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FACTORS INFLUENCING AVIAN COMMUNITY STRUCTURE IN BOTTOMLAND HARDWOOD FORESTS OF THE SOUTHEASTERN UNITED STATES

By

Michael Scott Husak

A Dissertation Submitted to the Faculty of Mississippi State University in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Biological Sciences in the Department of Biological Sciences

Mississippi State, Mississippi

May 2007

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SOUTHEASTERN UNITED STATES

By

Michael Scott Husak

Approved:

Eric T. Linder Assistant Professor of Biological Sciences (Director of Dissertation) Christopher M. Taylor Professor of Biological Sciences (Committee Member)

Gary N. Ervin Assistant Professor of Biological Sciences (Committee Member) Terry C. Maxwell Professor of Biological Sciences (Committee Member)

Dwayne A. Wise Professor of Biological Sciences and Graduate Coordinator (Committee Member) Philip B. Oldham Dean of College of Arts and Sciences Name: Michael Scott Husak

Date of Degree: May 5, 2007

Institution: Mississippi State University

Major Field: Biological Sciences

Major Professor: Dr. Eric T. Linder

Title of Study: FACTORS INFLUENCING AVIAN COMMUNITY STRUCTURE IN BOTTOMLAND HARDWOOD FORESTS OF THE SOUTHEASTERN UNITED STATES

Pages in Study: 117

Candidate for the Degree of Doctor of Philosophy

Bottomland hardwood forests (BHF) are a disappearing habitat of importance to numerous migratory and non-migratory birds of conservation concern. Thus, understanding variables of bottomland hardwood forests that affect avian assemblage patterns are of great interest. I examined factors influencing avian assemblage and guild patterns in BHF of Noxubee National Wildlife Refuge in east-central Mississippi by conducting winter and spring fixed-radius avian point counts and vegetation surveys from 2002 – 2004. The goals of this project were to 1) determine effects of greentree reservoir (GTR) management on breeding and wintering non-game bird community structure, 2) test hypotheses regarding plant structural complexity and avian assemblage patterns, and 3) examine the effects of landscapes on local bird assemblages within BHF.

Greentree reservoirs have subtle effects on avian communities. Sites within GTRs, sites in BHF adjacent to GTRs, and random, unimpounded BHF sites differed significantly in breeding bird diversity, richness, and evenness. However, the patterns

exhibited were a decreasing continuum of these variables with sites peripheral to GTRs demonstrating intermediate values. No differences were found among abundance, conservation status, or habitat specialization of breeding birds. Guild parameters did not differ except for a decreasing continuum in species richness among unimpounded BHF, BHF to GTRs, and GTR sites. The canopy nesting and ground gleaning foraging guilds were the only guilds found to differ among sites. Patterns could indicate that given the inherent structural variation of BHF, GTRs are within the expected range of variation, or GTR management could be indirectly affecting the surrounding landscape. GTR management did not affect community parameters for wintering birds, and only the bark gleaning foraging guild varied among sites (higher in GTRs). These results reflect the ubiquitous nature of wintering birds in east-central Mississippi forests.

There was direct support for the structural vertical heterogeneity hypothesis; however, regression analyses of principal component scores derived from sixty structural descriptor metrics suggest that avian communities and guilds are more directly influenced by overall local plant structural complexity, as predicted by the spatial heterogeneity hypothesis. Avian community and guild parameters did not differ among the three landscape contexts defined by 1,000 and 1,500m buffers.

DEDICATION

This dissertation is dedicated to my parents, Genevieve Matejicek Husak and the late Jerry Joe Husak III, to whom I attribute my interest in and curiosity about life and natural systems. Their unyielding support and belief in what I could accomplish have remained a source of strength for which I will always be grateful.

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TABLE OF CONTENTS

DEDICA	TION	ii
ACKNO	WLEDGEMENTS	. iii
LIST OF	TABLES	viii
LIST OF	FIGURES	xii
СНАРТЕ	ER	
I.	INTRODUCTION	1
	LITERATURE CITED	4
II.	EFFECTS OF GREEN TREE RESERVOIR MANAGEMENT ON BREEDING BIRD COMMUNITIES OF BOTTOMLAND HARDWOOD FORESTS IN MISSISSIPPI	6
	ABSTRACT	6
	INTRODUCTION	7
	STUDY AREA	. 10
	METHODS	. 11
	Point-Count Surveys.	. 11
	Analyses	. 13
	RESULTS	. 16
	Community Composition	. 16
	Conservation-Concern Rankings.	. 17
	Nesting Guilds.	. 18
	Foraging Guilds.	. 19
	Species Composition	. 20
	DISCUSSION	. 21
	Effects of GTR Management on General Avian Community Structure	. 23
	Effects of GTR Management on Species of Conservation Concern and	
	Habitat Specialists	. 25
	Effects of GTR Management on Nesting and Foraging Guild Richness	25
	and Adundance	23
	Effects of GTK Management on Species Composition.	. 20

	Management Implications. ACKNOWLEDGEMENTS LITERATURE CITED	. 27 . 28 . 28
III.	WINTER BIRD COMMUNITIES IN IMPOUNDED AND UNIMPOUNDED BOTTOMLAND HARDWOOD FORESTS: EFFECTS OF LONG-TERM GTR MANAGEMENT IN MISSISSIPPI	. 33
	ABSTRACT INTRODUCTION STUDY AREA METHODS Point-Count Surveys Analyses RESULTS General Community Structure Conservation-Concern Rankings. Habitat Specialization Foraging Guilds Before and After Inundation Foraging Guilds Before and After Inundation Foraging Guilds Without Seasonal Effects DISCUSSION Management Implications ACKNOWLEDGEMENTS LITERATURE CITED	. 33 . 34 . 37 . 37 . 37 . 39 . 43 . 43 . 43 . 43 . 43 . 44 . 48 . 55 . 56
IV.	TESTING THE RELATIONSHIP BETWEEN VEGETATION STRUCTURAL COMPLEXITY AND AVIAN ASSEMBLAGE STRUCTURE IN BOTTOMLAND HARDWOOD FORESTS	. 61 . 62 . 65 . 66 . 67 . 69 . 70 . 70 . 70 . 70 . 71 . 71 . 75

CHAPTER

Page

V. LANDSCAPE HETEROGENEITY AND AVIAN ASSEMBLAGE CHARACTERISTICS IN BOTTOMLAND HARDWOOD FORESTS		General Plant Complexity and Guild Parameters DISCUSSION ACKNOWLEDGEMENTS LITERATURE CITED	76 77 81 81
ABSTRACT.87INTRODUCTION88STUDY AREA90METHODS91Point-Count Surveys91Landscape Parameters91Community Parameters92Analyses94RESULTS95DISCUSSION96ACKNOWLEDGEMENTS99LITERATURE CITED99VI.CONCLUSIONS103LITERATURE CITED108APPENDIX10A.BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES110B.WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES113	V.	LANDSCAPE HETEROGENEITY AND AVIAN ASSEMBLAGE CHARACTERISTICS IN BOTTOMLAND HARDWOOD FORESTS	S 87
METHODS 91 Point-Count Surveys. 91 Landscape Parameters 91 Community Parameters 92 Analyses 94 RESULTS 95 DISCUSSION 96 ACKNOWLEDGEMENTS 99 LITERATURE CITED 99 VI. CONCLUSIONS 103 LITERATURE CITED 108 APPENDIX A. BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES 110 B. WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES 110		ABSTRACT INTRODUCTION STUDY AREA	87 88 90
Analyses 91 Community Parameters 92 Analyses 94 RESULTS 95 DISCUSSION 96 ACKNOWLEDGEMENTS 99 LITERATURE CITED 99 VI. CONCLUSIONS 103 LITERATURE CITED 108 APPENDIX 108 A. BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED 110 B. WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL 110		METHODS Point-Count Surveys	91 91
Analyses		Landscape Parameters Community Parameters	91 92
DISCUSSION 96 ACKNOWLEDGEMENTS 99 LITERATURE CITED 99 VI. CONCLUSIONS 103 LITERATURE CITED 108 APPENDIX 108 A. BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL 110 B. WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED 110 B. WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL 110 B. MINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL 113		Analyses	94 95
ACKNOWLEDGEMENTS 99 LITERATURE CITED 99 VI. CONCLUSIONS 103 LITERATURE CITED 108 APPENDIX A. BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES 110 B. WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES 113		DISCUSSION	95 96
VI. CONCLUSIONS		ACKNOWLEDGEMENTS LITERATURE CITED	99 99
LITERATURE CITED	VI.	CONCLUSIONS	103
 APPENDIX A. BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES		LITERATURE CITED	108
 A. BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES	APPENI	DIX	
B. WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES	A.	BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES	110
	B.	WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES	113

C.	VEGETATION VARIABLES MEASURED AT NOXUBEE	
	NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI11	17

LIST OF TABLES

TABLE

Page

2.1.	Avian community mean (± SE) diversity (Shannon-Weiner Diversity Index), species richness, abundance, and evenness (Jaccard Index) among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results	. 17
2.2.	Mean (± SE) conservation values, avian wetland dependency values, and habitat specialist values of unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results	. 18
2.3.	Nesting guild mean (± SE) species richness and abundance among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (GTR-Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.	. 19
2.4.	Foraging guild mean (± SE) species richness and abundance among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.	. 20
2.5.	DCA axis scores (mean ± SE) for avian species composition among unimpounded bottomland hardwood forest (BHF), greentree reservoirs (GTR), and bottomland hardwood forest adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters	

TABLE

3.1.	Repeated measure ANOVAs on mean community traits for avian winter community structure comparing pre- and post-flood (seasons) parameters among unimpounded bottomland hardwood forest stands (BHF; N = 25, greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) at Noxubee National Wildlife Refuge, Mississippi
3.2.	Repeated measure ANOVAs on mean community traits for avian winter community structure (with-in winter data combined) among unimpounded bottomland hardwood forest stands (BHF; N = 25, greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) at Noxubee National Wildlife Refuge, Mississippi
3.3.	 Avian winter community mean (± SE) diversity (Shannon-Weiner Diversity Index), species richness, abundance, and evenness (Jaccard Index) among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (GTR-Peripheral) at Noxubee National Wildlife Refuge, Mississippi 47
3.4.	Repeated measure ANOVAs on mean community traits for avian winter concervation-concern rankings among unimpounded bottomland hardwood forest stands (BHF; N = 25, greentree reservoirs (GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) at Noxubee National Wildlife Refuge, Mississippi. Because no seasonal effects were found, within-winter counts were combined to test for effects of habitat and year
3.5.	Repeated measure ANOVAs on mean foraging guild traits for avian winter communities among unimpounded bottomland hardwood forest stands (BHF; N = 25), greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) immediately before and after seasonal water impoundment at Noxubee National Wildlife Refuge, Mississippi
3.6.	Repeated measure ANOVAs on mean foraging guild traits for avian winter communities among unimpounded bottomland hardwood forest stands (BHF; N = 25), greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) in which there were no direct effects of flooding on local assemblages at Noxubee National Wildlife Refuge, Mississippi (i.e., within winter counts pooled)

TABLE

Page

3.7.	Mean (± SE) species richness and abundance of bark foraging species in unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs (GTR), and BHF stands adjacent to GTRs (GTR-Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.	. 54
4.1.	Principal component scores for vegetation characteristics of bottomland hardwood forest stands at Noxubee National Wildlife Refuge, Mississippi.	. 72
4.2.	Component matrix for vegetation variables in bottomland hardwood forest stands at Noxubee National Wildlife Refuge, Mississippi with scores >0.50.	. 73
4.3.	Stepwise regression model for avian foraging guild diversity (dependent variable) and principal component scores of local vegetation characteristics (Independent variables) at Noxubee National Wildlife Refuge, Mississippi.	. 75
4.4.	Stepwise regression model for avian nesting guild diversity (dependent variable) and principal component scores of local vegetation characteristics (Independent variables) at Noxubee National Wildlife Refuge, Mississippi	. 76
5.1.	Mean (± SE) values for breeding season avian community variables associated with bottomland hardwood plots located within a pure bottomland hardwood landscape (BHF; > 90% bottomland), pine-hardwood landscape (> 40% pine), and open-hardwood landscape (> 40% pastures and fields) at Noxubee National Wildlife Refuge, Mississippi (2002 – 2004)	. 95

TABLE

- A.1. Conservation concern rankings, habitat specificity scores, wetland dependency scores, and guilds of species in unimpounded BHF, GTR, and GTR-peripheral sites. Conservation concern scores are Partners in Flight rankings. Habitat specificity and wetland dependency ranks follow Croonquist and Brooks (1991) and Snell-Rood and Cristol (2003) and when not available, author experience. Habitat Specificity: 1 = generalist, 3 = selection basedupon general landscape features, not a single habitat type, 5 = habitat specialist. Wetland dependency: 0 =upland, 1 =occassionally uses wetlands, 3 = usually uses wetlands, 5 = found in wetlands only. Nesting guild (Ehrlich et al. 1988): 1 = ground, 2 = shrub, 3 = understory, 4 = canopy, 5 = cavity, 6 = bank, 7 = nest parasites. Foraging guild (Ehrlich et al. 1988): 1 = foliage gleening insectivore, 2 = bark gleening insectivore, 3 = ground gleening insectivore, 4 = ground gleening granivore, 5 = ground gleening omnivore, 6 = flycatching, 7 = nectarivores, 8 = aerial divers, 9 = raptorial,
- B.1. Conservation concern rankings, habitat specificity scores, wetland dependency scores, and Foraging guilds of species in unimpounded BHF, GTR, and GTR-peripheral sites. Conservation concern scores are Partners in Flight rankings. Habitat specificity and wetland dependency ranks follow Croonquist and Brooks (1991) and Snell-Rood and Cristol (2003) and when not available, author experience was used. Habitat Specificity: 1 = generalist, 3 = selection based upon general landscape features, but not a single habitat type, 5 = habitat specialist. Wetland dependency: 0 = upland, 1 =occassionally uses wetlands, 3 = usually uses wetlands, 5 = found in wetlands only. Foraging guild (Ehrlich et al. 1988): 1 = foliage gleaning insectivore, 2 = bark gleaning insectivore, 3 = ground gleaning insectivore, 4 = ground gleaning granivore, 5 = ground gleaning omnivore, 6 = flycatching, 7 = nectarivores, 8 = aerial divers, 9 = raptorial, 10 = stalk and strike, 11 = dabblers. 114

LIST OF FIGURES

FIGURE

Page

2.1.	CCA bi-plot of species scores associated with Axes 1 and 2 for	
	unimpounded bottomland hardwood forests (Hab1), greentree	
	reservoirs (Hab2), and bottomland hardwood forests adjacent to GTRs	
	(Hab3) at Noxubee National Wildlife Refuge, Mississippi. Axes were	
	significant ($F = 2.038, P = 0.001$)	2

CHAPTER I

INTRODUCTION

Determining factors affecting assemblage structure and diversity is a fundamental goal of ecology. However, it has been shown that characteristics of assemblages are dependent upon the scale at which they are examined (e.g., Williams et al. 2002). While ecologists traditionally assumed that most important ecological processes affecting communities operated at the local spatial scale, scientists have recently come to understand that relevant factors occur across various spatial scale. For example, habitat fragmentation and landscape heterogeneity can affect local assemblages through differing effects on functional groups and altering population processes (Williams et al. 2002). Landscape context can also structure a community by influencing within patch dynamics as well as influence movement across the landscape (Kilgo et al. 1997). Developing an integrated theory of assemblage structure will require an integration of comparative research on community patterns across spatial scales.

