list. Wash., D.C. 27 pp.

Palmer, M. W. 1990. The estimation of species richness by extrapolation. Ecology 71:1195-1198.

Palmer, M. W. 1991. Estimating species richness: the second-order jackknife reconsidered. Ecology 72: 1512-1513.

Palmer, M. W. 1995. How should one count species? Nat. Areas J. 15: 124-135.

Parrett, C., N. B. Melcher and R. W. James Jr. 1993. Flood discharges in the Upper Mississippi River basin, 1993. U.S. Geolog. Surv. Circ., 14 pp.

Peck, J. H. and M. M. Smart. 1986. An assessment of the aquatic and wetland vegetation of the Upper Mississippi River. Hydrobiologia 136: 57-76.

Petit, L. J. 1989. Breeding biology of prothonotary warblers in riverine habitat in Tennessee. Wilson Bull. 101: 51-61.

Poole, A. and F. Gill. 1992-5. The birds of North America.: life histories for the 21st century. The American Ornithologists' Union and the Academy of Natural Sciences, Wash., DC and Philadelphia, PA. pp.

Robbins, C. S., D. K. Dawson and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildl. Monogr. 103: 1-34.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, 4th ed., vol. 2 SAS Institute, Inc. Cary, NC. 846 pp.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123-141.

Sparks, R. E. 1995. Need for ecosystem management of large floodplain rivers and their floodplains. BioScience 45: 168-182.

Swensen, A. R. 1994. Using capture-recapture methodology to estimate the number of bird species. Creative Component, M.S., Statistics. Iowa State Univ. 42 pp.

Thompson, F. R., S. J. Lewis, J. Green and D. Ewert. 1993. Status of neotropical migrant landbirds in the Midwest: identifying species of management concern. Pages 422 *In* D. M. Finch and P. W. Stangel, Eds. Status and management of neotropical migratory birds. USDA Forest Service, Rocky ,Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-229, Fort Collins, CO.

Wahl, K. L., K. C. Vining and G. J. Wiche. 1993. Precipitation in the Upper Mississippi River Basin, January 1 - July 31, 1993. US. Geolog. Surv. Circ., 13 pp.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-201 In B. R. L. and D. M. Sharpe, Eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY.

White, G. C., K. P. Burnham, D. L. Otis and D. R. Anderson. 1978. User's manual for program CAPTURE Utah State Univ. Press. Logan, UT. 40 pp.

Yin, Y. and J. C. Nelson. 1995. Modifications to the Upper Mississippi River and their effects on floodplain forests. Long Term Resource Monitoring Program technical report 95-T003. National Biological Service, Environmental Management Technical Center, Onalaska, WI. 17 pp.

Yin, Y., J. C. Nelson, G. V. Swenson, H. A. Langrehr and T. A. Blackburn. 1994. Tree mortality in the Upper Mississippi River and floodplain following an extreme flood in 1993. Pages 39-60 *In* J. W. Baxko and M. M. Wise, Eds. Long Term Resource Monitoring Program, 1993 flood observation report. National Biological Service, Illinois Natural History Survey, and Wisconsin Department of Natural Resources. Onalaska, WI.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice Hall, Englewood Cliffs, NJ. 718 pp-

Table 1. Differences in relative abundance (# birds/point) among years for flooded plots in 1993 (N[19921 = 31; N[19931 = 34; N[19941 = 34).

Species and categories (a)	1992 (b)	1993	1994
Total - all species"	18.23 (0.72) A	16.38 (0.69) AB	14.98 (0.69) B
Great Blue Heron *	0.05 (0.04) B	0.18 (0.04) AB	0.22 (0.04) A
Mourning Dove *	0.13 (0.03) A	0.05 (0.03) AB	0.01 (0.03) B
Ruby-throated Hummingbird *	0.06 (0.01) A	0.00 (0.01) B	0.02 (0.01) AB
Hairy Woodpecker**	0.20 (0.03) A	0.10 (0.03) B	0.08 (0.03) B
Northern FllCker***	0.28 (0.04) A	0.28 (0.04) A	0.05 (0.04) B
Eastern Wood-Pewee **	0. 65 (0.06) A	0. 64 (0.06) A	0. 43 (0.06) B
Tree Swallow *	0. 32 (0.07) AB	0. 10 (0.06) B	0. 33 (0.06) A
Blue Jay **	0.24 (0.04) A	0.18 (0.03) AB	0.09 (0.03) B
Black-capped Chickadee **	0.23 (0.04) AB	0.25 (0.04) A	0.09 (0.04) B
White-breasted Nuthatch ***@	0. 48 (0.06) A	0. 65 (0.06) A	0.25 (0.06) B
Brown Creeper***	0.26 (0.04) A	0.07 (0.03) B	0.04 (0.03) B
House Wren **	1.39 (0.10) A	1.14 (0.09) AB	0.96 (0.09) B
Yellow Warbler*	0.19 (0.04) A	0.05 (0.03) B	0.11 (0.03) AB
CeruleanWarbler*@	0.01 (0.02) AB	0.07 (0.02) A	0.01(0.02) B
Common Yellowthroat *	0.29 (0.05) A	0.20 (0.04) AB	0.11 (0.04)B
Indigo Bunting ***	0.14 (0.02) A	0.01 (0.02) B	0.01 (0.02) B
Song Sparrow ***	0.70 (0.10)B	1.14 (0.10) A	0.73 (0.10) B
Brown-headed Cowbird **	0.35 (0.06) AB	0.15 (0.06) B	0.39 (0.06) A
American Goldfinch **	0.21 (0.04) A	0.07 (0.04) B	0.04 (0.04) B
Wintering distribution, resident **	0.21 (0.02)A	0.17 (0.02) AB	0.14 (0.02) B
Management status, high *	0.20 (0.02) A	0.18 (0.02) AB	0.14 (0.02) B
Management status, low *	0.21 (0.01) A	0.19 (0.01) AB	0.17 (0.01) B
Habitat preference, interior-edge ***	0.2 (0.01) A	0.27 (0.01) A	0.21 (0.01) B
Habitat preference, water ***	0.01 (0.01) B	0.04 (0.01)A	0.06 (0.01) A
Territory size, 2-5 ha***	0.22 (0.01) A	0.20 (0.01) A	0.15 (0.01) B
Nesting location,hole ***	0.30 (0.02) A	0.27 (0.02) A	0.21 (0.02) B
Foraging guild, bark ***	0.30 (0.02) A	0.27 (0.02) A	0.19 (0.02)B

(a) Significance level of overall general linear model (*P < 0.05; **P < 0.01; ***P < 0.005). Underlines indicate species/categories with lowered abundance on flooded than on unflooded plots in 1993 (Table 3).

See Methods and Appendix for a description of management risk categories and guild associations.

(b) Mean relative abundances (S.E.) with different letters are statistically different (P < 0.05).

@ Increased in abundance on flooded vs. unflooded plots in 1993.

Table 2. Differences in relative abundance (# birds/point) among years for unflooded plots in 1993 (N[1992] = 29; N[1993] = 31; N[1994] = 31).