Over the past four decades, many songbirds have undergone significant declines in North America (Sauer et al. 2001). Nearly two-thirds of birds breeding in eastern North America are included among those species in peril. Within the East Gulf Coast Plain Physiographic Area, 46 species of Neotropical migrants have been identified as being in need of increased population conservation and/or habitat preservation (Hunter et al. 1993). Within this physiographic region, bottomland hardwood forests support the greatest overall diversity of breeding birds, including many Partners in Flight species of priority concern, and they serve as important migratory corridors and wintering habitats (Hunter et al. 1993). Due largely to variation in local hydrology, periodic windthrows, and adjacent habitat types, bottomland hardwood forests are a dynamic and heterogeneous assemblage of plants. This site-specific variation in plant structure results in a site-specific assemblage of birds (Sallabanks et al. 2000).

Once covering vast acreage in the southeastern United States, these forested wetlands have been lost to agricultural development, harvested for timber, converted to forest plantations, and impounded for flood control and recreation (Abernathy and Turner 1987, Sallabanks et al. 2000). Total loss and alteration of landcover have occurred at a rate nearly five times greater than any other forest type in the country over the last two centuries (Abernathy and Turner 1987). Degradation and loss of habitat have had a major impact on breeding bird communities, and thus bottomland hardwood ecosystems have been identified as requiring the highest conservation priority (Hunter et al. 1993). Mississippi remains among the most forested states east of the Rocky Mountains, with more than 7.3 million ha of timberland (about 62% of entire state), approximately 20% of which remains bottomland hardwood forests, though little is old-growth (Rosson 2001).

A relatively common land management practice in Mississippi, as well as much of the southeastern U.S., is the building and maintenance of greentree reservoirs (GTRs). GTRs are seasonally impounded bottomland hardwood forest stands, controlled by a series of levees and water control structures, for the purpose of providing wintering and migratory habitat for waterfowl (Wigley and Filer 1989). Such land use practices have been implicated in causing significant alteration to local vegetation composition and structure (e.g., King and Allen 1996, Kilgo et al. 1997), which may ultimately alter local bird species occurrence, abundance, and/or survival (Christman 1984). Only two studies have previously addressed potential effects of GTR management on non-game birds (Christman 1984, Deller and Baldassare 1998, 1999) and their results suggest some effect on breeding bird communities, but more work is needed. No winter studies of GTR impacts on non-game birds have been conducted thus far.

The goal of this dissertation was examine factors affecting avian community structure within bottomland hardwood forests across multiple spatial scales, including anthropogenic factors such as GTR management and landscape alteration. The structural heterogeneity of bottomland hardwood forests and resulting variation in local avian assemblage patterns make them ideal habitats for testing hypotheses regarding mechanisms of community structure. While numerous studies have addressed plant/bird assemblage issues in the past, few have done so across multiples spatial scales within bottomland hardwood forests (most are upland) or in bottomland hardwood forest stands within a primarily forested landscape matrix (many are of highly fragmented stands within agricultural or urban landscapes). In the following chapters I examine the effect of GTR management on breeding (chapter 2) and wintering (chapter 3) bird assemblages, the effect of variation in plant structural complexity on bird community structure (chapter 4), and the effects of landscape heterogeneity on local bird community structure (chapter 5).

3

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CHAPTER II

EFFECTS OF GREEN TREE RESERVOIR MANAGEMENT ON BREEDING BIRD COMMUNITIES OF BOTTOMLAND HARDWOOD FORESTS IN MISSISSIPPI

ABSTRACT

Greentree reservoirs (GTRs) are seasonal impoundments of bottomland hardwood forest (BHF) stands built for waterfowl management. While they have been shown to increase waterfowl abundance, they have also been shown to detrimentally affect vegetation characteristics, invertebrate diversity, and perhaps songbird community characteristics. The objective of this study was to assess the effect of long-term (40+ yr) GTR management on avian breeding assemblage patterns in east-central Mississippi. Four GTRs and surrounding unimpounded BHF within Noxubee National Wildlife Refuge were surveyed using point-count protocols from 2002 – 2004. Comparisons were made of general avian community structure (diversity, richness, abundance, and evenness), avian conservation values, habitat specialization, wetland dependency, nesting guilds, and foraging guilds. Sites within GTRs, sites in BHF adjacent to GTRs (GTRperipheral), and random BHF sites differed in diversity, richness, and evenness (p < 0.05 for all variables) with a continuum of decreasing diversity occurring from within GTRs to random BHF sites. No differences were found among measures of abundance, conservation status, or habitat specialization. Within guild richness and abundance were similar among sites except for a decreasing continuum in species richness among BHF, GTR-peripheral, and GTR sites. The canopy nesting guild was the only guild found to have significantly higher richness in BHF sites, and the ground gleaning foraging guild had a significantly lower abundance in GTRs. Previous studies lack consistent results regarding impacts of greentree reservoirs on bottomland hardwood forest avian assemblages, and the inclusion of sites peripheral to GTRs in my study underscores the need for more work to determine what long-term impacts, if any, may be present.

INTRODUCTION

Greentree reservoirs (GTR) are bottomland hardwood forest (BHF) stands that are seasonally flooded by levees and water control structures during the fall and winter to provide foraging and resting habitats for migrating waterfowl (Reinecke et al. 1989). The first of such impoundments were constructed in the 1930's by private duck hunting clubs in eastern Arkansas (Rudolph and Hunter 1964). A 1987 census documented 142 GTRs in the southeastern U.S. alone, many on public lands, averaging more than 300 ha each (Wigley and Filer 1989). More recent surveys are not available (S. King, pers. comm.). GTR management has proven to be an effective management tool for waterfowl (e.g., Reinecke et al. 1989), but impacts on non-game species are poorly understood (e.g., Wehrle et al. 1995, Christman 1987, Deller and Baldassarre 1999).

A number of potential long-term ecological problems associated with GTRs have also been identified. With GTR management regimes, flooding is typically less dynamic and of longer duration and greater depth than natural flooding regimes in BHF. Previous studies suggest that these factors likely result in conversion to more water tolerant plant assemblages over time (King and Allen 1996). For example, a study of GTRs in Mississippi indicated an increase in overcup oaks (*Quercus lyrata*) and red maples (*Acer rubrum*), and a corresponding decrease in red oaks (*Quercus* spp.), green ash (*Fraxinus pennnsylvanica*), and American elm (*Ulmus americana*) compared to un-impounded sites after 30 years of impoundment. Furthermore, a general decrease in sapling and understory recruitment and basal area, and an increase in windthrow density have also been noted (e.g., King 1995, King and Allen 1996, and King et al. 1998).

Once covering vast acreage in the southeastern United States, forested wetlands have been lost to agricultural development, harvested for timber, converted to forest plantations, and impounded for flood control and recreation (Abernethy and Turner 1987, Sallabanks et al. 2000). Total loss and alterations have occurred at a rate five times greater than any other forest type in the United States over the last two centuries (Abernethy and Turner 1987). Degradation and loss of habitat have had a major impact on breeding bird populations (Sallabanks et al. 2000). For these reasons, BHF ecosystems have been identified as requiring the highest conservation priority (Hunter et al. 1993). Today, Mississippi remains one of the most forested states in the eastern U.S. with more than 7,300,000 ha of timberland (62% of state), approximately 20% of which remains BHF (Rosson 2001).

Due largely to variation in local hydrology, periodic wind throws, and adjacent habitat types, BHF are a dynamic and heterogeneous assemblage of plants. This sitespecific variation in plant structure results in site-specific assemblages of birds (Sallabanks et al. 2000). Because GTRs may reduce vertical structural heterogeneity of vegetation, they may also in turn result in the loss of avian foraging and/or nesting substrates or cover (Kilgo et al. 1997, Martin 1993,), ultimately altering local bird species occurrence, abundance, or breeding success. Potential long-term shifts in avian assemblage patterns are important to land managers as protection of biodiversity has received an increased emphasis in recent decades. Thus, managers may consider different goals for GTRs in addition to, or in place of, an emphasis on waterfowl species.

Within the East Gulf Coast Plain Physiographic Area, 46 species of Neotropical migratory landbirds have been identified for increased habitat conservation and/or population conservation (Hunter et al.1993). In this region, BHF support the greatest overall diversity of breeding birds, a large number of which are Neotropical migrants and/or Partners in Flight (PIF) species of priority concern (Hunter et al. 1993). BHF also serve as important migration corridors and wintering habitat for numerous additional migrants (Hunter et al. 1993).

The only published studies examining the effect of GTR management on breeding bird communities were conducted by Christman (1987) in Arkansas and Deller and Baldassarre (1998, 1999) in New York. Christman (1987) examined a single 1,600 ha GTR and found that during the breeding season bird richness in the GTR was significantly lower than that observed in an adjacent BHF stand. Deller and Baldassarre (1998) conducted surveys of two GTRs a year before flooding and following one year of flooding. They found that community diversity and species abundance and richness did not differ, except for a minor reduction in Wood Thrushes (*Hylocichla mustelina*), and a slight increase in Common Grackles (*Quiscalus quiscula*) and Red-winged Blackbirds (*Agelaius phoeniceus*; Deller and Baldassarre 1998, 1999).

While these findings are important, a more detailed study of long-term GTR management is needed to determine how general results are and to better understand the impact, if any, that GTRs have on breeding birds, especially those of conservation concern. To address this knowledge gap, I examined the impact of GTR management on BHF breeding bird community structure. Specifically, I hypothesized that due to structural modification of vegetation resulting from GTR management (King 1995, King and Allen 1996, and King et al. 1998), GTRs and natural BHF will vary in avian breeding community structure. Specifically, I predicted that 1) GTRs will have overall lower breeding bird species richness and abundance than natural BHF, 2) BHF specialists will have decreased richness and abundance in GTRs compared to natural sites, and 3) ground foraging, ground nesting, and shrub nesting species will have overall lowest abundances in GTRs compared to natural sites.

STUDY AREA

This study was conducted on the Noxubee National Wildlife Refuge (NNWR) in east-central Mississippi (33°N, 88°W), covering portions of Oktibbeha, Noxubee, and Winston counties. As a whole, the study site is representative of low-gradient Gulf Coastal Plain floodplain forests, with an approximately 11m drop in elevation from west to east (Ervin et al. 2006). Of the nearly 19,400 ha of refuge land, about 6,300 ha are nearly contiguous bottomland hardwood forest crisscrossed by 10 small-order tributaries of the Noxubee River. A primary charge of NNWR is that of waterfowl management. To that end, two permanent reservoirs and four seasonal greentree reservoirs have been constructed. Greentree reservoirs 1 and 2 were constructed in 1955 and 1958 respectively, while GTR 3 and 4 were constructed in 1963. Flood duration of the GTRs has varied greatly over time, ranging from annual flooding from mid-November to mid-March, to occasional 5 - 7 day inundation events during this same time period. Soil of the GTRs and unimpounded bottomland hardwood forest stands is predominantly an Urbo-Mantachie association. The Urbo soils are generally found on the broad flats, while the Mantachie soils are found in higher areas, and generally near stream channels. Both soil types have high water capacities and moderate permeability. Runoff is generally slow (Young 1990). Previous studies on the refuge have examined the effect of GTR management on plant and invertebrate community structure (e.g., Young 1990, Young et al. 1995, Wehrle 1995, and Ervin et al. 2006). These studies found a significant difference in canopy tree composition and seedling recruitment between GTR and natural BHF stands, with an increased tendency towards more flood tolerant species in GTRs, such as bald cypress (*Taxodiium taxus*), overcup oaks (*Quercus lyrata*), and red maples (Acer rubrum; Young 1995, Ervin et al. 2006).

METHODS

Point-Count Surveys.

Fixed-radius (radius = 50m) point counts were used to assess avian community composition following standard survey protocol (Hamel et al. 1996) during the late spring and early summer of 2002 through 2004. Twenty five count stations were

randomly placed within stands of BHF and 23 count stations were randomly placed within the four GTRs with the constraint that all points were \geq 200m from the next nearest point and \geq 100m from any habitat edge. An additional eighteen count stations were placed within BHF stands, but along a 100m buffer zone surrounding GTRs. These peripheral sites (GTR-peripheral) were used to account for the potential that GTR sites differed as a result of location (i.e., topography and stream proximity) and not GTR management, a potential issue since GTRs are commonly constructed in lower lying areas for ease of flooding. Originally 20 points were planned in each of the stand types, but land use alteration and variable flooding regimes resulted in the loss of several points in and around GTRs and the addition of other points in BHF and GTR stands. However, the number and distribution of points did not differ among breeding seasons.

Actual surveys of point count sites began after a 2-minute waiting period to minimize effect of intrusion. Then all birds detected by sight or sound during a 10-min sampling period were recorded, excluding flyovers. Each count station was surveyed twice between 10 May and 15 June each year. Point count stations were not visited a second time until all other count stations had been completed once. Surveys were begun \geq 10-minutes after sunrise and conducted until 1000 central daylight savings time, weather permitting (e.g., no rain or wind > 19 km/hr). Size of plots and sampling time constraints were established to optimize sampling effort (Ralph et al. 1995, Hamel et al. 1996). Distance of each bird detected was also determined using a laser rangefinder (Bushnell Yardage Pro ©); however, it was decided to exclude distance sampling analyses for this study. While stand characteristics are compared, sites are all within a structurally similar habitat type and thus detection should be relatively consistent and would likely not benefit from estimates of detection probabilities (Buckland et al. 2001).

Analyses.

The following metrics were used to compare avian community characteristics among BHF, GTR, and GTR-peripheral sites: species abundance, species richness, species diversity, community evenness, community similarity, and conservation value scores. Species abundance and species richness were measured as the sum of the maximum number of individuals of all species observed in one sampling visit and the total number of species observed at each point, respectively. Species diversity was assessed using the Shannon Diversity Index (H'; Brower et al. 1998):

$$H' = -\Sigma p_i \log p_i$$

Where p_i is the proportion of species *i* within a community at a point. Community evenness (*J'*), or relative diversity, was measured as:

$$J' = H'/H_{max}'$$

Where H_{max}' is the natural log of the total number of species observed. Community similarity was measured using the Morisita Index of Overlap (I_M):

$$I_M = \frac{2\Sigma X_i Y_i}{(l_1 + l_2)N_1 N_2}$$

Where x_i is the abundance of a species in community 1, y_i is the abundance of that species in community 2, N_1 is the total number of individuals in community 1, N_2 is the total individuals in community 2, and l_1 and l_2 are Simpson's index values for community 1 and 2, respectively:

$$L_1 = \frac{\sum X_i(X_i - 1)}{N_l(N_l - 1)}$$

The Morisita index refers to the probability that individuals randomly drawn from different communities will belong to the same species. Scores range from 0 to 1, with 0 indicating no similarity and 1 indicating identical communities. This index was chosen because sizes and diversities of samples have little effect on results (Wolda 1981).

Because of the conservation concerns associated with bottomland hardwood forests in the southeastern U.S., several measures related to conservation status were considered, including conservation value indices, wetland dependency ranking, and BHF habitat specificity ranking of breeding birds. Breeding bird conservation value indices (*BBCV*) are useful in assessing avian communities because unlike general summary statistics, such as species richness or diversity, they incorporate demographic information about each species in the community (Götmark et al. 1986). Use of conservation values has increased in recent years, but there has been little agreement on the most appropriate indices to use when comparing communities. I used Partners in Flight composite index (*BBCV*_{PIFcomp}) because Partners in Flight scores have been shown to provide the most rigorous and objective weighting system available, and the composite method removes much of the dependence on sample size (Nuttle et al. 2003). Thus the index can be represented by:

$BBCV_{PIFcomp} = \sum_{i=1}^{s} a_i w_i$

Where *s* is the number of species in the community, a_i is the abundance of species *i*, and w_i is the weighting factor (i.e., PIF ranking). All PIF rankings follow those of Nuttle et al. (2003; Appendix A.1).

Wetland dependency and habitat specificity rankings are intended to evaluate the variation in site specific use by species requiring habitats of interest, in this case, bottomland hardwood forest residents (Snell-Rood and Cristol 2003). Such rankings reduce the effects of ubiquitous species on site comparisons. For both values, sites were ranked based upon how rich they were in species with traits that make them of high bottomland forest conservation interest. Each species was assigned a ranking for their wetland dependency and degree of habitat specificity following Croonquist and Brooks (1991) and Snell-Rood and Cristol (2003). When published rankings were not available, author experience was used. Wetland dependency rankings were: 0 = upland, 1 = sometimes uses wetlands, 3 = usually lives in wetlands, 5 = found only in wetlands. Habitat specificity rankings were: 1 = generalist, 3 = dependent upon the landscape (e.g., forest or grassland), but not a single habitat type (e.g., hardwood or pine forest), 5 = habitat specialist (see Appendix A.1 for species-specific rankings for all species). Site rankings were calculated by summing rankings for all species present at point-count sites.

Birds also were divided into nesting guilds (location of typical nest within vegetation strata) and foraging guilds (means of food acquisition) following Ehrlich et al. (1988). Species abundance and species richness within guilds were compared among BHF, GTR, and GTR-peripheral sites. Nesting guilds analyzed included: canopy nesters, understory nesters, shrub nesters, ground nesters, and cavity nesters. Foraging guilds included: flycatchers, foliage gleaners, bark gleaners, ground gleaners, and opportunistic omnivores. Raptorial, nectivorous, and aquatic foraging species were omitted due to small sample sizes. See Appendix A.1 for species-specific guild classification. All variables were analyzed using repeated measures Analysis of Variance (ANOVA) and post-hoc Tukey-Kramer pair-wise comparisons to test for forest stand and year effects. All analyses were done in SAS (PROC MIXED; 1990) and significance was set at $\alpha = 0.05$. All values are presented as mean \pm standard error. For ease of discussion, the use of habitat from this point forward refers to the different types of local forest (BHF, GTR, and GTR-peripheral) within a broader bottomland context.

Finally, exploratory analyses were used to examine potential variation in actual species composition among habitat types. Average abundance of species was compared among sites with detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) biplots using CANOCO, version 4.5 (ter Braak and Šmilauer 2002). DCA axes were compared among habitats with ANOVA and post-hoc Tukey-Kramer pair-wise comparisons using SAS (PROC MIXED; 1990).

RESULTS

Community Composition.

There were no effects of year, nor were there any interactions between year and habitat for any of the overall community variables examined (values available upon request). Total abundance of birds did not differ significantly among BHF, GTR, and GTR-peripheral sites (p = 0.16); however, they did differ in diversity (p < 0.0001), species richness (p = 0.0013), and species evenness (p = 0.0014; Table 2.1). Mean species diversity was higher per plot in BHF (2.500 ± 0.021) and GTR-peripheral (2.431 ± 0.035) sites than in GTRs (2.335 ± 0.029; p < 0.0001 and p = 0.05 respectively), but did

not differ from each other (p = 0.204). Richness was higher in BHF (13.33 ± 0.26) than in GTRs (11.61 ± 0.34; p = 0.0008), but not GTR-peripheral sites (12.51 ± 0.42; p =0.233), nor was richness greater in GTR-peripheral sites than GTRs (p = 0.174). Morisita's index of community similarity (I_M) were: BHF vs GTR = 0.49, BHF vs GTRperipheral = 0.51, and GTR vs GTR-peripheral = 0.49. Thus, I_M values indicate that all sites are in fact very similar in composition.

Table 2.1. Avian community mean (± SE) diversity (Shannon-Weiner Diversity Index), species richness, abundance, and evenness (Jaccard Index) among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.

Factor	BHF (N = 25)	GTR (N = 23)	Peripheral (N = 18)	F	Р
Diversity	$2.500\pm0.021^{\rm A}$	2.335 ± 0.029^{B}	$2.431 \pm 0.035^{\rm AB}$	9.62	< 0.0001
Richness	$13.33\pm0.26^{\rm A}$	11.61 ± 0.34^{B}	12.51 ± 0.42^{AB}	6.87	0.0013
Abundance	17.60 ± 0.45	16.19 ± 0.10	16.55 ± 0.64	1.85	0.1603
Evenness	$0.191 \pm 0.002^{\rm A}$	0.208 ± 0.004^{B}	$0.201 \pm 0.004^{\rm AB}$	6.85	0.0014

Conservation-Concern Rankings.

Conservation values (*BBCV*_{PIFcomp}) were higher in GTRs (18.02 ± 0.10) than BHF (17.66 ± 0.12; p = 0.05), but these differences were not significant (p = 0.639; Table 2.2). No differences were found in habitat specificity rankings or wetland dependency values among sites (Table 2.2).

Table 2.2. Mean (± SE) conservation values, avian wetland dependency values, and habitat specialist values of unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.

	BHF	GTR	Peripheral	F	Р
Conservation Value	17.66 ± 0.12	18.02 ± 0.10	17.88 ± 0.10	2.75	0.0667
Wetland Species Dependency Values	14.63 ± 0.581	14.51 ± 0.643	14.67 ± 0.879	0.01	0.9874
Habitat Specialist Values	30.36 ± 0.778	28.03 ± 0.892	29.57 ± 01.198	2.01	0.1376

Nesting Guilds.

Understory nesting, ground nesting, and cavity nesting species did not differ in richness or abundance among habitats (Table 2.3). Species richness and abundance differed among habitats for shrub nesting species. Species richness and abundance were higher in BHF than GTRs, but did not differ significantly from GTR-peripheral sites. Likewise, GTR-peripheral sites did not differ significantly from GTRs (Table 2.3). While abundance did not differ among habitats for canopy nesters, species richness did. Richness was higher in BHF than in GTRs and GTR-peripheral sites, which did not differ significantly from each other (Table 2.3).

Table 2.3. Nesting guild mean (± SE) species richness and abundance among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (GTR-Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.

Nesting Guild	Variable	BHF	GTR	GTR- Peripheral	F	Р
Canopy Nesting	Richness	$5.04\pm0.180^{\rm A}$	$4.43\pm0.173^{\text{B}}$	$4.39\pm0.198^{\text{B}}$	3.48	0.0357
	Abundance	6.41 ± 0.272	5.90 ± 0.262	5.55 ± 0.268	2.26	0.1100
Understory Nesting	Richness	1.74 ± 0.103	1.66 ± 0.094	1.65 ± 0.104	0.35	0.7052
	Abundance	2.30 ± 0.155	2.60 ± 0.182	2.18 ± 0.145	1.60	0.2043
Shrub Nesting	Richness	$2.76\pm0.131^{\rm A}$	1.94 ± 0.150^B	2.31 ± 0.162^{AB}	5.54	0.0051
	Abundance	$3.53\pm0.209^{\rm A}$	$2.48\pm0.195^{\text{B}}$	3.00 ± 0.273^{AB}	4.12	0.0189
Ground Nesting	Richness	$0.23\pm.0058$	0.15 ± 0.044	0.25 ± 0.062	1.18	0.3101
	Abundance	0.26 ± 0.070	0.27 ± 0.127	0.33 ± 0.091	0.76	0.4708
Cavity Nesting	Richness	4.80 ± 0.149	4.81 ± 0.199	5.14 ± 0.254	0.84	0.4367
	Abundance	6.86 ± 0.294	7.24 ± 0.385	7.20 ± 0.385	0.36	0.7002

Foraging Guilds.

Flycatching, bark gleaning, and opportunistic foraging species did not differ in species richness or abundance among habitats (Table 2.4). However, foliage gleaners exhibited higher diversity in BHF than in GTRs. Neither of these sites differed significantly from GTR-peripheral sites. Ground gleaner species richness in BHF was higher than GTRs, but not GTR-peripheral sites, which also did not differ significantly from GTRs. Abundance of ground gleaners was higher in GTR-peripheral sites than GTRs (Table 2.4).

Table 2.4. Foraging guild mean (± SE) species richness and abundance among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.

Nesting Guild	Variable	BHF	GTR	Peripheral	F	Р
Flycatching	Richness	1.44 ± 0.069	1.42 ± 0.080	1.57 ± 0.080	0.94	0.3934
	Abundance	2.03 ± 0.127	2.30 ± 0.133	2.12 ± 0.127	0.98	0.3803
Bark Gleaning	Richness	2.17 ± 0.120	2.37 ± 0.147	2.47 ± 0.182	0.89	0.4120
	Abundance	2.80 ± 0.183	3.19 ± 0.246	3.12 ± 0.227	0.78	0.4591
Opportunistic	Richness	0.27 ± 0.054	0.15 ± 0.044	0.27 ± 0.069	1.763	0.1740
	Abundance	0.37 ± 0.089	0.36 ± 0.148	0.45 ± 0.132	0.144	0.8660
Foliage Gleaning	Richness	$5.29\pm0.187^{\rm A}$	4.46 ± 0.196^{B}	4.61 ± 0.238^{AB}	3.69	0.0285
	Abundance	7.23 ± 0.271	6.33 ± 0.311	6.43 ± 0.351	2.03	0.1368
Ground Gleaning	Richness	$2.20\pm0.133^{\rm A}$	$1.37\pm0.116^{\text{B}}$	1.94 ± 0.133^{AB}	9.72	0.0001
	Abundance	$2.91\pm0.242^{\rm A}$	1.73 ± 0.177^{B}	$2.59\pm0.228^{\rm A}$	6.97	0.0013

Species Composition.

Of the four axes defined by the DCA, habitats varied significantly for axis 1 only (Table 2.5). GTRs had significantly higher axis 1 scores (F = 14.845, p < 0.001) than both BHF and GTR-peripheral sites, which did not differ (Table 2.1). Based upon species scores for axis 1, GTRs maintain a greater abundance of Common Grackles (species score = 4.50), Eastern Phoebes (3.41), Red-headed Woodpeckers (3.05), Yellow-crowned Night Herons (2.92), Wild Turkeys (2.91), American Redstarts (2.78), Brown Thrashers (2.75), Indigo Buntings (2.79), Pine Warblers (2.75), Prothonotary Warblers
2.72), Little Blue Herons (2.56), Yellow-throated Warblers (2.44) and Brown-headed Cowbirds (1.94) than BHF and GTR-peripheral sites, but fewer Kentucky (- 2.19), Hooded (- 1.95), and Swainson's (- 1.77) warblers (see Appendix A.1 for scientific names). This variation in overall species composition among habitats is supported by CCA biplots which suggest significant variation (F = 2.038, p = 0.001) in species data given the constraints of the three habitat types (Figure 2.1).

Table 2.5. DCA axis scores (mean ± SE) for avian species composition among unimpounded bottomland hardwood forest (BHF), greentree reservoirs (GTR), and bottomland hardwood forest adjacent to GTRs (Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.

Factor	BHF	GTR	Peripheral	F	Р
Axis 1	$0.507 \pm 0.063^{\rm A}$	0.898 ± 0.054^{B}	$0.575 \pm 0.035^{\rm A}$	14.84	< 0.0001
Axis 2	0.509 ± 0.047	0.546 ± 0.066	0.612 ± 0.057	0.74	0.4810
Axis 3	0.582 ± 0.049	0.570 ± 0.049	0.662 ± 0.051	0.86	0.4290
Axis 4	0.719 ± 0.143	0.867 ± 0.181	0.731 ± 0.177	3.11	0.0551

DISCUSSION

Previous studies on the impact of GTRs on avian community structure have found no effect after one year of flood management (Deller and Baldasarre 1999), but significant changes in diversity and richness following 14 years of flood management (Christman 1984). In particular, Christman (1984) found a decrease in understory and ground foraging species which he related to alterations in vegetation structure following long-term (14 years) alterations in hydrology of GTRs compared to natural BHF sites.