Species and categories (a)	**1992 (b)**	**1993**	**1994**
Total-all species***	16.11 (o.a7) AB	18.14 (0.84) A	13.71 (o.s4) B
Great Blue Heron **	0.02 (0.04) B	0.16 (0.03) A	0.16 (0.03) A
Mallard ***	0.01 (0.03) B	0.13 (0.03) A	0.03 (0.03) B
Ruby-throated Hummingbird **	0.03 (0.01) A	0.00 (0.01) B	0.00 (0.01) B
Red-headed Woodpecker***	0.14 (0.02) A	0.03 (0.02) B	0.02 (0.02) B
Red-bellied Woodpecker***	0.28 (0.06) B	0.49 (0.06) A	0.20 (0.06) B
Downy Woodpecker***	0.40 (0.04) A	0.13 (0.04) B	0.17 (0.04) B
Hairy Woodpecker *	0.18 (0.04) A	0.04 (0.03) B	0.09 (0.03) AB
Northern Flicker***	0.30 (0.05) A	0.32 (0.05) A	0.04 (0.05) B
Eastern Wood-Pewee *	0.80 (0.10) A	0.80 (0.09) A	0.48 (0.09) B
Least Flycatcher*	0.01 (0.01) AB	0.04 (0.01) A	0.00 (0.01) B
Great CrestedFlycatcher***	0.90 (0.11) B	1.27 (0.10) A	0.74 (0.10) B
American Crow **	0.14 (0.08) B	0.42 (0.07) A	0.12 (0.07) B
Black-Capped Chickadee *	0.29 (0.06) AB	0. 33 (0.06) A	0.14 (0.06) 8
White-breasted Nuthatch *	0.43 (0.06) A	0.40 (0.06) AB	0.21 (0.06) B
Gray Catbird*	0.75 (0.10) A	0.53 (0.10) AB	0.39 (0.10) B
Yellow Warbler *	0.17 (0.06) AB	0.30 (0 .06) A	0 . 09 (0.06) B
Ovenbird *	0.01 (0.01) As	0.03 (0.01) A	0.00 (0.01) B
Common Yellowthroat***	0.35 (0.10) B	0.75 (0.10) A	0.27 (0.10) B
Northern Cardinal ***	0.42 (0.07) B	0.72 (0.07) A	0.44 (0.07) B
Rose-breasted Grosbeak **	0.14 (0.05) B	0 . 33 (0.05) A	0 .14 (0.05) H
Song Sparrow **	0.47 (0.11) H	0.94 (0.11) A	0.62 (0.11) AB
Red-winged Blackbird *	0.48 (0.13) B	0.96 (0.12) A	0.57 (0.12) AB
American Goldfinch ***	0.30 (0.06) A	0 . 21 (0.06) AB	0. 02 (0.06) B
Winter distribution, neotropical local **	0.29 (0.03) AB	0.30 (0.03) A	0.18 (0.03) B
Winter distribution, resident ***	0.19 (0. 01) A	0.19 (0.01) A	0.13 (0.01)B
Population status, stable * **	0.18 (0.01) AB	0.22 (0.01) A	0.16 (0.01) B
Management status, high ***	0.17 (0.02) A	0.19 (0.02)A	0.11 (0.02) B
Management status, low ***	0.19 (0.01) AB	0.21 (0.01) A	0.15 (0.01) B
Habitat preference, edge *	0. 26 (0.02) AB	0.30 (0.02) A	0.23 (0.02) B
Habitat preference, interior-edge ***	0.24 (0.01) AB	0.27 (0.01) A	0.17 (0.01) B
Habitat preference,water***	0.01 (0.01) B	0.04 (0.01) A	0.03 (0.01) A
Territory size,>5 ha*	0.09 (0.01) AB	0.12 (0.01) A	0.09 (0.01) B
Territory size, 2-5 ha***	0.21 (0.01) A	0.22 (0.01) A	0.15 (0.01) B
Nesting location,ground***	0.08 (0.02) B	0.18 (0.02) A	0.09 (0.02) B
Nesting location, hole ***	0.26 (0.02) A	0.26 (0.02)A	0.18 (0.02) B
Foraging guild, bark ***	0.25 (0.02) A	0.20 (0.02) AB	0.15 (0.02) B
Foraging guild, ground *	0.14 (0.01) AB	0.18 (0.01) A	0.12 (0.01) B

(a) Significance level of overall general linear model (*P < 0.05; **P < 0.01; ***P < 0.005). Underlines indicate species/categories with lowered abundance on flooded plots in 1993 and among years for flooded plots. See Methods and Appendix for description of management risk categories and guild association

(b) Mean relative abundances (S.E.) with different letters are statistically different (P < 0.05).

Table 3. Differences in relative abundance (# birds/point) for flooded and unflooded plots in 1993.

Species and categories (a)	change (b)	Flooded (c)	Unflooded (c)
Total - all species	n.s.	16.38 (0.73)	18.14 (0.76)
Yellow-billed Cuckoo **	+	0.14 (0.03)	0.03 (0.03)
Yellow-bellied Sapsucker ***	+	0.72 (0.07)	0.40 (0.08)
Hairy Woodpecker **	+	0.10 (0.02)	0.04 (0.02)
Least Flycatcher *	-	0.00 (0.01)	0.04 (0.01)
Great Crested Flycatcher ***	-	0.63 (0.10)	1.27 (0.10)
Blue Jav **_*	-	0.18 (0.06)	0.47 (0.07)
White-breasted Nuthatch **@	+	0.65 (0.07)	0.40 (0.07)
Carolina Wren *	-	0.00 (0.01)	0.03 (0.01)
House Wren **	-	1.14 (0.13)	1.68 (0.14)
Veery *	-	0.00 (0.01)	0.04 (0.01)
Gray Catbird ***	-	0.16 (0.06)	0.53 (0.06)
Yellow Warbler ***	-	0.05 (0.06)	0.30 (0.06)
Cerulean Warbler **@	+	0.07 (0.02)	0.01 (0.02)
Prothonotary Warbler ***	+	1.09 (0.11)	0.30 (0.12)
Ovenbird *	-	0.00 (0.01)	0.03 (0.01)
CommonrYellow hmat ***	-	0.20 (0.09)	0.75 (0.10)
Northern Cardinal ***	-	0.32 (0.08)	0.72 (0.08)
Rose-breasted Grosbeak ***	-	0.04 (0.04)	0.33 (0.04)
Red-winged Blackbird *	-	0.55 (0.12)	0.96 (0.13)
Common Grackle ***	+	1.08 (0.12)	0.32 (0.12)
Brown-headed Cowbird ***	-	0.15 (0.07)	0.53 (0.07)
American Goldfinch *	-	0.07 (0.04)	0.21 (0.04)
Winter distribution, neotropical widespread **	-	0.68 (0.08)	0.96 (0.08)
Population status, mixed **	-	0.25 (0.02)	0.34 (0.03)
Habitat preference, edge **	-	0.23 (0.02)	0.30 (0.02)
Nesting location, lower canopy **	-	0.24 (0.03)	0.35 (0.03)
Nesting location, other **	-	0.05 (0.02)	0.14 (0.02)
Foraging guild, air *	-	0.14 (0.02)	0.22 (0.02)
Foraging guild, bark **	+	0.27 (0.02)	0.20 (0.02)
Foraging guild, ground **	-	0.13 (0.01)	0.18 (0.01)

(a) Significance level of overall general linear model (*P < 0.05; **P < 0.01; ***P < 0.005) in 1993. Underlines indicate species with lowered abundance on flooded plots among years. See Methods and Appendix for a description of management risk categories and guild associations.
(b) Change in relative abundance (+ increased on flooded plots; - decreased on flooded plots).
(c) Mean relative abundance (S.E.) for flooded and unflooded plots in 1993.
@ Abundance increased on flooded plots among years.

Table 4. Species and management risk/guild categories with significant differences (P < 0.05) in relative abundance (# birds/point) between flooded and unflooded plots in 1993 and significance of the same comparison in 1992 and 1994..

Species and categories (a)	change (b)	1992 (c)	1993 (c)	1994 (c)
Yellow-billed Cuckoo **	+	0.0460	0.0004	0.2168
Yellow-bellied Sapsucker ***	+	0.0264	0.0003	0.2853
Hairy Woodpecker **	+	0.6165	0.0393	0.7929
Least Flycatcher *	-	0.6480	0.0177	0.1893
Great Crested Flycatcher ***	-	0.6042	0.0002	0.2248
Blue Jar ***	-	0.3898	0.0084	0.0362
White-breasted Nuthatch **	+	0.6007	0.0084	0.5615
Carolina Wren *	-	0.3134	0.0181	0.8497
House Wren **	-	0.7149	0.0173	0.0285
Veery *	-	0.3665	0.0298	0.4171
Gray Catbird * * *	-	0.0125	0.0002	0.0273
Yellow Warbler ***	-	0.8199	0.0043	0.5914
Cerulean Warbler **	+	0.3672	0.0097	0.3436
Prothonotary Warbler ***	+	0.0020	0.0001	0.0001
Ovenbird *	-	0.3052	0 0298	0.2986
Common Yellowthrnat ***	-	0.4528	0.0005	0.0489
Northern Cardinal ***	-	0.5763	0.0002	0.0220
Rose-breasted Grosbeak ***	-	0.2670	0.0001	0.0842
Red-winged Blackbird *	-	0.9632	0.0548	0.3108
Common Grackle ***	+	0.2171	0.0001	0.0311
Brown-headed Cowbird ***	-	0.3766	0.0031	0.1208
American Goldfinch *	-	0.4021	0.0139	0.3797
Winter distribution, neotropical widespread **	-	0.4708	0.0138	0.3308
Population status, mixed **	-	0.8734	0.0072	0.6332
Habitat preference, edge * *	-	0.3302	0.0123	0.8407
Nesting location, lower canopy **	-	0.8832	0.0118	0.4199
Nesting location, other **	-	0.4235	0.0103	0.1846
Foraging guild, air *	-	0.8699	0.0187	0.8664
Foraging guild, bark **	+	0.1194	0.0084	0.0489
Foraging guild, ground **	-	0.8528	0.0127	0.8729

(a) Significance level of overall general linear model (*P < 0.05; **P < 0.01; ***P < 0.005) in 1993 Underlines indicate groups with lowered relative abundance in 1993 and 1994. (P < 0.05).
See Methods and Appendix for a description of management risk categories and guild associations.
(b) Change in relative abundance (+ increased on flooded plots; - decreased on flooded plots).
(c) P-values from GLM for differences in relative abundance. Underlines indicate P < 0.05.