Figure 2.1. CCA bi-plot of species scores associated with Axes 1 and 2 for unimpounded bottomland hardwood forests (Hab1), greentree reservoirs (Hab2), and bottomland hardwood forests adjacent to GTRs (Hab3) at Noxubee National Wildlife Refuge, Mississippi. Axes were significant (F = 2.038, P = 0.001).

The work presented here is only the third study (to my knowledge) to address the effects of GTR management on bird community structure, and the first to do so following 40+ years of management practices. Given the results of the previous studies, I expected a

pronounced difference between sites because of the extended GTR management practices. However, the use of random BHF stands and BHF stands adjacent to GTRs as discrete habitat types has resulted in a more complex story.

Effects of GTR Management on General Avian Community Structure.

Similar to Christman's (1984) findings, natural BHF stands in east-central Mississippi do support greater species diversity and richness than GTRs, as I predicted. Conversely, species evenness was higher among GTR sites than natural BHF sites. However, these differences are complicated by the fact that they were not consistently seen when natural BHF stands immediately adjacent to GTRs (GTR-peripheral) were considered. In this study, BHF adjacent to GTRs were intermediate, or perhaps transitional in avian community structure compared to to that of GTRs and BHF. These results could be interpreted in several different ways. The first interpretation suggests that differences detected between GTRs and BHF are an effect of elevation and flood potential only made more pronounced by GTR management. GTRs tend to be constructed by land managers in areas of relatively low elevation and with numerous waterways (Wigley and Filer 1989). Thus, these areas may have historically supported a somewhat different assemblage of birds than higher elevations. Today this is reflected in the strong similarity between GTRs and GTR-peripheral locations. This could support the findings of Deller and Baldassare (1999) in which pre- and post-impoundment avian communities did not differ. While Ervin et al. (2006) did not find a significant difference in elevation and relative elevation between GTRs and unimpounded BHF at NNWR, these GTRs do contain a greater number of small order streams than surrounding BHF.

A second interpretation suggests that the scale of vegetation modification previously noted in theses GTRs are not sufficient to effect overall avian assemblage patterns. While absolute abundance of some species does vary among habitats, very few species exhibit specialization on one habitat type or another (Appendix A.1). Furthermore, the Morisita Index confirms that all three areas have very similar species presence. Because birds may select for habitat characteristics beyond that of local patch characteristics (e.g., focusing on landscape characteristics such as composition or arrangement, Lee et al. 2002), it may be that alterations resulting from impoundment do not affect birds while the waters are withdrawn during the breeding season. Third, it may be that these general measures of community structure fail to acknowledge the actual changes in avian species that may occur (i.e., replacement of typical BHF species by generalists or extreme wetland specialists). Finally, a fourth explanation could be that GTR management has significantly altered the hydrology of sites immediately adjacent to GTR levees, resulting in a vegetative community, and thus avian assemblage, intermediate between that of natural BHF and GTRs. My observations in the field suggest that during periods of heavy rainfall, GTR levees often result in considerable overflow into areas surrounding GTRs for extended periods of time compared to BHF stands at greater distances. Unfortunately, I lack data describing local plant and bird assemblages prior to initial impoundment, and thus the degree to which GTR management directly effects local assembly patterns may never be known. Mine is the first study to survey sites immediately adjacent to GTRs to test for these potential issues.

Effects of GTR Management on Species of Conservation Concern and Habitat Specialists.

GTR management appears to have no effect on overall *BBCV* scores, wetland dependency values, or BHF habitat specialist values. These results were surprising in light of previous studies in forested wetlands which have found that hydrological cycles have a greater effect on community structure than do details of vegetation structure (Swift et al. 1984). This may be due to the degree of hydrological variation in natural BHF stands (related to variation in topography), whereby seasonal flooding of GTRs still falls within the realm of variation exhibited by BHF.

Effects of GTR Management on Nesting and Foraging Guild Richness and Abundance.

The lack of an effect of GTR management on cavity nesting, flycatching, bark gleaning, or opportunistic foraging guilds was not surprising. The decrease in species richness between BHF and GTR sites for shrub-nesting and ground gleaning species was predicted. But the decreasing continuum among BHF, GTR-peripheral, and GTR sites, similar to many of the general community parameters, was not expected. The canopy nesting guild also had its highest richness in BHF, and the ground gleaning foraging guild had its lowest abundance in GTRs. Therefore, my prediction that GTR management would decrease ground nesting and foraging birds was supported, while the effect on shrub species is less clear, and an effect on understory species was absent. Christman (1984) predicted that long-term GTR management would decrease avian diversity as thinning of understory vegetation decreased habitat structure necessary for ground and low-level guilds. However, while GTR management may initially decrease understory recruitment (King 1995, King and Allen 1996), over several decades understory growth may increase as more water-tolerant species colonize GTRs and/or increased canopy gaps (Ervin et al. 2006) promote understory growth. Thus, while plant community composition may change, patch-scale vertical structure may be similar (Husak and Linder, unpublished data).

Effects of GTR Management on Species Composition.

While many species appear to be relatively evenly dispersed among bottomland forest types examined in this study, DCA and CCA results imply at least some speciesspecific variation in habitat occupancy. In particular, GTRs appear to maintain a higher abundance of several disturbance associated species (e.g., Indigo Buntings, Brownheaded Cowbirds, and American Redstart) and fewer species associated with mature BHF habitat (i.e., Swainson's and Hooded warblers) than do unimpounded BHF or sites peripheral to GTRs. Results of previous studies would imply that the GTRs have a greater frequency of windthrows (King et al. 1998) and thus maintaining more early successional vegetation patches compared to the surrounding landscape. However, Ervin et al. (2006) found that canopy gaps were no more frequent in these particular GTRs than they were in unimpounded BHF. However, an important component of GTRs that is often overlooked with regard to avian communities is the presence of anthropogenic gaps for the purpose of hunting. Land managers maintain large clearings which are seeded during the late summer with vegetation to attract waterfowl (Wigley and Filer 1989). These clearings vary in size among GTRs, but those at NNWR are generally 50-100m in diameter. The presence of such openings appears to structurally mimic early

26

successional stages seen in natural gaps during the breeding season, and produces edges in otherwise contiguous forest (personal observation).

GTRs also maintain a greater abundance of species more closely associated with more inundated conditions (e.g., Little Blue Herons and Prothonotary Warbler) than did unimpoinded BHF and GTR-peripheral sites. Of greatest concern is the increased abundance of Brown-headed Cowbirds in GTRs which have been implicated in the decline of many local Neotropical migrant populations (Morgan et al. 2006).

Management Implications.

Had I conducted a simple comparison between BHF and GTRs, I would have concluded that GTR management appears to have a dramatic effect on local avian parameters, likely as a result of modification to habitat structure following changes in hydrological patterns. However, the addition of BHF sites adjacent to GTRs suggests a more complicated story. Caution should be used as what remains unclear is whether or not sites peripheral to GTRs are also impacted, directly or indirectly, by the construction and maintenance of GTRs or if the similarities between GTRs and GTR-peripheral sites is the result of similar elevational characteristics and therefore similar historical hydrology. Future studies should consider sampling birds along transects radiating outward from GTR centers to uplands to explore the potential of a topographic related transition. Furthermore, as new GTRs are planned for construction, preliminary surveys should be conducted *a priori* and monitored post completion.

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CHAPTER III

WINTER BIRD COMMUNITIES IN IMPOUNDED AND UNIMPOUNDED BOTTOMLAND HARDWOOD FORESTS: EFFECTS OF LONG-TERM GTR MANAGEMENT IN MISSISSIPPI

ABSTRACT

Previous studies of Greentree reservoirs (GTRs), seasonal impoundments of bottomland hardwood forest (BHF) stands, have been shown to increase local migratory and wintering waterfowl abundance. However, they have also been shown to alter vegetation characteristics, invertebrate abundance and composition, and sometimes breeding songbird populations. Studies have yet to address the effects of such seasonal impoundment on winter communities of non-game birds. Thus, the objective of my study was to assess the effect of long-term GTR management on avian winter assemblage patterns in east-central Mississippi. Comparisons were made of general avian community structure (diversity, richness, abundance, and evenness), avian conservation values, habitat specialization (bottomland hardwood and wetland specialization), and foraging guilds. My results suggest local GTR management does not significantly affect general community structure, conservation rankings, or habitat specialization characteristics. While ground gleaning birds did exhibit a seasonal shift in habitat use, this change was study-wide and appears to reflect a more general movement of birds away from the hydrologically dynamic bottomland hardwood forests and not necessarily a direct response to GTR management. The overall results may reflect the ubiquitous nature of many birds wintering in east-central Mississippi.

INTRODUCTION

Bottomland hardwood forests (BHF) exhibit significant temporal variation in hydrology, often producing ephemeral wetland forests. Fluctuations in precipitation and variation in local topography play important roles in the longevity of this site-specific inundation. As a result of localized hydrology, BHF stands exhibit pronounced horizontal heterogeneity in vegetational structure (King and Allen 1996). Historically, seasonally inundated BHF served as important migratory stopover sites and/or wintering grounds for waterfowl in the eastern United States. Once covering vast acreage in the southeastern United States, forested wetlands were greatly reduced in the 19th and 20th centuries as land was lost to agricultural development, harvested for timber, converted to forest plantations, and impounded for flood control and recreation (Abernethy and Turner 1987, Sallabanks et al. 2000). Total loss and alterations have been estimated to have occurred at a rate five times greater than for any other forest type in the United States over the last two centuries (Abernethy and Turner 1987).

In an attempt to manage waterfowl in the diminishing BHF of the southeastern United States, private duck hunting clubs began constructing greentree reservoirs (GTRs) in the 1930's in eastern Arkansas (Rudolph and Hunter 1964). GTRs are bottomland hardwood forest stands that are seasonally flooded by levees and water control structures during the fall and winter to provide foraging and resting habitats for migrating waterfowl in the form of forested wetlands (Reinecke et al. 1989). These early attempts proved successful, and over the following decades many other private organizations and government agencies adopted similar land-use practices. A 1987 census documented 142 GTRs in the southeastern U.S. alone, many on public lands, averaging more than 300 ha each (Wigley and Filer 1989; more recent surveys are unavailable, S. L. King pers. Comm.). GTR management has proven to be an effective management tool for waterfowl (e.g., Reinecke et al. 1989, Sherman et al. 1995); however, a number of potential long-term ecological problems associated with GTRs have been identified.

GTR management regimes impose flooding that is typically less dynamic and of longer duration and greater depth than natural flooding in BLH. Previous studies suggested that these factors result in conversion to more water tolerant plant assemblages over time (King and Allen 1996). For example, a study of GTRs in Mississippi indicated an increase in overcup oaks (*Quercus lyrata*) and red maples (*Acer rubrum*), and a corresponding decrease in red oaks (*Quercus spp.*), green ash (*Fraxinus pennnsylvanica*), and American elm (*Ulmus americana*) compared to un-impounded sites (Young 1990, Young et al. 1995). A general decrease in sapling and understory recruitment and basal area, and an increase in windthrow density have also been noted in GTRs in general (e.g., King 1995, King and Allen 1996, and King et al. 1998).

Impacts of GTR management on non-game avian species remains poorly understood (e.g., Wehrle et al. 1995, Christman 1987, Deller and Baldassarre 1999). Generally, site-specific variation in forest plant structure results in site-specific

assemblages of birds (Sallabanks et al. 2000). Because GTRs may alter plant assemblage structure and reduce the vertical structural heterogeneity of vegetation, they may result in a loss of avian foraging substrates and/or cover (Kilgo et al. 1997, Martin 1993,), ultimately altering local bird species occurrence and abundance. Potential longterm shifts in avian assemblage patterns are important to land owners and managers as maintenance of ecosystem function has become an objective of forest management, including protection of biodiversity (Bengtsson et al. 2000, Hamel 2003). Thus, managers may consider different goals for GTRs in addition to, or in place of, an emphasis on waterfowl species. The only published studies that I am aware of examining the effect of GTR management on non-game birds have focused solely on breeding bird communities (Christman 1987, Deller and Baldassarre 1998, 1999). While findings of these studies are important, they fail to address the long-term effects of GTR management on an entire seasonal bird community. To my knowledge, there have been no previous studies of non-game, winter avian assemblages in GTRs. Furthermore, there has been a growing interest in winter bird community structure (e.g., Hamel et al. 2002, Rubenstein et al. 2002, Hamel 2003). For these reasons, I examined the impact of GTR management on BHF winter bird community structure. I hypothesized that due to structural modification of vegetation and the prolonged presence of water, GTRs and natural BHF will vary in avian winter community structure. I predicted that 1) GTRs will have overall lower diversity, species richness, and abundance than natural BHF, 2) BHF specialists will have decreased richness and abundance in GTRs compared to natural sites, 3) wetland specialists will have increased diversity, richness, and abundance in

GTRs than BHF, 4) ground and understory foraging species will have overall lowest richness and abundances in GTRs compared to natural sites, and 5) the impoundment of water will result in an abrupt within-season shift in GTR community structure as species evacuate inundated territories.

STUDY AREA

This study was conducted on the Noxubee National Wildlife Refuge (NNWR) in east-central Mississippi (33° N, 88° W), covering portions of Oktibbeha, Noxubee, and Winston counties. The 19,400 ha of refuge land contain about 6,300 ha of nearly contiguous BHF along small-order tributaries of the Noxubee River. Two permanent reservoirs and four seasonal GTRs have been constructed at NNWR (GTR 1 and 2 in 1955 and 1958 respectively, and GTR 3 and 4 in 1963) for the primary purpose of managing migratory and wintering waterfowl. Flood duration of the GTRs has varied greatly over time, ranging from annual flooding from mid-November to mid-March, to 5 – 7 day inundation events during this same time period. Details of local topography and soil conditions can be found in Ervin et al. (2006).

METHODS

Point-Count Surveys.

Fifty meter fixed-radius point counts were used to assess avian community composition following standard survey protocol of Hamel et al. (1996) during the late fall and winter from November 2002 through January 2004. After a 2-minute waiting period at point-count stations, all birds detected by sight or sound during a 10-min sampling

period were recorded, excluding flyovers. Twenty five count stations were randomly placed within stands of BHF and 23 count stations were randomly placed within the four GTRs under the condition that all points were at least 200m from the next nearest point and 100m from any habitat edge. An additional 18 count stations were placed within BHF stands, but 100m adjacent to GTRs (GTR-peripheral). These peripheral sites served two purposes: 1) to account for the potential that GTR sites differ as a result of location (i.e., topography and stream proximity), a potential issue since GTRs are commonly constructed in lower lying areas for ease of flooding, and 2) to see if the mid-winter inundation results in certain foraging guilds of birds moving from fall territories in GTRs to adjacent sites once flooding begins. Each count station was surveyed twice per winter to allow for the analyses of within season inundation effects; once prior to closing of flood gates and inundation with water and once while GTRs were inundated. Surveys were begun no sooner than 10-minutes after sunrise and conducted until 1000 CST. Size of plots and time constraints were established to optimize sampling effort (Ralph et al. 1995, Hamel et al. 1996). No surveys were conducted during rainy or windy (> 12 mph) conditions. Travel between GTR points was frequently done by kayak. While much of the GTR waters remain below 1-m in depth, deeper streams and sink-holes along the most direct routes between points precluded walking in most cases. To minimize the potential impacts of a kayak on approach to a point-count site, a neutral color (blue) was used and the last 100 m of the route to a point were concluded at a considerably slower pace. Distance of each bird detected was also determined using a laser rangefinder (Bushnell Yardage Pro ©); however, it was decided to not use distance sampling analyses for this study. While we are comparing stand characteristics, sites are all within a structurally similar habitat type and thus detection probabilities should be relatively consistent. Furthermore, my goal was not to address population-specific variation among sites, and community and guild parameters would likely not benefit from estimates (Buckland et al. 2001).

Analyses.

The following variables were used to compare avian community characteristics: species abundance, species richness, species diversity, community evenness, and conservation value scores. Because non-game species were the target of my study, all waterfowl species were omitted from all analyses. Species abundance and species richness were measured as the sum of the maximum number of individuals of all species observed in one sampling visit and the total number of species observed at each point respectively. Species diversity was derived using the Shannon Diversity Index (H'; Brower et al. 1998):

$$H' = -\Sigma p_i \log p_i$$

Where p_i is the proportion of species *i* within a community at a point. Community evenness (*J'*), or relative diversity, was measured as:

$$J' = H'/H_{max}'$$

Where H_{max}' is the natural log of the total number of species observed. Community similarity was measured using the Morisita Index of Overlap (I_M):

$$I_M = \frac{2\Sigma X_i Y_i}{(l_1 + l_2)N_1 N_2}$$

Where x_i is the abundance of a species in community 1, y_i is the abundance of that species in community 2, N_1 is the total number of individuals in community 1, N_2 is the total individuals in community 2, and l_1 and l_2 are Simpson's index values for community 1 and 2 respectively:

$$L_1 = \frac{\Sigma X_i (X_i - 1)}{N_l (N_l - 1)}$$

The Morisita index refers to the probability that individuals drawn randomly from different communities will belong to the same species. Scores range from 0 to 1, with 0 indicating no similarity and 1 indicating identical communities. This index was chosen because sizes and diversities of samples have little effect on results (Wolda 1981).

Because of the conservation concerns associated with BHF in the southeastern U.S. (Hamel 2003), measures related to conservation status were considered. Conservation value indices (*CVI*) are useful in assessing avian communities because unlike general summary statistics, such as species richness or diversity, they incorporate demographic information about each species in the community (Götmark et al. 1986). While use of conservation values has increased in recent years, there has been little agreement on the most appropriate indices to use when comparing communities. I used Partners in Flight composite index ($CVI_{PIFcomp}$) because Partners in Flight scores have been shown to provide the most rigorous and objective weighting system available, and the composite method removes much of the dependence on sample size (Nuttle et al. 2003). Thus the index can be represented by:

$$CVI_{PIFcomp} = \sum_{i=1}^{s} a_i w_i$$

Where *s* is the number of species in the community, a_i is the abundance of species *i*, and w_i is the weighting factor (i.e., PIF ranking). All PIF rankings follow those of Nuttle et al. (2003; Appendix B.1).

Wetland dependency and habitat specificity rankings are intended to evaluate the variation in site specific use by species requiring habitats of interest, in this case, BHF residents (Snell-Rood and Cristol 2003). Such rankings reduce the effects of ubiquitous species on site comparisons. For both values, site rankings were based upon relative richness of species with traits that make them of high bottomland forest conservation interest. Each species was assigned a ranking for their wetland dependency and degree of habitat specificity following Croonquist and Brooks (1991) and Snell-Rood and Cristol (2003), and when not available, author experience was used. Wetland dependency rankings were: 0 = upland, 1 = sometimes uses wetlands, 3 = usually lives in wetlands, 5 = found only in wetlands. Habitat specificity rankings were: 1 = generalist, 3 = dependent upon the landscape (e.g., forest or grassland), but not a single habitat type (e.g., hardwood or pine forest), 5 = habitat specialist (see Appendix B.1 for species-specific rankings for all species). Site rankings were calculated by summing rankings for all species present at point-count sites.

In addition to the metrics describing the entire community, birds were also divided into foraging guilds (means of food acquisition) following Ehrlich et al. (1988). Guilds were used in analyses to account for the fact that general community metrics may overlook the effects of variables that only contribute to variation in species using specific attributes of a habitat, such as a stratum within a forest profile. Species abundance and species richness within guilds were compared among BHF, GTR, and GTR-peripheral sites, as well as among years and seasons (i.e., pre- and post-inundation). All species were placed into one of the following foraging guilds: foliage gleaning insectivore, bark gleaning insectivore, ground gleaning insectivore, ground gleaning granivore, ground gleaning omnivore, flycatching, nectarivores, aerial divers, raptorial, stalk and strike, and dabblers (Ehrlich et al. 1988; see Appendix B.1 for species-specific guild classification). Due to small samples sizes, flycatchers, nectarivores, aerial divers, raptorial, stalk and strike and strike, and strike, and dabblers were omitted from all analyses.

All variables were analyzed using repeated measures Analysis of Variance (ANOVA) and post-hoc Tukey-Kramer pair-wise comparisons to test for forest stand and year effects using SAS (PROC MIXED; 1990). Pre-inundation and post-inundation counts were compared (seasons) to examine direct effects of seasonal inundation. When no within season effects were found, counts were combined as overall winter habitat comparisons. In such cases, abundance was determined as the maximum number of individuals of each species observed during a single visit, not an average or sum. Values are presented as mean \pm SE. For ease of discussion, the use of habitat from this point forward refers to the different types of stands (BHF, GTR, and GTR-peripheral) within a broader bottomland context.

RESULTS

General Community Structure.

No differences were found in community metrics between pre- and postinundation conditions (Table 3.1). Thus, surveys were combined within winters for analyses of year and habitat effects. Within-winter pooled data exhibited no significant interactions or differences between years for general community structure (Table 3.2). General community metrics, including diversity, evenness, richness and abundance, were not significantly different among the three habitats (Table 3.2 and 3.3).

Conservation-Concern Rankings.

No differences were found in Conservation rankings between pre- and postinundation conditions (Table 3.4), so surveys were combined within winters for analyses of year and habitat effects. Subsequently, no effects of year, habitat, or interactions were found for *CVI*_{PIFComp} (Table 3.4).

Habitat Specialization.

No differences were found in wetland dependency scores or habitat specialization scores between pre- and post-inundation conditions (Table 3.4), so surveys were combined within winters for analyses of year and habitat effects. No effects of year, habitat, or interactions were found (Table 3.4). Though not significantly different, it should be noted that mean (\pm SE) wetland dependency scores were as follows: BHF = 6.37 ± 0.52 , GTR = 7.98±0.68, GTR-peripheral = 7.06±0.65 implying that very few wetland dependent species occupy bottomland hardwood forests during the winter (excluding waterfowl). Habitat specialization scores were: $BHF = 28.55 \pm 1.02$; $GTR = 29.82 \pm 1.21$, GTR-peripheral = 26.00 ± 1.47 ; suggesting that most of the species present are landscape dependent (e.g., require forest structure), but are tolerant of a wide range of local structure (e.g., bottomland forests or upland forests).

Foraging Guilds Before and After Inundation.

Ground gleaning granivores, flycatchers, nectarivores, aerial divers, raptorial, and all aquatic foraging species were omitted due to small sample sizes. However, all ground gleaning species were pooled into a single ground gleaning guild for analysis. Bark gleaning insectivores, foliage gleaning insectivores, and ground gleaning omnivores had no change in abundance or richness following inundation. However, ground gleaning insectivores and all ground gleaners combined varied in overall abundance and richness between seasons (Table 3.5). For the ground gleaning insectivorous guild, there was an overall general decrease in species abundance following inundation (3.58±0.33 preinundation vs 2.58 \pm 0.21 post-inundation; p = 0.016), but no significant change in species richness (1.94 \pm 0.12 versus 1.94 \pm 0.11; p = 0.442). However, this trend was not habitat specific, indicating that individuals were not moving away from flooded areas at a different rate than at other locations within the forest. For all ground gleaners combined, abundance and richness decreased in value from pre- to post-inundation $(3.94\pm0.36$ pre versus 2.79 ± 0.24 post, p = 0.05 and 2.31 ± 0.12 pre versus 1.92 ± 0.13 post, p = 0.013respectively). Again this trend was general and not habitat specific.

Table 3.1. Repeated measure ANOVAs on mean community traits for avian winter community structure comparing pre- and post-flood (seasons) parameters among unimpounded bottomland hardwood forest stands (BHF; N = 25, greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) at Noxubee National Wildlife Refuge, Mississippi.

	Diversity			Richness				Abunda	nce		Evenness			
Source	DF	F	Р	DF	F	Р	DF	F	Р	DF	F	Р		
Season	1	1.590	0.2077	1	3.340	0.0685	1	0.270	0.6017	1	0.640	0.4249		

Table 3.2. Repeated measure ANOVAs on mean community traits for avian winter community structure (within winter data combined) among unimpounded bottomland hardwood forest stands (BHF; N = 25, greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) at Noxubee National Wildlife Refuge, Mississippi.

		Divers	ity		Richness			Abundance			Evenness		
Source	DF	F	Р	DF	F	Р		DF	F	Р	DF	F	Р
Habitat	2	1.230	0.2947	2	1.310	0.2741		2	1.240	0.2919	2	1.520	0.2234
Year	1	0.450	0.5050	1	0.020	0.8777		1	3.000	0.0858	1	0.600	0.4420
Habitat*Year	2	0.390	0.6770	2	0.280	0.7566		2	0.580	0.5636	2	0.260	0.7703

Table 3.3. Avian winter community mean (± SE) diversity (Shannon-Weiner Diversity Index), species richness, abundance, and evenness (Jaccard Index) among unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs(GTR), and BHF stands adjacent to GTRs (GTR-Peripheral) at Noxubee National Wildlife Refuge, Mississippi.

Factor	BHF (N = 25)	GTR (N = 23)	GTR- Peripheral $(N = 18)$	F	Р
Diversity	2.280 ± 0.039	2.234 ± 0.049	2.170 ± 0.053	1.23	0.6770
Richness	11.930 + 0.398	12.000 + 0.452	10.970 + 0.599	1.31	0.2741
Abundance	22710 ± 1581	23.820 ± 1.720	20.350 ± 2.012	1.31	0.2919
Evenness	0.196 ± 0.005	0.196 ± 0.006	0.209 ± 0.007	1.52	0.2234

Table 3.4. Repeated measure ANOVAs on mean community traits for avian winter conservation-concern rankings among unimpounded bottomland hardwood forest stands (BHF; N = 25, greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) at Noxubee National Wildlife Refuge, Mississippi. Because no seasonal effects were found, within-winter counts were combined to test for effects of habitat and year.

Source		CVI		Spec	Habita ializatio	nt n Scores	Wetland Dependency Scores			
	DF	F	Р	DF	F	Р	DF	F	Р	
Season	1	0.84	0.3606	1			1			
Habitat	2	1.240	0.2939	2	2.440	0.0919	2	1.840	0.1639	
Year	1	0.010	0.9033	1	0.350	0.5541	1	1.470	0.2278	
Habitat*Year	2	0.580	0.5613	2	1.510	0.2264	2	2.340	0.1006	

Foraging Guilds Without Seasonal Effects.

Because ground gleaning omnivores and bark and foliage gleaning insectivores exhibited no seasonal effect, counts were pooled within winters to examine effects of year and habitat. Bark gleaning insectivores varied in richness and abundance among habitats (Table 3.6 and 3.7), with an overall lower abundance and richness of species in GTR-Peripheral sites (Table 3.7). The remaining guilds exhibited no effect of year or habitat (Table 3.6).

DISCUSSION

This is the first comprehensive study of non-game bird use of GTRs during winter months. My results indicate that GTR management has little to no effect on winter, nongame avian community and guild structures, including habitat specialization, within BHF of east-central Mississippi. Even mid-season impoundment of water, which renders the forest floor inaccessible to most birds well after the establishment of winter home ranges did not significantly impact community or guild structure. Among the differences that were found, none reflect a direct link to GTR management. I had predicted a reduction in ground foraging birds in GTRs compared to BHF and GTR-peripheral sites as foraging habitat was lost during inundation, and thus expected differences between pre- and postflooding samples, as well as between impouned and unimpounded sites. I was surprised to see that variation in these particular guilds appears to be a function of bottomland hardwoods as a system in general, not an artifact of management regimes. Few ground foraging birds were recorded throughout the study (see Appendix B.1). Given the hydrological dynamics and unpredictable temporal aspect of water within BHF during

Table 3.5.	Repeated measure ANOVAs on mean foraging guild traits for avian winter communities among
	unimpounded bottomland hardwood forest stands (BHF; N = 25), greentree reservoirs(GTR; N = 23), and
	BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) immediately before and after seasonal water
	impoundment at Noxubee National Wildlife Refuge, Mississippi.