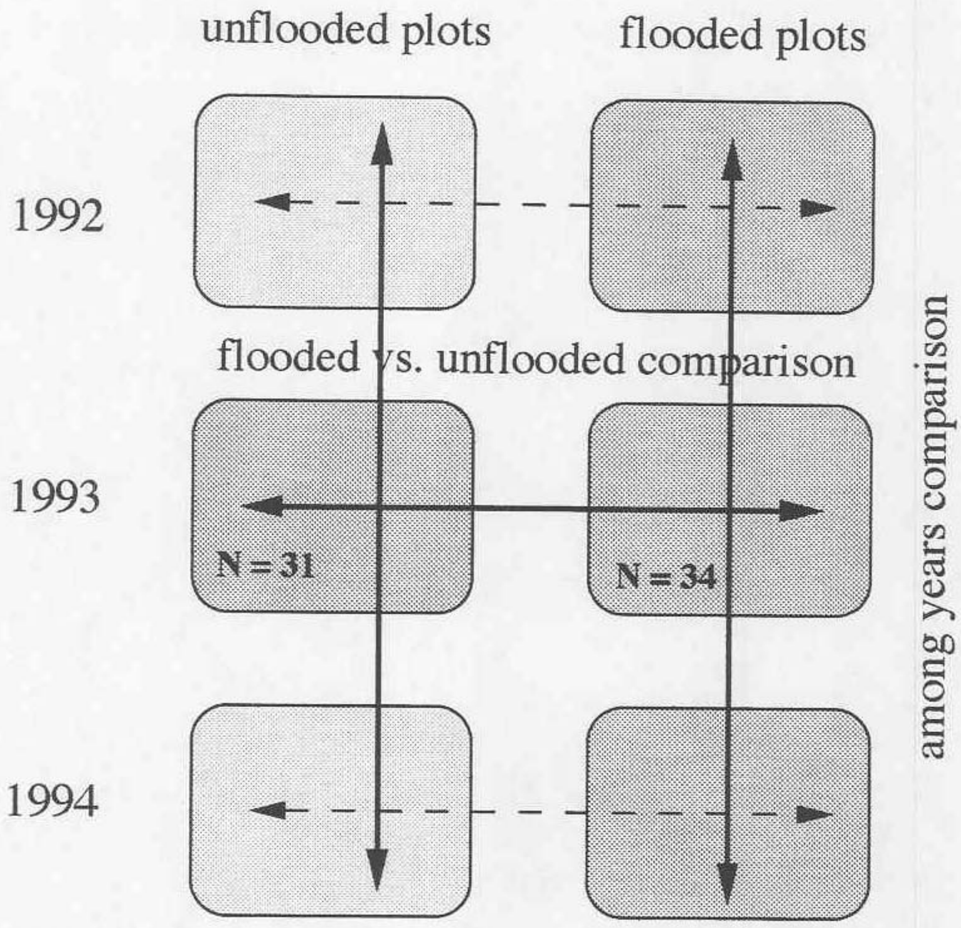

Figure 1. Study design testing effects of the 1993 flood on the Upper Mississippi River bird community.

Appendix. Management risk categories and guild associations of Upper Mississippi River birds.

Family	Common name	Scientific name	N (a)	Winter (b)	Pop. (c)	Status (d)	Habitat (e)	Territory (f)	Nesting (g)	Foraging (h)
ArtJeidae	Great Blue Heron	Ardea herodias	40	T	S	L	W	L	UC	P
	Great Egret	Casmecodius albus	1	T	S	L	W	L	UC	P
	Green-hacked Hers	Butorides striatus	2	T	M	L	W	L	UC	P
Anatidae	Canada Goose	Branta canadamsis	2	T	S	L	W	L	G	G
	Wood Duck	Aix sponsa	35	T	S	L	W	L	H	G
	Mallard	Ams platyrhynchos	16	T	S	L	W	L	G	G
	Hooded Merganser	Lophodytes cucullatus	2	T	ND	L	W	L	H	P
Accipitridae	Bald Eagle	Haliaeetus leucocephalus	6	R	M	H	W	L	UC	P
	Red-shouldered Hawk	Buteo lineatus	5	R	M	H	I	L	UC	C
Ralfidae	Sora	Pormna Carolina	2	T	M	L	W	S	O	G
Charadriidae	Killdeer	Chacadrius vociferus	3	T	S	L	E	S	G	G
Scolopacidae	American Woodcock	Scolopax minor	2	T	D	L	E	M	G	G
Columbidae	MoumingDove	Zenaidamacroura	25	R	M	L	E	M	UC	G
Cucu<idae	Black-billed Cuckoo	Coccyzus erytluopthalmus	4	NL	M	H	IE	M	LC	LC
	Yellow-billed Cuckoo	Coccyzusamericanus	35	NI	D	H	IE	M	LC	LC
Stagidae	Great Homed Owl	Bubo virgirrianus	1	R	S	L	IE	L	UC	C
	Barred Owl	Strix varia	6	R	S	L	I	L	H	C
Apodidae	Chimney Swift	Chaeturapelagica	13	NI	D	M	E	S	H	A
Trochilidae	Ruby-throated Hummingbird	Archilochus colubris	13	NI	S	M	IE	M	UC	LC
Alcediricdae	Belted Kingfisher	Ceryle alcyon	8	T	M	L	W	L	O	P
Piadae	Red-headed Woodpecker	Melanerpes erythrocephalus	31	R	D	L	IE	L	H	B
	Red-bellied Woodpecker	Melanetpes carolirrus	52	R	S	L	IE	L	H	B
	Yellow-bellied Sapsucker	Sphyrapicus varius	55	T	ND	L	IE	M	H	B
	Downy Woodpecker	Picoidespubescens	SS	R	M	L	IE	M	H	B
	Hairy Woodpecker	Picoides villosus	45	R	S	L	I	L	H	B
	Northern Flicker	Colapta auratus	48	R	D	L	IE	M	H	B
	Pileated Woodpecker	Dryocopus pileatus	16	R	S	L	I	L	H	B
Tyraimidae	Eastern Wood-Pewee	Contopu virens	56	NL	D	H	IE	M	UC	A
	Acadian Flycatcher	Empidonax virescens	6	NL	D	H	I	S	UC	A
	Least Flycatcher	Empida>ax minimus	12	NI	D	M	E	5	UC	A
	EascemPhoebe	Sayomisphoebe	3	T	S	L	IE	S	O	A
	Great Crested Flycatcher	Myiarchus ccinitus	55	NL	M	H	IE	M	H	A
	Eastern Kingbird	Tyramrus tyrannies	3	NI	D	M	E	M	LC	A
Hirundinidae	Purple Martin	Progne subis	2	NI	D	H	E	S	H	A
	Tree Swallow	Tachyaneta bicolor	44	T	M	L	E	5	H	A
Cmvidae	Blue Jay	Cyanoatha aistata	46	R	D	L	IE	M	UC	UC
	American Crow	Corvus brachyrhynchos	46	R	S	L	E	L	UC	G
Paridae	Black-capped Chickadee	Paris abicapillus	51	R	M	L	lE	M	H	LC
	Tufted Titmouse	Panubicolor	2	R	S	L	IE	M	H	LC
Sittidae	White-breasted Nuthatch	SiCa carolinensis	53	R	M	L	IE	L	H	B
Certhiidae	Brown Creeper	Certhia ameritana	34	R	S	L	I	M	H	B
Troglodytidae	Carolina Wren	Thryothorus ludovicianus	8	R	S	L	IE	S	LC	LC
	House Wren	Troglodytes aedon	56	NW	S	L	E	S	H	LC

(a) Number of plots species was identified from in 1992.
(b) Wintering distribution: R = resident; T = temperant migrant; NW = neotropical, widespread; NI = neotropical, intermediate; NL = neotropical, local.
(c) Population status: S = stable, increasing (Thompson, et al. 1993, categories 1 or 2); M = mixed (categories 3 or 4); D = decreasing (category 5); ND = no data.
(d) Management states: L = low (Thompson, et al. 1993, rank 1 -1.99); M = medium (rank 2 - 2.99); H = high (rank 3 - 5.00).
(e) Habitat preference: I = interior forest; lE = interior-edge; E = edge; W = near water.
(f) Territory size: S = < 2 ha; M = 2-5 ha; L = > 5 ha.
(g) Nesting location: G = ground; LC = lower canopy; UC = upper canopy; H = hole; O =other.
(h) 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, saltier, screener; B = bark gleaner, excavator.

Appendix continued.