			Baı	k Gleanin	g Insect	ivores		Foliage Gleaning Insectivores						
			Richnes	SS	To	Total Abundance			Richness			Total Abundance		
	Source	DF	F	Р	DF	F	Р	DF	F	Р	DF	F	Р	
~	Season	1	1.46	0.228	1	1.66	0.199	1	0.59	0.445	1	0.53	0.467	
49	Habitat	2	2.300	0.793	2	1.330	0.265	2	1.090	0.337	2	1.170	0.314	
	Year	1	0.070	0.793	1	1.050	0.306	1	0.001	0.975	1	2.020	0.156	
	Habitat*Year	2	1.230	0.295	2	0.880	0.414	2	0.150	0.859	2	0.770	0.462	
	Habitat*Season	2	0.260	0.770	2	0.250	0.780	2	0.390	0.674	2	0.001	0.996	
	Year*Season	2	0.030	0.872	2	0.020	0.883	2	1.620	0.205	2	1.830	0.177	
	Habitat*Year* Season	2	0.690	0.501	2	1.100	0.335	2	0.830	0.439	2	0.500	0.609	

	Ground Gleaning Insectivores							Ground Gleaning Omnivores					
		Richne	SS	Tot	Total Abundance			Richness			Total Abundance		
Source	DF	F	Р	DF	F	Р	DF	F	Р	DF	F	Р	
Season	1	0.6	0.442	1	5.91	0.016	1	0.17	0.684	1	1.03	0.312	
Habitat	2	5.500	0.005	2	2.910	0.056	2	0.490	0.614	2	0.230	0.793	
Year	1	0.340	0.559	1	0.030	0.873	1	0.120	0.735	1	2.870	0.092	
Habitat*Year	2	3.730	0.026	2	0.060	0.944	2	1.370	0.256	2	0.090	0.913	
Habitat*Season	2	0.090	0.913	2	0.070	0.936	2	0.260	0.775	2	0.870	0.420	
Year*Season	2	2.200	0.139	2	0.820	0.367	2	0.850	0.358	2	1.250	0.264	
Habitat*Year* Season	2	0.800	0.449	2	1.690	0.187	2	0.260	0.775	2	0.550	0.580	

Table 3.5. Continued

50

	All Ground Gleaners								
		Richne	SS	Tot	al Abun	dance			
Source	DF	F	Р	DF	F	Р			
Season	1	3.87	0.050	1	6.34	0.013			
Habitat	2	1.230	0.294	2	1.850	0.160			
Year	1	3.460	0.064	1	0.410	0.524			
Habitat*Year	2	1.560	0.213	2	0.150	0.862			
Habitat*Season	2	2.300	0.102	2	0.250	0.775			
Year*Season	2	0.280	0.597	2	0.120	0.726			
Habitat*Year* Season	2	0.750	0.473	2	1.910	0.150			

Table 3.5. Continued

Table 3.6. Repeated measure ANOVAs on mean foraging guild traits for avian winter communities among unimpounded bottomland hardwood forest stands (BHF; N = 25), greentree reservoirs(GTR; N = 23), and BHF stands adjacent to GTRs (GTR-Peripheral; N = 18) in which there were no direct effects of flooding on local assemblages at Noxubee National Wildlife Refuge, Mississippi (i.e., within winter counts pooled).

			Bar	k Gleanin	g Insect	ivores		Foliage Gleaning Insectivores						Gr	Ground Gleaning Insectivores		
	Richness			Total Abundance		Richness		Total Abunda		dance	Richne		SS				
_	Source	DF	F	Р	DF	F	Р	DF	F	Р	DF	F	Р	DF	F	Р	
52	Habitat	2	4.52	0.013	2	3.41	0.037	2	1.470	0.234	2	1.080	0.343	2	1.700	0.188	
	Year	1	0.08	0.779	1	0.090	0.762	1	3.130	0.080	1	6.540	0.012	1	3.290	0.073	
	Habitat*Year	2	0.29	0.751	2	0.530	0.590	2	0.310	0.732	2	0.920	0.400	2	1.560	0.215	

Table 3.6. Continued.

			Ground G	leaning	eaning Omnivores							
		Richnes	S	. <u> </u>	Total A	bundance						
Source	DF	F	Р	DF	F	Р						
Habitat	2	0.790	0.458	2	0.190	0.828						
Year	1	0.010	0.923	1	2.240	0.137						
Habitat*Year	2	1.220	0.299	2	0.100	0.906						

Table 3.7. Mean (± SE) species richness and abundance of bark foraging species in unimpounded bottomland hardwood forest stands (BHF), greentree reservoirs (GTR), and BHF stands adjacent to GTRs (GTR-Peripheral) at Noxubee National Wildlife Refuge, Mississippi. Superscript letters reflect Tukey-Kramer pairwise comparison results.

	BHF	GTR	GTR-Peripheral	F	Р
Species Richness	2.70 ± 0.137^{AB}	$2.92\pm0.135^{\rm A}$	$2.48\pm0.162^{\rm B}$	4.52	0.013
Species Abundance	4.26 ± 0.246^{AB}	$4.44\pm0.248^{\rm A}$	$3.86\pm0.255^{\rm B}$	3.41	0.037

winter months, perhaps ground foraging birds simply have a natural tendency to abandon such sites for upland conditions where flooding is rare throughout the season.

Bark gleaners may be less abundant and exhibit decreased richness due to structural differences of peripheral sites. Woodpeckers, which dominate the winter bark foraging guild, tend to reach peak abundances and diversity in mature stands of trees where there is a variety of potential substrates and an increase in dead and dieing vegetation (Winkler et al. 1995). Peripheral sites on this study site contain fewer mature trees and snags and have a greater frequency of windthrows than did BHF or GTR sites (Husak and Linder, unpublished data), perhaps rendering GTR-peripheral sites less attractive to bark gleaners. Whether or not adjacent GTRs have an influence on these characteristics of GTR-peripheral sites is unclear.

It should also be noted that wetland dependency scores and habitat specialization scores observed during the winter months were not only similar among habitats, but also relatively low (Snell-Rood and Cristol 2003). Locally, wetland dependency and habitat

specialization scores for wintering year-round residents and short-distance temperate migrants found at NNWR were considerably lower than was observed during the breeding season when numerous Neotropical migrants were present (see chapter 2). Furthermore, all species used in analyses and observed in bottomland hardwood stands were also observed in other habitat types, including upland hardwood forests and pinehardwood mixed forests, and most were observed in pine forest stands (MSH, personal observation). Thus winter birds occupying sites surveyed during this study, which are typical of winter birds in bottomland hardwood forests of the southeastern United States (e.g., Hamel 2003), are generally of a ubiquitous nature and likely have minimal potential to be impacted by modifications to bottomland hardwood stands.

Management Implications.

It may be concluded that while GTR management may negatively impact vegetation characteristics of local BHF stands, the non-game birds occupying BHF during the winter months at NNWR are not significantly affected, even after more than 40 years of flood regimes. This may well be the result of the ubiquitous nature of winter residents and a low abundance of species that might be directly effected by inundation; however, it must be stressed that this is the first study to address winter communities in GTRs, and the general applicability of the findings are unclear. It is recommended that similar studies be conducted at other locations among GTRs of varying age to test for the presence of general patterns. Furthermore, surveys conducted prior to the construction of planned GTRs could provide invaluable future comparisons of potential impacts.

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CHAPTER IV

TESTING THE RELATIONSHIP BETWEEN VEGETATION STRUCTURAL COMPLEXITY AND AVIAN ASSEMBLAGE STRUCTURE IN BOTTOMLAND HARDWOOD FORESTS

ABSTRACT

Previous studies have shown a relatively consistent pattern between avian species richness and diversity and habitat complexity. Such relationships have been explained in terms of increased food availability, foraging substrates, and nesting substrates resulting from the increased complexity. I tested hypotheses relating structural diversity and vertical heterogeneity to an increase in overall avian diversity and guild diversity in bottomland hardwood forest stands in east-central Mississippi. Regression analyses of vertical vegetation structural heterogeneity suggest a direct positive relationship between woody plant structure and avian assemblage structure as predicted by long standing hypotheses. However, regression analyses of principal component scores derived from numerous structural descriptor metrics suggest that avian communities and guilds in bottomland hardwood forests in east-central Mississippi are more directly influenced by site maturity and structural complexity of understory plants, indirectly supporting a greater importance of point-scale spatial heterogeneity. Specifically, sites with increased tree and shrub density in multiple understory levels appear to support the greatest

richness and diversity of communities and foraging and nesting guilds. Variation in abundance of species was found to increase with mature canopies, understories with increased plant diversity, and trees in states of good health.

INTRODUCTION

Understanding mechanisms that generate and ultimately maintain patterns of assemblage diversity and structure (e.g., richness, abundance, and evenness of species) is a fundamental topic in community ecology (e.g., MacArthur and MacArthur 1961, Ricklefs and Schluter 1993, Gaston 2000, Williams et al. 2002). While there is a general agreement that habitat complexity and heterogeneity positively affect diversity, there is no general rule relating the two across habitats and taxa. Relating bird community characteristics to habitat structure in particular has received much attention in ecological literature (e.g., MacArthur 1964, Cody 1974, Willson 1974, Balda 1975, Swift et al. 1984, Mills et al. 1991, Martin 1993). Although many exceptions have been documented, one widely accepted pattern in avian assemblages is a positive correlation between species diversity and spatial heterogeneity and vegetation density (e.g., Martin 1993). This relationship has been explained in terms of food availability and competition, in which areas with greater foliage density have more food, and areas with greater structural complexity provide more types of foraging sites to partition or minimize competition. Others have emphasized a similar relationship for nesting substrates (Martin 1993). Historically, authors implied a simple linear relationship between foliage height diversity and bird species diversity (e.g., MacArthur 1961). However, such conclusions were rarely substantiated by fieldwork (e.g., Tomoff 1974,

62

Willson 1974, James and Wamer 1982). More recently, Martin (1993) and Steele (1993) have demonstrated that individuals of some species may select areas of greater vegetation density to increase reproductive success within a given habitat. Additionally, areas of greater structural complexity provide a greater variety of nest sites, thereby potentially increasing the diversity of species that can utilize said habitat. Southwood (1996) argued that spatial heterogeneity (measured as overall physical structure), whether at regional or local scales, was a more important factor than simple vertical complexity for terrestrial vertebrates as a whole. Holmes et al. (1979) found that plant species composition was a better predictor of avian community and foraging guild diversity and richness in northern hardwood forests than was vertical or general physical, structural complexity. Wiens and Rotenberry (1981) found little effect of habitat structure or species composition on bird species abundances or diversity in shrub-steppe vegetation of the western United States, and suggested such habitats are structurally too simple and species-poor to exhibit such relationships. Therefore, despite a long standing tradition of such structural patterns, more work in a variety of habitats is needed.

Bottomland hardwood forests (BHF) exhibit considerable vertical and horizontal structural heterogeneity (Kellison and Young 1997), due largely to variation in hydrology, sedimentation, age, and disturbance frequency and intensity (such as windthrows and seasonal flooding; Pashley and Barrows 1993). As such, BHF are a good habitat for testing hypotheses about the effects of microhabitat variation as it becomes possible to test effects of structural variation without the potential for overlying effects of surveying different ecosystems. Additionally, within the East Gulf Coast Plain Physiographic Area, BHF support the greatest overall diversity of breeding birds, a large number of which are Neotropical migrants and/or Partners in Flight (PIF) species of priority concern (Hunter et al. 1993). Total loss and alteration to BHF have occurred at a rate five times greater than any other forest type in the United States over the last two centuries (Abernethy and Turner 1987). Thus, understanding structural factors contributing to avian community structure within these habitats is of considerable conservation interest.

The goal of this study was to test hypotheses regarding the effects of local habitat structural complexity on avian community and guild characteristics in bottomland hardwood forests of the southeastern United States. While numerous studies have addressed this issue, they have generally tended to use comparisons among different habitat types (e.g., Rotenberry et al. 1979, Mitchell et al. 2005, but see Swift et al. 1983, and references therein), or they have assessed habitat diversity by simplifying complexity as the number of plant contact points at various height categories along linear transects (e.g., Cody 1974) or used multiple variables, each of which were compared to diversity or richness in simple linear regression models. Here, I have used a single habitat type with inherent structural heterogeneity among local sites, and attempted to address complexity by quantifying in more detail the structure provided by vegetation. Thus, I was able to test two competing, though not mutually exclusive, mechanisms of maintaining diversity: 1) a positive relationship between vertical structural complexity and avian diversity (Martin's 1993 vertical heterogeneity hypothesis) and 2) a positive relationship between overall local spatial heterogeneity and avian diversity (Southwood's 1996 spatial

heterogeneity hypothesis). To do this, I use a greater variety of height categories than previous studies within three-dimensional volumes of habitat and then use complexity indices and multivariate analyses to examine combined effects on avian community and guild structure. Understanding such relationships in bottomland hardwood forests of the southeastern U.S. is important given the rapid loss of this habitat over the last 200 years (Abernethy and Turner 1987, Sallabanks et al. 2000) and the number of birds of high conservation concern that utilize the habitat for nesting and/or migratory habitat (Hunter et al.1993).

STUDY AREA

This study was conducted on the Noxubee National Wildlife Refuge (NNWR) in portions of Oktibbeha, Noxubee, and Winston counties of east-central Mississippi (33°N, 88°W). A primary charge of NNWR is waterfowl management, and thus much has been done to preserve BHF habitat that functions as seasonal forested wetlands for waterfowl. For a more detailed description of the study area soils and vegetation, see Ervin et al. (2006). Approximately 6,300 ha of nearly contiguous bottomland hardwood forest dissected by 10 small-order tributaries of the Noxubee River remain on the 19,400 ha of refuge land. As a result, this heterogeneous habitat persists in a relatively homogeneous landscape, providing the opportunity for a better direct test of the effects of structural complexity on avian assemblage structure while minimizing underlying effects of general habitat or landscape factors. Four greentree reservoirs constructed during the 1950s and 1960s are maintained within the larger BHF at NNWR. Because these specific greentree reservoirs have recently been found to fall within the range of vegetational variation associated with natural BHF, albeit the extreme edge of the spectrum, and do not appear to have modified avian community structure in a consistent fashion (see chapter 2 and 3), random points within such microhabitats were surveyed during this study and data included in all analyses.

METHODS

Avian Community Data.

Relative abundance of avian species was determined using fixed-radius (radius = 50m) point counts following standard survey protocol (Hamel et al. 1996) during the late spring and early summer of 2002 through 2004. All birds detected by sight or sound during a 10-min sampling period were recorded, excluding flyovers. Each of 61 count stations was surveyed twice between 10 May and 15 June each year. Point count stations were not visited a second time until all other count stations had been completed once. Surveys were begun no sooner than 10-minutes after sunrise and conducted until 1000 central time. Point-count size and durations used were intended to maximize sampling effort within BHF stands (Ralph et al. 1995, Hamel et al. 1996). No surveys were conducted during inclement weather, including rainy or windy (> 19 km/hr) conditions.