Family	Common name	Scientific name	N (a)	Winter (b)	Pop. (c)	Status (d)	Habitat (e)	Territory (f)	Nesting (g)	Foraging (b)
Troglodytidae	Winter Wren	Troglodytes troglodytes	1	T	S	L	I	M	G	G
Muscicapidae	Blue-gray Gnatcatcher	Polioptila caerulea	53	NJ	S	M	IE	S	UC	UC
	Eastern Bluebird	Sialia sialis	1	T	S	L	E	S	H	G
	Veery	Cathans fuscescens	16	NJ	D	H	I	S	G	G
	Wood Thrush	Hylocid>(amuscelina	6	NL	M	H	IE	S	*LC*	G
	American Robin	Turdus migratorius	56	T	S	L	E	S	UC	G
Mimidae	Gray Catbird	Dumetella cardinensis	50	NJ	S	M	E	S	LC	G
	Brown Thrasher	Toxostomarofum	2	T	D	L	E	M	G	G
Bombycillidae	Cedar Waxwing	Bombycitla cemonun	10	R	S	L	E	M	UC	A
Snanidae	European Starling	Sturnus vulgaris	11	R	D	L	E	S	H	G
Vin;oitidae	Yellow-tiuoated Vireo	Vireo flavifrons	46	NJ	S	H	IE	S	UC	UC
	Warbling Vireo	Vireo gilvus	51	NJ	D	M	IE	M	UC	UC
	Red-eyed Vireo	Vireo olivaceta	47	NJ	S	M	IE	S	UC	UC
Emberizidae	Yellow Warbler	Dendroicapetechia	37	NW	S	L	E	S	LC	LC
	Yellow-throated Warbler	Dendroica domiirica	1	NJ	3	M	IE	S	UC	UC
	Cemiean Warbler	Dendroica ceNlea	1	NL	D	H	I	S	UC	UC
	American Redstart	Setophaga ruticilla	53	NW	M	M	I	S	LC	LC
	ProUionotary Warbler	Protonotuia atrea	50	NL	S	H	IE	S	H	LC
	Ovenbird	Seiuna amocapillus	10	NJ	S	H	I	S	G	G
	CommonYellowthroat	Gedhlypistriclms	47	NW	M	M	E	S	G	LC
	Scarlet Tanager	Piranga olivacea	5	NL	S	H	I	M	UC	UC
	Northern Cardinai	Cwdinalisiis	54	R	S	L	IE	S	LC	G
	Rose-breasted Grosbeak	Phcuctiaaludoviciama	38	NJ	M	H	IE	M	UC	UC
	Indigo Bunting	Passetina cyanea	18	NJ	D	M	E	M	LC	LC
	Rufous-sidedTowhee	Pipilo erytiitophthalmus	1	T	D	L	IE	M	LC	G
	Chipping Sparrow	Spizella passeiina	1	NW	S	L	E	S	LC	G
	Field Sparrow	Spiulla pusilla	3	T	D	L	E	S	G	G
	Song Sparrow	Melospiza melodic	54	T	S	L	E	S	G	LC
	Swamp Sparrow	Melospiza georgiana	2	T	S	L	W	S	O	G
	Red-winged Blackbird	Agelaius phoeniceus	50	T	D	L	E	S	LC	G
	Common Grackle	Quiscalus quiscula	56	R	D	L	E	S	UC	G
	Brown-headed Cowbird	Molotlaus afar	53	R	M	L	E	L	O	G
	Northern Oriole	Ictenus galbula	55	NJ	D	M	E	M	UC	U
Fringillidae	American Goldfinch	Cardue)istristis	44	R	M	L	E	S	LC	LC

CHAPTER 6. NEST PREDATION IN LARGE VERSUS SMALL FLOODPLAIN FOREST TRACTS

A paper to be submitted to Oikos

Melinda G. Knutson[1,2] and Erwin E. Klaas[1]

Abstract

We studied predation on artificial nests in large floodplain forests of the Upper Mississippi River in 1993 and 1994, comparing large and small forest tracts, effects of time during the nesting season, and distance from edge. We monitored 431 nests evenly divided between large and small forest tracts over the two years. Contrary to many similar studies, large forest tracts had higher predation rates than small forest tracts (52.3% vs. 36.3%). Furthermore, there was no significant difference in predation rates among nests placed 25, 50, 100 or 200 m from the forest edge. Predation rates decreased over the nesting season. Calculated artificial nest "survival", derived from observed predation rates in 1993-94, was similar to natural nest survival for several species for the same study area in 1992. Nest losses did not differ among several habitat variables measured at the nest sites. We hypothesize that floodplain predators are different than upland predators and that edges in the floodplain do not support large numbers of predators, especially mammals.

Introduction

Many species of songbirds breeding in North America are experiencing population declines, according to Breeding Bird Survey data (Robbins et al. 1989, Askins et al. 1990, Sauer and Droege 1992). High rates of nest predation may be partially responsible for these population declines (Wilcove 1985, Temple and Cary 1988). Predation is considered the largest cause of nest failure in passerine birds in some regions of North America (Ricklefs 1969, Best and Stauffer 1980), accounting for 55 - 79% of all nest losses. One method of examining sources of predation and relative rates of nest loss among habitats is to experimentally manipulate nest locations with

---

[1] Graduate student and Professor, respectively, Iowa State University, Department of Animal Ecology and National Biological Service, Iowa Cooperative Fish and Wildlife Research Unit, Ames, IA. Research conducted and manuscript written by Knutson with consultation from Klaas.

[2] Author for correspondence. Address after 1 September 1995: National Biological Service, Upper Mississippi Science Center, P.O. Box 2226, Lacrosse, WI 54601.

artificial nests. Artificial nests are designed to mimic the size, shape, and location of natural nests. Eggs are placed in them, and they are left in place for a specific time interval and checked for evidence of predation.

Although artificial nests can provide an estimate of predation rates on real songbird nests, there are limitations (Martin 1987, Willebrand and Marcstrom 1988, Roper 1992). Care must be taken to avoid leaving unnatural visual or olfactory cues, which might attract or repel more predators than would real nests. Also, it is impossible to mimic parental bird movements to and from the nest which may be significant cues to predators of natural nests. Natural nests are also subject to predation over a longer time interval than is usual in an artificial nest study.

The primary advantage of artificial nests is that many more artificial nests than natural nests can be monitored for the same effort. Artificial nest studies allow control over sample sizes and nest locations and can be considered analogous to laboratory studies. As in a laboratory study, control is achieved at the expense of altering processes that occur under more natural conditions. If the objective is to compare predation rates on artificial nests among different treatments, the relative rates of predation among the treatments can indicate which conditions lead to higher rates of predation on natural nests (Roper 1992).

Few studies of nest predation have been conducted in riparian habitats (Best and Stauffer 1980), and fewer still have examined large floodplain forests. These forests on the Upper Mississippi River (UMR) provide habitat for at least 84 species of birds during the breeding season and may be important in maintaining some bird populations, especially birds absent from or declining in adjacent upland habitats (Chapter 3). We examined the effect of floodplain forest tract size, nest distance from the forest edge, and time during the nesting season on predation rates on artificial nests. We also tested whether small-scale habitat features, which vary from nest-to-nest, affect predation rates.

Study area

The study area consisted of forested habitat in river navigation Pools 6-9 of the UMR from Winona, MN to Lansing, IA (NW Universal Transverse Mercator (UTM) E602000, N4883000; SE UTM E655000, N4785000), a distance of about 110 km, following the main channel of the river. Floodplain forests in the study area are generally not found in discrete patches; patch shapes are sinuous and interconnected, and forests are interspersed with marshes, grassy openings, pools and channels. Large forest tracts were selected from the largest tracts of contiguous forest available. Forested habitat composed an average of 62% of the landscape within 800 m of the center of the large tracts, with 60% of this area was > 50 m from an edge (core area). Mean forested area within the 800-m zone for large patches was 214 ha (range: 196-226 ha). Small patches were mostly surrounded by water (islands or narrow forest strips) and forested habitat composed an average of 35% of the surrounding land, with 25% as core area. The mean forested area within the 800-m zones of small patches was 104 ha (range: 70-159 ha). The amount of forested area was measured from geographic information system (GIS) coverages of the study area using the FRAGSTATS spatial analysis program (McGarigal and Marks 1994).

Silver maple *(Acer saccharinum)* was the dominant tree species in the study area, along with green ash *(Fraxinus pennsylvanica)* and elm *(Ulmus* spp.). (See Chapter 2 for a detailed description of floodplain forest vegetation.) Most shrubs were sparse, but thick patches of poison ivy *(Toxicodendron radicans)* and prickly ash *(Zanthoxylum americanum)* were common. The understory of the closed canopy forest was dominated by tall nettles *(Urtica dioica)* and canopy gaps were dominated by reed canary grass *(Phalaris arundinaceae).*

Methods

We monitored 431 (1993 = 175; 1994 = 256) artificial nests from late May through early July of 1993 and 1994. Half of the open-cup artificial nests were placed in large forest tracts and half in small tracts. We conducted 3 trials, spaced over the nesting season, in 1993 (28 & 29 May [N = 56], 9 & 10 June [N = 56], 2 July [N = 63]) and 4 trials in 1994 (24 & 25 May [N = 64], 8 & 9 June [N = 64], 21 & 22 June [N = 64], 5 & 6 July [N = 64]). We placed all nests for a single trial within 2 days. Each trial was identified by the week of the nesting season. Week 1 corresponds to the 4th week of May and week 6 corresponds to the first week of July. Different locations for both large and small tracts were used for each trial in 1993; we were forced to conduct the week 6 trial in flooded plots, because the entire floodplain was flooded. In 1994, two locations of large and small tracts were used; nests for weeks 1 and 5 were placed in the first location and nests for weeks 3 and 6 were placed in the second.