Avian community parameters calculated for comparisons included richness (total number of species recorded), abundance (based upon maximum number of individuals observed at each point for each species), diversity, and evenness. Species diversity was derived using the Shannon Diversity Index (H'; Brower et al. 1998). Community evenness (J'; Brower et al. 1998), or relative diversity, was measured as:

$J' = H'/H_{max}'$

Where H_{max} is the natural log of the total number of species observed.

Avian Guild Data.

Birds were divided into nesting guilds (location of typical nest within vegetation strata) and foraging guilds (means of food acquisition) following descriptions by Ehrlich et al. (1988). Nesting guilds analyzed included: canopy nesters, understory nesters, shrub nesters, ground nesters, and cavity nesters. Foraging guilds analyzed were: foliage gleaning insectivore, bark gleaning insectivore, ground gleaning insectivore, ground gleaning granivore, ground gleaning omnivore, and flycatching (for all species-specific guild classifications, see Appendix A.1). Because their presence could not be tied directly to vegetation characteristics, aerial divers, stalk and strike foragers, and aquatic dabbling species were omitted from guild analyses. Richness and abundance values were calculated and used to derive nesting and foraging guild diversity (H') scores for each location.

Vegetation Data.

Vegetation structure of each count station was determined annually. Two types of plots were used to assess vegetation at each station, "tree plots" and "understory plots," the combination of which were used to assess vertical structural diversity and general plot structural complexity. Two 11.1-m radius tree plots were established at each count station, one in the center and one 25 m from the center in a random direction determined by a blind twist of a compass. Within these plots all trees with a diameter at breast height

(DBH) greater than 8.5 cm were identified to species and their height, DBH, and health recorded. Other variables recorded include canopy coverage, mean canopy height, mean subcanopy height, the number of small (<10 cm diameter) failed logs, the number of large (>10 cm diameter) failed logs, the number of stumps (< 1.5 m ht), distance to nearest canopy gap, total number of woody plants between 1–1.5m, 1.5–2.0 m, 2–2.5 m, and >2.5 m, total number of canopy trees, total number of subcanopy trees, total number of understory trees, mean DBH of canopy trees, mean DBH of subcanopy trees, mean DBH of understory trees, average canopy tree health, average subcanopy tree health, average understory tree health, average health of all trees in plot. Tree health was measured as a subjective scale (1 – 5) modified from Daniel et al. (1979), where 1 = trees with < 10% branch death, 2 = trees with 10% – 50% branch death, 3 = trees with > 50% branch death, but leaves retained on some branches, 4 = trees in which all branches appear dead but minor limbs remain intact, 5 = snags with only primary limbs or no limbs remaining.

Four 4-m² squares were placed at random distances from the count station centers in the four cardinal compass directions to assess understory characteristics. Distances from point centers were determined using a random number table. Within each plot, the number of terminal stems of oaks, other trees, shrubs, cane, ferns, and other herbaceous stems terminating at 0–0.3 m, 0.3–1m, 1–2m, 2 – 2.5m, and > 2.5m were recorded. Percentage of area covered by shrubs and trees, herbaceous plants, cane, ferns, vines, and other organic material (e.g., logs, cypress knees, fungi) at each height category were recorded to the nearest percent. Percent of overall ground covered by bare ground, leaf litter, grass, water, roots, moss, cypress knees, and fungi were also recorded.

Analyses.

To test Martin's vertical structural heterogeneity hypothesis (1993), the number of terminal plant stems in each of the surveyed height categories were used to develop diversity scores for each point count station. The Shannon diversity index (H') was used:

$$H' = -\sum p_i \log p_i$$

Where p_i was the proportion of terminal stems in height category *i* within a complete vertically sampled column within point count plots. Thus, scores took into account the relative abundance of terminal stems within and among height categories, depicting the degree to which each point was structurally layered, as described by Martin (1993). A high H' score depicts a more structurally diverse location relative to vegetation. H' values were first calculated by combining all vegetation types (herbaceous and woody) and then by using only trees and shrubs. Trees and shrubs were examined separately because they may represent better indicators of vertical heterogeneity than more ephemeral herbaceous growth relative to bird habitat selection (Wiens and Rotenberry 1981). Simple linear regression was used to compare vertical plant diversity (reflecting vertical complexity) with avian community and guild parameters.

Then, I tested Southwood's spatial heterogeneity hypothesis (1996) for overall combined effects of vegetation characteristics on community and guild parameters. The more than 60 vegetation variables (all variables except for terminal stem counts used above, see Appendix C.1) were reduced using principal component analysis (PCA).

Variables used quantitatively described overall spatial arrangement, density, and diversity of plants at each point. Thus, they represent those factors, Southwood (1996) suggested were better predictors of avian assemblage patterns than simple vertical, structural complexity alone. Sample scores from principal components (PC) with eigenvalues >1.0 and individually contributing \geq 5% of overall variance in the PCA were entered into stepwise linear regressions to determine which factors and their underlying variables had the greatest effect on community and guild parameters, and to see if any factors were consistently more important (i.e., consistently loaded first).

Finally, because I wanted to know if vertical structural complexity was a better indicator of avian community and guild parameters than overall site attributes (i.e., general spatial heterogeneity), as implied by Martin (1993), vegetation diversity scores (see above) were entered into the stepwise regression model. Factors contributing to greater overall variance, should load earlier. Consequently, the order in which PC scores are loaded will determine the importance of vegetation diversity relative to spatial heterogeneity. All analyses were conducted using SPSS version 13.0.

RESULTS

Vertical Structural Heterogeneity.

Vertical Structural Diversity and Avian Community Parameters. There were no significant relationships between overall plant structural diversity and species diversity $(R^2 = 0.024, P = 0.214)$, evenness $(R^2 = 0.006, P = 0.530)$, richness $(R^2 = 0.020, P = 0.259)$, or abundance $(R^2 < 0.0001, P = 0.953)$. Using H' scores for only shrubs and trees 70

plants, there was no significant relationship between structural plant diversity and evenness ($R^2 = 0.027$, P = 0.192), richness ($R^2 = 0.047$, P = 0.082), or abundance ($R^2 = 0.002$, P = 0.750). However, there was a significant positive relationship between shrub and tree structural diversity and avian community diversity ($R^2 = 0.079$, P = 0.023).

Vertical Structural Diversity and Guild Parameters. There were no significant relationships between vertical structural diversity scores for all plants and nesting guild diversity ($R^2 = 0.043$, P = 0.096) or foraging guild diversity ($R^2 < 0.0001$, P = 0.898). While there was no relationship between shrub and tree vertical structural diversity scores and foraging guild diversity ($R^2 = 0.001$, P = 0.823), there was a significant positive relationship with nesting diversity ($R^2 = 0.109$, P = 0.007). Thus, sites with an increased number of woody plant layers among the numerous height categories supported a greater diversity of nesting microhabitats.

General Structural Complexity.

PCA Results. A total of 20 components were extracted, accounting for a total of 87% of overall variance. However, only six principal components (PC) accounted for \geq 5% of overall variation (Table 4.1), and thus only these PC were used in subsequent stepwise regressions. Table 4.2 summarizes the component matrix for these five, including variables contributing the most to each principal component (variables with a score > +/- 0.5). PC 1 is primarily defined by the density of switchcane (*Arundinaria gigantean*) and its coverage from the ground to heights exceeding 2 m, PC 2 is defined by the number of woody stems (trees and shrubs) in height categories above 1.5 m, implying subcanopy

and understory structure, PC 3 is determined primarily by the number and size of mature trees, PC 4 is related to coverage by vine and other non-woody plants below 1 m, and PC 5 is related to size and health of understory trees.

	Eigenvalues				
Principal Component	Total	% of Variance	Cumulative %		
1	6.88	10.75	10.75		
2	5.69	8.88	19.63		
3	4.45	6.95	26.58		
4	4.07	6.36	32.94		
5	3.44	5.38	38.32		
6	3.31	5.17	43.49		
7	2.99	4.67	48.17		
8	2.65	4.14	52.31		
9	2.26	3.53	55.84		
10	2.14	3.34	59.18		
11	1.92	3.00	62.17		
12	1.84	2.87	65.05		
13	1.70	2.65	67.70		
14	1.59	2.48	70.18		
15	1.52	2.38	72.56		
16	1.37	2.14	74.70		
17	1.30	2.03	76.73		
18	1.23	1.92	78.65		
19	1.15	1.80	80.45		
20	1.02	1.60	82.05		

Table 4.1. Principal component scores for vegetation characteristics of bottomland hardwood forest stands at Noxubee National Wildlife Refuge, Mississippi.

	PC1		PC2		PC3	
Rank						
	Variable	Score	Variable	Score	Variable	Score
	% area covered				DBH of	
1	in cane 1-2 m	0.91	# of trees >2m	0.67	understory trees	0.61
	# of cane stems		# of trees/shrubs		# of canopy	
2	0.3-1 m	0.87	1.5-2m	0.60	trees	0.56
	% area covered		# of trees/shrubs		Total # plants 0-	
3	in cane 0-0.3 m	0.79	2-2.5m	0.59	0.3m	0.55
	# - f		# of two of /ab wab a		# = f + = = = / = h == h =	
4	# of cane stems $0-0.3 \text{ m}$	0.77	# of trees/shrubs $>2.5m$	0.55	# of trees/shrubs $0-0.3m$	0.51
5	% area covered	0.75				
5		0.75	_	_	_	_
	% area covered					
6	in cane 0.3-1m	0.711	-	_	_	—
	# of cane stems >					
7	2m	0.66	_	_	_	_
	# of the oc/abruba					
8	# 01 trees/stirubs 0.3-1m	0.66	_	_	_	_
0	# of cane stems	0.63	_	_	_	_
,	1 2111	0.05				
	% area covered					
10	0.3-1m	0.59	_	_	_	_
-						
11	Canopy cover	-0.55	_	_	_	

Table 4.2. Component matrix for vegetation variables in bottomland hardwood forest stands at Noxubee National Wildlife Refuge, Mississippi with scores >0.50.

Table 4.2. Continued.

	PC4			PC5		PC6	
Rank	Variable	Score		Variable	Score	Variable	Score
1	% area covered by vines >2m	0.71	1	Health of understory trees	0.61	# of small logs	0.54
2	% area covered by vines 1-2m	0.70	1	DBH of understory trees	-0.51	_	_
3	% area covered by vines 0.3-1m	0.62	:	# of oaks saplings 0-0.3m	0.50	_	_
4	% area covered by herbaceous plants 0.3-1m	0.51		_	_	_	_
5	_	_		_	_	_	_
6	_	_	_	_	_	_	_
7	_	_	_	_	_	_	_
8	-	_	_	_	_	_	_
9	_	_	_	_	_	_	_
10	_	_	_	_	_	_	_
11	_	_	_	_	_	_	_

Table 4.3. Stepwise regression model for avian foraging guild diversity
(dependent variable) and principal component scores of local
vegetation characteristics (Independent variables) at Noxubee
National Wildlife Refuge, Mississippi.

Mo	lel	R^2	F	Р	Model Variables	В	Р
1	0.	081	5.53	0.022	PC 4	-0.284	<0.0001

General Plant Complexity and Community Parameters. PC 1, 4, and 6 did not load into (i.e., did not significantly contribute to observed variance) any of the best-fit models for community parameters. PC 2 was included in models for all but one parameter, total abundance of birds (Table 4.3). For diversity and species richness, PC 2 was the only significant factor loaded ($R^2 = 0.162$, P = 0.001 and $R^2 = 0.109$, P = 0.007 respectively) and it demonstrated a positive relationship in both cases. For evenness, PC 5 loaded into the model first, exhibiting a positive relationship, followed by PC 2 which exhibited a negative relationship ($R^2 = 0.167$, P = 0.003). For total abundance, only PC 5 was significant ($R^2 = 0.091$, P = 0.014) and it exhibited a negative relationship. Thus, the general structure of avian communities in these BHF is dependent upon density of woody understory plants, size of understory trees, and the relative health of those trees.

When vertical plant diversity scores were included in stepwise regression analyses with PCs, they failed to load into any of the models for community parameters. Thus, factors reflecting overall structural complexity were more important than simple vertical structural diversity. *General Plant Complexity and Guild Parameters.* For foraging guild diversity, only PC 4 was found to be significant (Table 3; $R^2 = 0.081$, P = 0.022). The nesting guild diversity model included (in order of loading) PC 2, PC 4, and PC 3 ($R^2 = 0.288$, P < 0.0001; Table 4.4). Thus, while foraging guild diversity is a function of mid-level coverage by vines and herbaceous plants, nesting diversity is more closely tied to tree community structure and vegetation complexity below 1m. As with community parameter models, vertical structural complexity failed to load in any guild models when included among PC variables, suggesting again that general structural elements of the local habitat are more important to avian structure than vertical structuring alone.

Table 4.4. Stepwise regression model for avian nesting guild diversity
(dependent variable) and principal component scores of local
vegetation characteristics (Independent variables) at Noxubee
National Wildlife Refuge, Mississippi.

Model	R^2	F	P-Value	Model Variables	В	Р
1	0.175	13.329	0.001	PC 2	0.418	0.001
2	0.238	9.688	< 0.0001	PC 2	0.418	0.001
				PC 4	0.252	0.027
3	0.288	8.238	< 0.0001	PC 2	0.418	0.001
				PC 4	0.252	0.027
				PC 3	0.224	0.042

DISCUSSION

Bottomland hardwood forests of Noxubee National Wildlife Refuge, MS support a diverse assemblage of birds. I documented 62 species (Appendix A.1), which included a variety of resident, short-distance migrant, and long-distant migrant species, with representations from all nesting and forging guilds considered. Birds considered generalist species and edge species (Miller et al. 2004) dominated my overall samples (Appendix A.1), but several species considered forest interior specialists (following Robbins et al. 1989) were recorded. Among the forest interior specialists were species such as Prothonotary, Swainson's, and Hooded warblers, which are Partners in Flight species of high conservation concern and associated with structurally mature forested wetlands (Petit 1999, Brown and Dickson 1994, Evans Ogden and Stutchbury 1994). Thus, my sampled sites likely reflect a broad-scale spatial heterogeneity expected in welldeveloped, contiguous BHF systems.

Vertical structural complexity of vegetation, measured as a composite variable of stems terminating at various height categories, had a direct affect on species richness and diversity. These results support Martin's hypothesis that vertical vegetation structure is a primary factor in determining breeding bird community parameters in forested habitats (1993). Yet the addition of other structural elements, such as herbaceous growth, had no significant additional effects. These results are comparable to previous studies which have indicated that layering of woody vegetation, via increased nesting and/or foraging substrates and microhabitats, are strong predictors of avian community parameters (Wiens and Rotenberry 1981, and citations therein).