Nests were placed along transects running perpendicular to the forest edge at 25, 50, 100, and 200 m distances from the forest-water edge, 100 m apart in large tracts. In small tracts, nests were similarly placed at 25 and 50 m from the edge. Nests were placed 2 - 3 m above the ground in trees. Ground nests were not used because few ground-nesting songbirds are found in these forests. The artificial nests were designed to simulate some features of American redstart *(Setophaga ruticilla)* nests, one of the most common lower canopy nesters in these forests. Nests were made of 2.5-cm wire mesh and lined with leaves or grass from the placement site. Finished dimensions were approximately 10 cm in diameter and 7 cm in height. Two fresh northern bobwhite *(Colinus virginianus)* eggs were monitored in each nest. Northern bobwhite egg shells are thinner than Japanese quail *(Coturnix coturnix)* shells, reducing a potential bias against small predators that may be deterred by thick shells (Reitsma et al. 1990, Roper 1992). The eggs were dulled with mud from the site to simulate natural egg speckling and minimize visual detection. Field workers handled the eggs and nests with rubber gloves and wore rubber waders to minimize human scent. Nest locations were recorded in reference to a flag placed about 10 m from the nest. No special effort was made to conceal the nests, however, they were often difficult to find without referring to specific notes on their locations. Nests were checked on the 6th day after placement. This time period is similar to that used by other researchers (Wilcove 1985). Other studies have shown that most predation occurs within this interval of time (Martin 1988) .

We recorded the height of the artificial nest and estimated the degree of camouflage around the nest by recording the percentage of the nest not visible due to leaves within 0.5 rn of the nest on the top and two sides. The means of the three leaf cover estimates were used in the analysis. Habitat variables at the nest site were measured within an 11.3-m (0.04 ha) radius circle surrounding the tree in which the nest was placed. We recorded the nest tree species and nest tree diameter at breast height (dbh) in 4 size classes: 8 -15, 16 - 30, 31 - 50 and > 50 cm. Tree canopy cover within the circle was recorded in 3 classes: 0 - 50, 51 - 75, and 76 - 99%. We also recorded the three most frequent tree species. Understory density was defined as shrub cover (plants 0.5 - 4 m tall with a woody stem) in 3 classes: 0 - 5, 6 -30, and > 30%. To obtain means for the class variables, we assigned the midpoint of the class to the observation (Bonham 1989). We also recorded the distance from the nest to the marking flag to test whether this influenced predation.

Disturbances to the artificial nest were recorded when the nests were checked. Classes of disturbance included (a) weather damage with no predation, (b) 1 or 2 eggs missing with no damage to the nest lining, (c) eggs pecked or broken with no damage to the nest lining, (d) eggs missing or broken with damage to the nest lining or support material, and (e) all other disturbance.

We compared predation rates (# nests disturbed) between years using the Chi-square test with probabilities given by Fisher's Exact Test (PROC FREQ (SAS Institute Inc. 1989)), a modification of the Chi-square test suitable for testing differences in proportions (Zar 1984). Differences in predation rates between flooded vs. unflooded trials in 1993 and among locations in 1994, weeks of the nesting season, and distances to forest edge also were tested using Fisher's Exact Test. We used log-linear models to assess the relative contributions of forest size, week of the nesting season, and distance to forest edge. The full model including all three main effects was contrasted with reduced models, dropping one of the variables each time. Differences in full and reduced models follow a Chi-square distribution with one degree of freedom and indicate the dropped variable's contribution to the model. A stepwise logistic regression model also was developed for size, week, and distance to edge. We tested the effect on predation rates of variables measured at the nest site using a log-linear model. Differences between intact and depredated nests in the species of nest tree or the species of trees surrounding the nest tree were tested using Fisher's Exact Test. Differences between large and small forest plots in types of predation were tested using Fisher's Exact Test.

Results

There was no difference in overall predation rates between 1993 (45.7%) and 1994 (43.4%) (X2 = 0.234, 1 df, $P < 0.693$), so we pooled the 1993 and 1994 data. Large forest plots (52.3%; n = 216) had higher predation than small forest plots (36.3%; n = 215) ($X^2 = 11.228$, 1 df, $P < 0.0009$). Weeks of the nesting cycle were different ($X^2 = 7.759$, 3 df, $P < 0.052$); predation was highest in the third week of the nesting season (52.5%; n = 120), followed by week 1 (47.5%; n = 120), week 6 (37.8%; n = 127) and week 5 (35.9%; n = 64). No significant differences between artificial nest distances to the forest edge were detected ($X^2 = 6.578$, 3 df, $P < 0.087$), however, there was a trend of increasing predation rates with distance from edge (25m: 40.5%, n = 178; 50m: 41.4%, n = 145; 100m: 51.9%, n = 54; 200m: 57.4%, n = 54). When large and small plots were considered separately, predation rates did not differ with distance from edge in either the large (44.4 - 57.4%; n = 54) ($X^2 = 2.134$, 3 df, $P < 0.558$) or the small plots (33.9 - 39.6%; n = 91-124) ($X^2 = 0.735$, 1 df, $P < 0.394$.).

When forest patch size, week of the nesting season and distance to edge were entered as the full logistic model and each variable's contribution was considered alone, patch size ($X^2 = 6.121$, 1 df, $P < 0.0134$) explained more variation than week ($X^2 = 4.541$, 1 df, $P < 0.0331$) or distance to edge ($X^2 = 0.697$, 1 df, $P < 0.4038$). Stepwise logistic regression resulted in a 2-variable model ($X^2 = 15.689$, 2 df, $P < 0.0004$) with patch size ($X^2 = 11.228$, 1 df, $P < 0.0008$) and week ($X^2 = 4.580$, 1 df, $P < 0.0324$) meeting the alpha = 0.05 criterion for entering and staying in the model.

The full logistic model for variables measured at each nest with predation as the dependent variable was not significant ($X^2 = 9.50$, 6 df, $P < 0.1473$, n = 239). Mean values for these variables were: nest height = 2.5 m (S.D. = 0.5 m), tree dbh = 21.7 cm (S.D. = 14.7 cm), leaf cover within 0.5 m of the nest = 32.3% (S. D. = 42.4%), tree canopy cover = 78.1% (S.D. = 18.5%), shrub cover = 21.2% (S.D. = 18.0%), and flag distance = 9.7 m (S.D. = 3.1 m). The most common tree species surrounding the nests included *Acer saccharinum, Fraxinus pennsylvanica, Ulmus spp.,* and *Celtis occidentalis.* There was no difference between intact and depredated nests in the species of tree the nest was placed in ($X^2 = 3.365$, 4 df, $P < 0.499$) or the species of trees surrounding the nest tree ($X^2 = 1.224$, 4 df, $P < 0.874$).

The types of disturbance in depredated nests did not differ between large and small forest plots ($X^2 = 3.088$, 4 df, $P < 0.538$). In most depredated nests, the eggs were missing with the nest itself left undisturbed (74.4%; n = 142). Some nests were damaged in addition to loss of eggs (16.2%; n = 31). In some nests, the eggs were pecked or broken (4.2%; n = 8), and 2 nests (1.0%) were lost to weather-related causes.

Discussion

The overall nest predation rates we observed are similar to those found in other studies of above-ground nests (Yahner and Scott 1988, Yahner and Voytko 1989, Yahner and DeLong 1992). We compared our artificial nest results with actual data we collected on natural open-cup nests in 1992 (M. Knutson, unpublished data). Natural nests were found and followed in large forest tracts in the same study area; some tracts were the same ones used in the present study. To compare the artificial nest predation rate with natural nest survival, it was necessary to adjust for nest losses from causes other than predation and convert the predation rate to a "survival" rate. We assumed our 45% predation rate represented 60% of all losses real nests experience, a figure within the range estimated in the literature (Ricklefs 1969, Best and Stauffer 1980). Therefore, our calculated total losses were estimated at 45% / 60% = 75%. Our artificial nest "survival" was then about 1 - 75% = 25%. If we consider only the large forest tracts (52% predation), corresponding to the forest tract size where the natural nest data were collected, the calculated artificial nest "survival" is about 13%. We recorded American redstart survival over the corresponding egg and incubation period in 1992 in the same study area at 28.3% (N = 23); American robin *(Turdus migratorius)* survival was 18.5% (N = 13), gray catbird *(Dumetella carolinensis)* survival was 73.0% (N = 11), and yellow warbler survival was 21.0% (N = 6). Based on these comparisons, artificial nests may be a reasonably reliable method of assessing predation in these forests, at least for lower canopy, cup-nesting birds. Yahner (1989) found similar predation rates between artificial nests placed at nest sites previously used by birds vs. randomly placed nests, while Reitsma et al. (1990) found higher predation rates for artificial nests than natural nests.

We found predation rates higher earlier in the nesting season than later. Some studies of real nests have also shown that predation decreases over the nesting season (Howell 1942, Nice 1957). Other studies report no difference in predation rates over time (Best and Stauffer 1980, Yahner et al. 1989, Nour et al. 1993, L.eimgruber et al. 1994). We did not find that small-scale habitat variables differed between intact and depredated nests. Others have had similar results (Best and Stauffer 1980, Yahner and Voytko 1989, Reitsma et al. 1990), although a few researchers have found that nest concealment is important in reducing predation (Angelstam 1986, Leimgruber et al. 1994).

The types of disturbance to nests can indicate which predators are responsible. When eggs are missing from a nest, but the nesting material is undisturbed, birds or snakes are the most likely culprits (Best 1978, Best and Stauffer 1980, Hensley and Smith 1986). House wrens *(Troglodytes aedon)* are usually responsible for pecked eggs, as they are interspecifically territorial (Belles-Isles and Picman 1986a, 1986b). When a nest is torn up and destroyed, the culprits are more likely mammals such as squirrels *(Sciurus* and *Glaucomys* spp.), skunks *(Mephitis mephitis),* raccoon *(Procyon lotor)* or fox (*Vulpes fulva or Urocyon cinereoargenteus)* (Best 1978, Best and Stauffer 1980, Westmoreland and Best 1985). Since most of our depredated nests were intact, it is likely that bird predators are the major source of nest loss in the floodplain, although snakes, mink and weasels *(Mustela* spp.) cannot be ruled out. Potential snake predators in these forests include the black rat snake *(Elaphe obsoleta)* (Hensley and Smith 1986), a known climber, and the western fox snake *(Elaphe vulpina).* However, our study area. is on the northern edge of the distribution range for the rat snake, and neither species was observed during field work. Nest losses to these predators, if any, are likely to be minor. In a largely unsuccessful effort (due to technical difficulties) to photograph visitors to artificial nests placed in the study area (nests additional to the ones used in this study), all photographs obtained were of birds (n = 6); we recorded no mammal or snake visitors. Other potential avian nest predators or destroyers common in these forests include the American crow *(Corvus brachyrhynchos)* (Sugden and Beyersbergen 1986), common grackle *(Quiscalus quiscala),* blue jay *(Cyanocitta cristata),* brown-headed cowbird *(Molothrus ater),* and gray catbird (Belles-Isles and Picman 1986a). In censuses of the study area, none of these birds showed a preference for large forest tracts (Chapter 4). Other studies have also found birds to be the major nest predators in forest habitats (Andrea et al. 1985, Nilsson et al. 1985, Yahner and Cypher 1987, Yahner and Scott 1988, Yahner et al. 1989, Yahner and DeLong 1992, Nour et al. 1993).

Our findings of higher predation rates in large forest tracts are in contrast to most other artificial nest studies, which have found lower predation in large forest tracts (Andrea et al. 1985, Wilcove 1985, Andrea and Angelstarn 1988, Small and Hunter 1988, Yahner and Scott 1988) (but see Yahner and Voytko 1989, Nour et al. 1993, Leimgruber et al. 1994). Most of these studies were conducted in upland habitats. Our results may be due to differences in predator-prey distributions in upland and lowland forests. It is likely that the lowland predator community is somewhat different than the upland predator community. Mammals such as mink are more common near water. Our data indicate that birds, rather than mammals, are the main floodplain forest predators.

In addition, the upland pattern of predator preference for edge habitats does not appear to be true in the floodplain. The landscape pattern of floodplain forests is patchy, with small, grassy openings in even the largest forest tracts. Some upland studies indicate that edge effects are present at 200 m or more from an edge (Angelstam 1986, Wilcove et al. 1986); one explanation for the absence of edge effects in our study might be that 200 rn was an inadequate maximum distance because the floodplain is functionally all "edge". We were unable to use longer distances because there is little land in the floodplain farther than 200 m from an edge. However, Paton (1994), in a review of the effect of edge on nest success, concludes edge effects within 50 m of the edge are well-supported, while evidence for effects beyond that are weak. Furthermore, if the floodplain is all edge, large and small plots should have similar predation rates, the null hypothesis that we rejected. The floodplain forest edges we studied are not anthropogenic (except for indirect effects of lock and dam construction) and can be considered "inherent" rather than "induced" (Yahner and Scott 1988). The biological implications of this distinction, however, are not clear. Predation along forestwater edges may differ from forest-field edges. Small and Hunter (1988) also found lower predation rates on artificial nests near a forest-water edge.

In general, the overall number of predators is determined by food supplies as well as available nesting or denning habitat. If large areas of the floodplain (water and marsh habitats) are unsuitable for predators, the floodplain forests represent a patchy resource in a matrix of unproductive habitat. In contrast, bird and mammal nest predators in uplands find open or edge habitats most productive, and the forests are exploited secondarily (Whitcomb et al. 1981, Wilcove 19$5, Andren and Angelsta.m 1988, Paton 1994, Askins 1995). Large forest tracts in the floodplain may have higher predation rates because they are large enough to support at least a small population of nest predators. Predators exploiting small forest tracts in the floodplain axe required to cross marsh and water habitats to gain access to these resources, if the tracts are smaller than their home range. This energy expenditure is likely to be especially high for mammals. If mammal predation alone is higher in large floodpla.in tracts vs. small tracts, that might be enough to account for the higher predation in large tracts.

Theoretical models have been developed that address predator-prey dynamics in patchy habitat complexes (Morris 1988, Oksanen 1990, Oksanen et al. 1992). Productive habitats are those that provide adequate food and other resources to sustain predator populations. When productive habitats dominate the landscape (as in uplands), exploitation of prey tends to "spill over" into unproductive habitats (Oksanen 1990, Oksanen et al. 1992). The patterns of exploitation are influenced by whether habitat patches are larger or smaller than predator home ranges. If they are smaller (as is likely in small floodplain tracts but not large tracts), the habitat is exploited in a fine-grained manner with predators roaming widely in search of food (Oksanen et al. 1992). Angelstam (1986) recognized the relationship between landscape context and nest predation rates and proposed a productivity gradient model to explain why an edge-effect is not always observed. If predator productivity is larger in the habitat surrounding the forest than the forest itself, then "spill over" predation into the forest occurs and an edge-effect will be found. If the landscape context is similar in productivity or less productive than the forest (or is dominated by forest), then the edgeeffect disappears (but see Small and Hunter 1988).

We hypothesize that in uplands, predators "spill over" from more productive adjacent habitats into relatively unproductive large forest tracts when competition or territorial behavior forces subordinate individuals into suboptimal habitats. In the floodplain, the forests may be more productive for predators than adjacent habitats. If so, it is reasonable to assume that predation would be higher in larger tracts and there would be no reason to expect higher predation near edges.

Although we did not compare predator densities in upland vs. lowland habitats, we can make some predictions about relative numbers of predators in the two locations. Water covers more of the floodplain than any type of vegetation in the pools we studied (27-44% of the total floodplain area) (Laustrup and Lowenberg 1994), yet forests may be the principal habitat for predators there. In the uplands, predators are found in many habitats, with lower densities in large forest tracts. Therefore, we would expect lower numbers of predators overall in the floodplain vs. the uplands. Furthermore, numerous studies indicate that forests, in general, are marginal habitats for most nest predators, especially mammals (Whitcomb et al. 1981, Wilcove 1985, Andren and Angelstam 1988, Paton 1994, Askins 1995). Therefore, on a larger scale than we addressed, the floodplain as a whole may represent a patchy, seasonal habitat for many nest predators. These predators may be supported primarily in the adjacent uplands but forage in the floodplain when food sources are available. The relative difficulty in accessing these habitats, especially for mammals, may keep predation pressure down in lowland forests. Predation patterns in the larger UMR watershed may be an important factor defining the relative importance of upland and lowland forests for bird populations, especially interior forest specialists experiencing population declines.

Management implications

Our understanding of predator-prey dynamics and the population ecology of floodplain forest birds is still too sketchy to allow clear recommendations regarding which components of the floodplain are of highest conservation priority. This study points out the dangers of assuming that patterns observed in upland habitats can be extrapolated to large floodplain forests without testing. It is likely that differences in nest predation patterns are produced by differences in the underlying processes of predator-prey dynamics. The specifics of those processes remain to be worked out.

Acknowledgements

Funding was provided by the National Biological Service (Patuxent Environmental Science Center, Branch of Migratory Birds Research), Iowa State University, U.S. Fish and Wildlife Service (Region 3 Nongame Program), and the Minnesota Department of Natural Resources Nongame Program. Ms. Knutson also was supported by a Cooperative Education Agreement with the Patuxent Center. Classified Thematic Mapper databases were provided by NBS, Upper Mississippi Science Center, Environmental Management Technical Center. Special thanks to Ms. Knutson's doctoral committee members Louis Best, Brent Danielson, Kirk Moloney, and Thomas Jurik. James Majure and Todd Bishop provided technical GIS consultation. Field, office, and data management assistance were provided by Ingrid Moore, Mark Krom, Rebecca Peak, Julie Schreiber, Fredrick Keith, Jesse Audette, Brenda VanBeek, and Sara Handrick. David Ford and Richard Trump assisted with the camera set-up. Michael Erwin, Deanna Dawson, and Tim Bergin provided helpful comments on earlier drafts of the paper .

Literature Cited

Andren, H. and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69: 544-547.

Andren, H., P. Angelstam, E. Lindstrom and P. Widen. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos 45: 273-277.

Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47: 365-373.

Askins, R. A. 1995. Hostile landscapes and the decline of migratory songbirds. Science 267: 1956-1957.

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

Belles-Isles, J. C. and J. Picman. 1986x. Destruction of heterospecific eggs by the Gray Catbird. Wilson Bull. 98: 603-605.

Belles-Isles, J. C. and J. Picman. 1986b. House Wren nest-destroying behavior. Condor 88: 190-193.

Best, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95: 9-22.

Best, L. B. and D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. Condor 82: 149-158.

Bonham, C. D. 19$9. Measurements for terrestrial vegetation. John Wiley & Sons, New York, NY. 338 pp.

Hensley, R. C. and K. G. Smith. 1986. Eastern Bluebird responses to nocturnal black rat snake nest predation. Wilson Bull. 98: 602-603.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (Turdus migratorius L.). Am. Midl. Nat. 29: 529-603.

Laustrup, M. S. and C. D. Lowenberg. 1994. Development of a systematic land cover/land use database for the Upper Mississippi River System derived from Landsat thematic mapper satellite data. National Biological Survey, Environmental Management Tech. Center, Onalaska WI. 90 pp.

Leimgruber, P., W. J. McShea and J. H. Rappole. 1994. Predation on artificial nests in large forest blocks. J. Wildl. Manage. 58: 254-260.

Martin, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. Condor 89: 925-928.

Martin, T. E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. Proc. Natl. Acad. Sci. 85: 2196-2199.

McGarigal, K. and B. J. Marks. 1994. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure v2.0. Kevin McGarigal, P.O. Box 606, Dolores, CO 81323-9998. Corvallis, OR. pp.

Morns, D. W. 1988. Habitat-dependent population dynamics and community structure. Evol. Ecol. 2: 253-269.

Nice, M. M. 1957. Nesting success in altricial birds. Auk 74: 305-321.

Nilsson, S. G., C. Bjorkman, P. Forslund and J. Hoglund. 1985. Egg predation in forest bird communities on island and mainland. Oecologia 66: 511-515.

Nour, N., E. Matthysen and A. A. Dhondt. 1993. Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. Ecography 16: 111116.

Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. Evol. Ecol. 4: 220-234.

Oksanen, T., L. Oksanen and M. Gyllenberg. 1992. Exploitation ecosystems in heterogeneous habitat complexes II: impact of small-scale heterogeneity on predatorprey dynamics. Evol. Ecol. 6: 383-398.

Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conserv. Biol. 8: 17-26.

Reitsma, L. R., R. T. Holmes and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudronicus,* and eastern chipmunks, Tamias striates, on nest predation in a northern hardwood forest: an artificial nest experiment. Oikos 57: 375-380.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smiths. Contrib. Zool. 9: 148.

Robbins, C. S., J. R. Sauer, R. S. Greenberg and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. Proc. Natl. Acad. Sci. 86: 76587662.

Roper, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? Oikos 65: 528-530.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, 4th ed., vol. 2 SAS Institute, Inc. Cary, NC. 846 pp.

Sauer, J. R. and S. Droege. 1992. Geographic pattemms in population trends of neotropical migrants in North America. Pages 26-42 In J. M. Hagan III and D. W. Johnston,

Eds. Ecology and conservation of neotropical migrant landbirds. Manomet Bird Observatory, Woods Hole, MA.

Small, M. F. and M. L. Hunter. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia 76: 62-64.

Sugden, L. G. and G. Beyersbergen. 1986. Effect of density and concealment on American Crow predation of simulated duck nests. J. Wildl. Manage. 50: 9-14.

Temple, S. A. and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conserv. Biol. 2: 340-347.

Westmoreland, D. and L. B. Best. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102: 774-780.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-201 In B. R. L. and D. M. Sharpe, Eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Wilcove, D. S., C. H. McLellan and A. P. Dobson. 19$6. Habitat fragmentation in the temperate zone. Pages 237-256 In M. E. Soule', Eds. Conservation biology. Sinauer Associates, Sunderland, MA.

Willebrand, T.. and V. Marcstrom. 1988. On the danger of using dummy nests to study predation. Auk 105: 378-379.

Yahner, R. H. and B. L. Cypher. 1987. Effects of nest location on depredation of artificial arboreal nests. J. Wildl. Manage. 51: 178-181.

Yahner, R. H. and C. A. DeLong. 1992. Avian predation and parasitism on artificial nests and eggs in two fragmented landscapes. Wilson Bull. 104: 162-168.

Yahner, R. H., T. E. Morrell and J. S. Rachael. 1989. Effects of edge contrast on depredation of artificial avian nests. J. Wildl. Manage. 53: 1135-1138.

Yahner, R. H. and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. J. Wildl. Manage. 52: 158-161.

Yahner, R. H. and R. A. Voytko. 1989. Effects of nest-site selection on depredation of artificial nests. J. Wildl. Manage. 53: 21-25.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice Hall, Englewood Cliffs, NJ. 718 pp.

CHAPTER 7. GENERAL CONCLUSIONS

Lock and dam construction, agriculture, and urban development have resulted in the conversion of about half the presettlement UMR floodplain forests to non-forested habitats (Peck and Smart 1986, Laustrup and Lowenberg 1994, Yin and Nelson 1995). The remaining forests have changed in species composition and structure; species richness is lower and tree density has declined (Moore 1988). *Acer saccharinum is* the dominant tree species, followed by *Ulmus* spp., *Fraxinus pennsylvanica,* and *Quercus bicolor.* The sapling layer is dominated by *Ulmus* spp. and *F. pennsylvanica,* followed by *A. saccharinum, Celtis occidentalis,* and *Q. bicolor. Ulmus spp.* and *F. pennsylvanica* have a large cohort of saplings, whereas *A. saccharinum* has fewer saplings. Populus *deltoides* has declined in importance along with some hardwood species. The changes in tree species dominance and sapling composition I observed may signal a change in forest structure. The present tall, closed-canopy forests could be replaced by forests with smaller trees and more grass and shrub habitats. These changes in forest height and structure could, in turn, change the composition of the floodplain forest bird community. Many members of the present bird community are heavily dependent on tall-canopied forests for breeding and feeding and would be adversely affected by large-scale change toward a small-statured forest. Upper canopy nesters and feeders and cavity-nesting birds would be most affected.

A total of 84 bird species was identified over the three census years. Some common bird species in UMR floodplain forests include the American robin *(Turdus migratorius),* house wren *(Troglodytes aedon),* great crested flycatcher *(Myiarchus crinitus),* northern oriole *(Icterus galbula),* American redstart *(Setophaga ruticilla),* eastern wood-pewee *(Contopus virens),* and yellow-bellied sapsucker *(Sphyrapicus varies).* Floodplain forest specialist species on the UMR include the prothonotary warbler *(Protonotaria citrea),* redshouldered hawk *(Buteo lineatus),* and bald eagle *(Haliaeetus leucocephalus).* Several floodplain species are at risk because of population declines regionally or continentally (Breeding Bird Survey, unpublished data). These species include the red-headed woodpecker *(Melanerpes erythrocephalus),* northern flicker *(Colaptes aerates),* downy woodpecker *(Picoides pubescens),* eastern wood-pewee, great crested flycatcher, tree swallow *(Tachycineta bicolor),* black-capped chickadee *(Pares atricapillus),* white-breasted nuthatch *(Sitta carolinensis),* blue-gray gnatcatcher (*Polioptila caerulea),* gray catbird *(Dumetella carolinensis),* warbling vireo *(Vireo gilvus),* yellow-throated vireo *(Vireo flavifrons),* redeyed vireo *(Vireo olivacems),* American redstart, prothonotary warbler, common yellowthroat *(Geothlypis trichas),* rose-breasted grosbeak *(Pheucticus lzulovicianzsr),* northern oriole, Acadian flycatcher *(Empidonax virescens),* least flycatcher *(Empidonax minimus),* willow flycatcher *(Empidonax traillii),* veery *(Catharus furcescens),* cerulean warbler *(Dendroica cerulea),* and ovenbird *(Seiurus aurocapillus).*

Floodplain forests also provide important habitat for cavity and bark-nesting species because of the abundance of large snags. This is particularly true for species that require large cavities, such as the pileated woodpecker (*Dryocopus pileatur).* On the UMR, 23 species use cavities for nesting, including 7 woodpecker species, the house wren, greatcrested flycatcher, white-breasted nuthatch, prothonotary warbler, black-capped chickadee, tree swallow, brown creeper *(Certhia americana),* wood duck (*Aix sponsa*), barred owl (Strix *varia),* chimney swift *(Chaetura pelagica),* European starling *(Sturnus vulgaris),* Carolina wren *(Thryothorus ludovicianus),* hooded merganser *(Lophodytes czicullatus),* eastern bluebird *(Sialia sialis),* and purple martin *(Progne subis).* The abundance and size of snags is probably higher in the floodplain than in the adjacent upland forests because of differences in timber harvesting intensity and because hydrologic changes influence floodpla.in tree survival.

We found that about 35010 of the species changed in abundance or frequency of occurrence over the study period. Species richness overall and relative abundances of several groups of birds classified by management risk categories and guild associations declined in 1994. Lowered abundance and species richness in 1994 may have resulted from effects of the 1993 flood. A few groups of birds increased over the period, including birds preferring habitats near water and piscivores. The National Biological Service's Breeding Bird Survey identifies similar patterns at a regional and continental scale, but because the survey is conducted from roadside counts, floodplain and wetland habitats, in general, are underrepresented. My research provides detailed baseline information on the floodplain forest bird community along with estimates of annual variation, which will serve as a benchmark for future monitoring efforts in the study area.

To my knowledge, no previous study has examined the effect of a major flood on breeding birds of large northern floodplain forests. We found that species richness did not differ among the plots tested, but abundance was lower in 1994 overall and for several individual species and species groups. Species with the strongest evidence of lowered abundance during flooding include the blue jay *(Cyanocitta cristata),* house wren, yellow warbler *(Dendroica petechia),* common yellowthroat, brown-headed cowbird *(Malothrus ater),* and American goldfinch *(Carduelis tristis).* For the blue jay, house wren, and common yellowthroat, we present evidence that lowered abundance coincident with the flood persists into the following breeding season. These birds constitute a relatively small percentage of the total floodplain bird community. Relative abundances of most floodplain birds were little affected. Abundances of birds within management risk categories or guild associations did not show similar strong evidence of flood sensitivity. Not all flood effects were negative; some species increased in abundance on flooded plots, including the cerulean warbler and white-breasted nuthatch. Major flooding may maintain appropriate habitat for prothonotary warblers in the face of nest-site competition from house wrens.

I found that species diversity of floodplain birds, and the abundance and richness of hole-nesting and bark-gleaning bird guilds, are associated with mature forests within a landscape matrix dominated by forest. Within the floodplain, vegetation (small scale) variables had a larger influence on bird distributions than landscape matrix (large scale) factors. Area-sensitivity follows a different pattern in the floodplain than in uplands. Species considered area-sensitive in the floodplain and previously identified as area-sensitive in upland studies include the yellow-billed cuckoo (*Coccyzus americanus),* ruby-throated hummingbird *(Archilochus colubris),* red-bellied woodpecker *(Melanerpes carolinus),* hairy woodpecker (*Picoides villosus*), white-breasted nuthatch, and brown creeper. Many species identified as area-sensitive in uplands do not show these patterns in the floodplain. I suggest that the landscape matrix of the floodpiain, which is predominantly water and marsh rather than agricultural fields or urban land, may change predator and nest parasite dynamics. If relative abundance and species richness are reliable indicators of habitat quality, the UMR floodplain provides important habitat for area-sensitive species, including some neotropical migrants.

In an artificial nest study I found that, contrary to many similar studies, large forest tracts had higher predation rates than small forest tracts (52.3% vs. 36.3%). Furthermore, there was no significant difference in predation rates among nests placed 25, 50, 100 or 200 m from the forest edge. Predation rates decreased over the nesting season. Calculated artificial nest "survival", derived from observed predation rates in 1993-94, was similar to natural nest survival for several species for the same study area in 1992. Nest losses did not differ among several habitat variables measured at the nest sites. We hypothesize that floodplain predators are different than upland predators and that edges in the floodplain do not support large numbers of predators, especially mammals.

Patterns of distribution and abundance of area-sensitive bird species on the UMR differ from those reported in numerous studies of upland forest birds. In addition, patterns of nest predation are different than those observed in upland bird communities. These findings indicate that the processes underlying these patterns may also be different. A priority for future research is demographic study of songbird populations, which will clarify differences in reproductive success between upland and lowland habitats, especially for species at risk of population decline. Little is known about how cowbird parasitism affects floodplain birds, and such studies would also clarify these relationships. Since predation is a major source of reproductive failure in songbirds, research aimed at understanding differences in the effects of predators on avian reproductive success in upland vs. lowland forests of the UMR region should also be undertaken. Since some members of the present floodplain bird community require floodplain forests of adequate size and vegetative structure, predictive models should be developed to anticipate changes in the floodplain forest plant community that would adversely affect these birds.

Our current understanding of predator-prey dynamics and the population ecology of floodplain forest birds is still too sketchy to allow clear recommendations regarding which components of the floodplain are of highest conservation priority. My research points out the dangers of assuming that patterns observed in upland habitats can be extrapolated to large floodplain forests without testing. It is likely that the patterns of species distribution and abundance and nest predation that I observed in the large floodplains of the UMR indicate that there are fundamental differences between uplands and lowlands in some underlying ecological processes. The specifics of those processes remain to be worked out.

Since our current understanding of the role of floodplain forests as wildlife habitats is simplistic and limited primarily to birds, the most prudent management recommendation is to conserve the existing forests in as close to their present state as possible, with no additional loss of forest. Forest management should focus on encouraging natural forest successional processes linked to the hydrology of the floodplain. River fluvial processes, altered by navigation structures, should be managed to provide mud flats where early successional species can become established and grow. In addition, a healthy floodplain forest should have some areas of young trees and shrubs as well as mature forests with large standing snags. Efforts should be made to expand the area occupied by floodplain forests and increase species diversity to compensate for the major floodplain forest losses since European settlement. Restoration of higher-elevation terrace forests could provide nearly the full complement of tree species present before large-scale forest conversion, including some flood-intolerant species. Trees adapted to these sites in our study area include *Q. bicolor,* Q. *alba, Q. rubra, Carya* spp., *Gleditsia triacanthos, A. saccharum, C. occidentalis; Prunus serotina, Juglans nigra, J. cinerea,* and *Robinia pseudo-acacia* (Galatowitsch and McAdams 1994, Yin et al. 1994). Regeneration techniques such as clear-cutting and tree removal deprive cavity-nesting birds of critical habitat and satisfactory tree regeneration on cut-over areas may be retarded due to competition from *P. arundinaceae* .

LITERATURE CITED

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

Brittingham, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33: 31-35.

Decamps, H., J. Joachim and J. Lauga. 1987. The importance for birds of the riparian woodlands within the alluvial corridor of the River Garonne, S. W. France. Regulated Rivers: Research and Management 1: 301-316.

Emlen, J. T., M. J. DeJong, M. J. Jaeger, T. C. Moermond, K. A. Rusterholtz and R. P. White. 1986. Density trends and range boundary constraints of forest birds along a latitudinal gradient. Auk 103: 791-803.

Finch, D. M. 1991. Population ecology, habitat requirements, and conservation of neotropical migratory birds. General Technical Report RM-205. June 1991. U.S.D.A. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 26 pp.

Freemark, K. E., J. B. Dunning, S. J. Hejl and J. R. Probst. in press. A landscape ecology perspective for research, conservation and management. Pages 1-105 In T. Martin and D. Finch, Eds. Ecology and management of Neotropical migratory birds: a synthesis and review of the critical issues. Oxford University Press, New York, NY.

Galatowitsch, S. M. and T. V. McAdams. 1994. Distribution and requirements of plants on the Upper Mississippi River: literature review. Unpublished project report to U.S. Fish and Wildlife Service. June, 1994. Iowa Cooperative Fish and Wildlife Research Unit, Ames, IA. 175 pp.

Grettenberger, J. 1991. Habitat fragmentation and forested wetlands on the Upper Mississippi River. Potential impacts on forest interior birds. Passenger Pigeon 53: 227-241.

Laustrup, M. S. and C. D. Lowenberg. 1994. Development of a systematic land cover/land use database for the Upper Mississippi River System derived from Landsat thematic mapper satellite data. National Biological Survey, Environmental Management Technical Center, Onalaska WI. 90 pp.

Lynch, J. F. and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation 28: 287-324.

Moore, G. F. 1988. Plant communities of Effigy Mounds National Monument arid their relationship to presettlement regional vegetation. Master's thesis. University of Wisconsin, Madison. 148 pp.

Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8: 17-26.

Peck, J. H. and M. M. Smart. 1986. An assessment of the aquatic and wetland vegetation of the Upper Mississippi River. Hydrobiologia 136: 57-76.

Rappole, J. H. and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. Auk 111: 652-660.

Robbins, C. S., D. K. Dawson and B. A. Dowell. 1989a. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildlife Monographs 103: 1-34.

Robbins, C. S., J. R. Sauer, R. S. Greenberg and S. Droege. 1989b. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences 86: 7658-7662.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987-1957.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-201 *In* B. R. L. and D. M. Sharpe, Eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Yin, Y. and J. C. Nelson. 1995. Modifications to the Upper Mississippi River and their effects on floodplain forests. Long Term Resource Monitoring Program technical report 95-T003. National Biological Service, Environmental Management Technical Center, Onalaska, WI. 17 pp.

Yin, Y., J. C. Nelson, G. V. Swenson, H. A. Langrehr and T. A. Blackburn. 1994. Tree mortality in the Upper Mississippi River and floodplain following an extreme flood in 1993. Pages 39-60 *In* J. W. Barko and M. M. Wise, Eds. Long Term Resource Monitoring Program, 1993 flood observation report. National Biological Service, Illinois Natural History Survey, and Wisconsin Department of Natural Resources. Onalaska, WI.