Effects of other structural elements of local microhabitat describing general spatial diversity and complexity, suggest that such simple measures of heterogeneity (i.e., terminal stems alone) may oversimplify patterns of local diversity as predicted by Southwood (1996). Regression analyses using principal components derived from combining multiple habitat variables suggest that avian community richness and diversity are determined primarily by a cumulative increase in tree and shrub density in the understory and canopy of BHF plots. Swift et al. (1984) found similar results in forested wetlands of Massachusetts which they were able to link to hydrological cycles. Swift et al. (1984) and Kilgo et al. (1999) found a positive correlation between understory density and primary productivity and fleshy resource (e.g., fruit) availability which they suggest further promotes avian species richness by increasing food abundance and diversity.

Models produced by Baker (1997) for BHF in south-east Mississippi found that avian species richness was most strongly correlated with an increase in dominant tree DBH and percentage of bare ground, with number of epiphytes, presence of water, number of decaying stumps, number of logs, and percent canopy cover of the understory contributing significant, but proportionally minor roles. Baker (1997), and similarly Hunter (1992), suggested that the increase in DBH within stands could be attributed to late-successional stages which would provide an increase in resource availability to an increasing number of species. Though not related to diversity or richness in this study, understory DBH was a predictor of overall abundance, which could be inferred to support Baker's (1997) conclusions. It should be noted that Baker's (1997) results were based upon multiple simple linear regression, and thus may hide effects of colinearity and potential combined effects, which my use of PCA was intended to reduce.

Overall abundance was also determined by an increase in tree health, decreasing canopy tree size, and increasing oak sapling abundance. Thus, sites with a more mature (i.e., larger trees) and developmentally diverse (i.e., local sapling recruitment is not limited to oaks) understory promote local avian abundance. It has been previously shown that while moderate disturbance promoted diversity, climax communities may provide greater resource abundance, thus allowing for a greater local abundance of consumers, even if richness declines (Morin 1999). Buffington et al. (1997) found that late-successional BHF habitats exhibit greater vegetative diversity, including multiple vegetation layers, high vegetation density, edges, snags, and interspersion of habitats which provide more potential nesting and foraging sites. Such descriptors are similar to the factors found to be meaningful in this study through PCA. They also found that structural diversity was paralleled by bird density and species diversity in riparian habitats and generally are greatest in late-successional habitats such as second-growth bottomland forests (Buffington et al. 1997). Thus, my results suggest a peak in measured community parameters associated with features of BHF of late-succession (Smith et al. 1995).

I did find support for the hypothesized relationship between structural complexity of plants and diversity of birds. However, my results also suggest that such approaches to diversity may overlook important elements often excluded from studies. My use of PC scores demonstrated that much of the effects of structural complexity are dependent upon the functional identity of the structural components and underlying spatial heterogeneity of habitats, factors that could prove critical in conservation of restoration efforts. Such factors should be considered in future studies associated with avian community and guild structure in BHF systems.

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CHAPTER V

LANDSCAPE HETEROGENEITY AND AVIAN ASSEMBLAGE CHARACTERISTICS IN BOTTOMLAND HARDWOOD FORESTS

ABSTRACT

While studies considering the effects of landscape-scale effects have increased dramatically over the last decade, most continue to consider the role of land cover and landscape heterogeneity on fragmented habitats. Few studies have considered such effects on contiguous landscapes. In this study, effect of land cover on community structure at 500-m, 1,000-m, and 1,500-m scales of birds in bottomland hardwood forests was examined. The landscape matrix included pure bottomland hardwood stands (> 90% bottomland hardwood forest), pine-hardwood mix (> 40% pine forest), and open-hardwood mix (> 40% agricultural land and/or fields). Comparisons of species diversity, richness, abundance, conservation values, wetland dependency, and habitat specialization using ANOVAs did not differ among land cover categories. Similarly, detrended correspondence analysis and canonical correspondence analysis found no significant patterns of variation in species composition among land cover types. These results are in contrast to several previous studies, but consistent with work suggesting land cover effect is scale-dependent and perhaps species-specific.

INTRODUCTION

Over the past two decades, studies have increasingly begun to consider avian assemblage structure in a landscape context. Traditionally, ecologists assumed that the most important ecological processes affecting communities operated at the local spatial scale, where quality and availability of food (e.g., Martin 1987), vegetation structure (e.g., James and Warner 1982, Martin 1993, Southwood 1996), floristics (e.g., Rotenberry 1985), and nest predation (e.g., Sieving and Willson 1998) could be correlated with variation in avian assemblage patterns. However, scientists have recently come to understand that relevant factors typically occur across various spatial scales and characteristics of assemblages are dependent upon the scale at which they are examined (e.g., Williams et al. 2002). For example, habitat fragmentation and landscape heterogeneity can affect local assemblages through differing effects on functional groups and altering population processes (Williams et al. 2002). Landscape context also can structure a community by influencing within-patch and metapopulation dynamics, as well as influence movement across the landscape (Kilgo et al. 1997). Yet investigations seldom address proximate causes of landscape associations, and thus few empirical data are available to evaluate alternative mechanisms responsible for assemblage structure at landscape scales (Rodewald and Yahner 2001). Developing an integrated theory of assemblage structure will require an integration of comparative research on community patterns across spatial scales.

While the number of studies of landscape-scale effects on avian assemblage has continued to increase substantially, most have focused on associations with the arrangements of patches, corridors, and matrix elements on landscapes and with patch area, fragmentation, and isolation (Rodewald and Yahner 2001), the conclusions of which remain ambiguous. Furthermore, studies evaluating avian diversity commonly do so within highly contrasting landscapes, such as forests, agriculture, and/or suburban environments. These studies have found numerous effects of landscape metrics on avian assemblages (e.g., Robbins et al. 1989, Villard et al. 1999, Sallabanks et al. 2000). Studies of more subtly contrasting landscapes, such as varying forest types, ages, management regimes, or silvicultural practices (e.g., Drolet et al. 1999, Penhollow and Stauffer 2000, Lichstein et al. 2002) have identified fewer effects.

Silviculture and agriculture are common land use practices outside urban centers in the largely rural state of Mississippi. Mississippi remains one of the most forested states in the eastern U.S., with more than 7,300,000 ha of timberland (62% of state), approximately 20% of which is bottomland hardwood forest (Rosson 2001). However, much of the remaining naturally forested areas are restricted to state parks, national forests, or federal wildlife refuges deeply embedded in a matrix of silvicultral (e.g., pine or pine-hardwood) and agricultural (e.g., corn, soybean, and hay) habitats. Yet the landscape-scale effects of the common land use practices on wild populations within forests remains poorly understood (but see Kilgo et al. 1997).

The purpose of this study was to determine the effects of landscape heterogeneity on structural characteristics of avian assemblages in bottomland hardwood forests in eastcentral Mississippi. I hypothesized that mixed landscapes would support a greater diversity of species, but more homogeneous landscapes would result in a more specialized collection of species. I also hypothesized that differences will be more pronounced in contrasting landscapes (bottomland hardwood forest within a agricultural matrix) than within more subtly contrasting landscapes (bottomland hardwood forest within a pine or pine-hardwood matrix) and therefore support Kilgo et al.'s (1997) forest buffer hypothesis, which states that "harder" edges (e.g., forest/grassland transition) have a stronger impact on local communities than do soft edges (e.g., two adjacent forest types). Thus I predicted that: 1) points within pure bottomland hardwood stands would have an increased number of forested wetland species and overall habitat specialists, 2) points within a bottomland hardwood forest landscape would maintain lower overall diversity and species richness than those within a mixed bottomland/pine forest matrix, which in turn would be lower than points within a bottomland/field matrix; and 3) species abundance would not vary among stand types.

STUDY AREA

This study was conducted on the Noxubee National Wildlife Refuge (NNWR) in portions of Oktibbeha, Noxubee, and Winston counties of east-central Mississippi (33°N, 88°W). NNWR covers nearly 19,400 ha of mostly forested lands, about 6,300 ha of which are nearly contiguous bottomland hardwood forest along the Noxubee River and 10 of its tributaries. Other habitats include pine forests, mixed pine/hardwood forests, upland hardwood forests, fields, and lakes. Surrounding NNWR, and within its boundaries, are private land holdings used predominantly for agriculture and silviculture. Thus, the contiguous nature of the focal habitat reduced the effects of confounding factors such as fragmentation and connectivity, while simultaneously providing a relatively heterogeneous landscape.

METHODS

Point-Count Surveys.

I used standard fixed-radius (radius = 50m), silent point counts following survey protocol of Hamel et al. (1996) during the late spring and early summer of 2002 through 2004. A total of 66 random points were stratified across a contiguous bottomland hardwood forests to insure some buffer overlap with other habitat types (i.e., pine forests and open fields) at distances \geq 500m with the constraint that all points were \geq 200m from the next nearest point and \geq 100m from any habitat edge. All birds detected by sight or sound during a 10-min sampling period were recorded, excluding flyovers. Each count station was surveyed twice between 10 May and 15 June each year. Point count stations were not visited a second time until all other count stations had been completed once. Surveys were conducted during the first four hours following local sunrise, weather permitting (e.g., no rain or wind > 19 km/hr). Size of plots and count time constraints were established to optimize sampling effort (Ralph et al. 1995, Hamel et al. 1996).

Landscape Parameters.

Landscape parameters were measured using landcover data from the Mississippi Gap Program, with a $30m \times 30m$ resolution. Fifty three random points were ground truthed to insure relative accuracy of maps. ArcGIS 9.1 was used to establish 500-m, 1,000-m, and 1,500-m buffers around each point count site. Each point count site was

categorized as pure bottomland hardwood forest if landcover was >90% bottomland hardwood forest, pine-hardwood landscape if landcover was >40% pine, and openhardwood landscape if landcover was greater than 40% pasture, cleared field, or agricultural land. However, because of the relatively contiguous nature of bottomland hardwood forests at NNWR, no points with 500-m buffers met criteria for pine or field landscapes and thus were not used in final analyses. Previous studies have shown that landscape characteristics of a 1,000 m buffer surrounding a habitat patch can significantly influence avian distribution, abundance, and reproductive success (e.g., Saab 1999). My point count placement resulted in the same classification of points with both 1,000-m and 1,500-m buffers, so results reflect both buffers simultaneously. Of the 66 point count survey sites, thirty points met pure bottomland criteria but only 12 met pine-hardwood criteria and seven met open-hardwood criteria. For the purpose of maintaining similar samples sizes for each land cover category, 10 pure bottomland hardwood landscape points and 10 pine-hardwood landscape points were randomly selected for analyses and all seven open-hardwood landscape points were used in analyses.

Community Parameters.

The following community metrics were used to compare avian community characteristics among landscape types: species abundance, species richness, species diversity, community evenness, community similarity, and conservation value scores. Species abundance and species richness were measured as the sum of the maximum number of individuals of all species observed in one sampling visit and the total number
of species observed at each point respectively. Species diversity was assessed using the Shannon Diversity Index (H'; Brower et al. 1998):

$$H' = -\sum p_i \log p_i$$

Where p_i is the proportion of species *i* within a community at a point. Community evenness (*J'*), or relative diversity, was measured as:

$$J' = H'/H_{max}'$$

Where H_{max} is the natural log of the total number of species observed.

Bottomland hardwood forests in the southeastern U.S. are of high conservation concern because of the numerous avian breeding residents considered Partners in Flight (PIF) species of priority concern (Hunter et al. 1993). For that reason, several measures related to conservation status were considered, including conservation value indices, wetland dependency ranking, and BHF habitat specificity ranking. Breeding bird conservation value indices (*BBCV*) were derived using a PIF composite index (*BBCV*_{PIFcomp}) following Nuttle et al. (2003). Thus the index can be represented by:

$$BBCV_{PIFcomp} = \sum_{i=1}^{s} a_i w_i$$

Where *s* is the number of species in the community, a_i is the abundance of species *i*, and w_i is the weighting factor (i.e. PIF ranking, see Appendix A.1).

Wetland dependency and habitat specificity rankings are intended to evaluate the variation in site specific use by species requiring bottomland hardwood forests (Snell-Rood and Cristol 2003). Such rankings reduce the effects of ubiquitous species on site comparisons. For both values, each species recorded was assigned a ranking for their wetland dependency and degree of habitat specificity following Croonquist and Brooks

(1991) and Snell-Rood and Cristol (2003), or author experience. Wetland dependency rankings were: 0 = upland, 1 = sometimes uses wetlands, 3 = usually lives in wetlands, 5 = found only in wetlands. Habitat specificity rankings were: 1 = generalist, 3 = dependent upon the landscape (e.g., forest or grassland), but not a single habitat type (e.g., hardwood or pine forest), 5 = habitat specialist (see Appendix A.1 for speciesspecific rankings for all species). Rankings were summed for all species present at each point-count site.

Analyses.

All variables were analyzed using repeated measures Analysis of Variance (ANOVA) and post-hoc Tukey-Kramer pair-wise comparisons to test for landscape and year effects using SAS (PROC MIXED; SAS Institute 1990). Multivariate analyses were used to explore potential variation in actual species composition among landscapes. Average abundance of species was compared among point count sites with detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) biplots using CANOCO, version 4.5 (ter Braak and Šmilauer 2002). DCA axes were compared among habitats with ANOVA and post-hoc Tukey-Kramer pair-wise comparisons using SAS (PROC MIXED; 1990). Rare species (those recorded fewer than five times) were excluded from analyses to reduce biases inherent in ordination techniques (ter Braak and Šmilauer 2002).

RESULTS

There were no significant differences in diversity, evenness, richness, abundance, conservation values, wetland dependency, or habitat specialization among sites in the three landscape contexts (Table 5.1). For DCA samples scores, only axes 1 and 2 described more than five percent of overall variance within samples (16% and 8.2% respectively) and thus were the only axes included in ANOVAs. However, no significant differences were found for axis 1 (df = 2, F = 2.505, P = 0.103) or axis 2, (df = 2, F = 0.038, P = 0.963). Four CCA axes were derived, which cumulatively accounted for 33%

Table 5.1. Mean (± SE) values for breeding season avian community variables associated with bottomland hardwood plots located within a pure bottomland hardwood landscape (BHF; > 90% bottomland), pine-hardwood landscape (> 40% pine), and open-hardwood landscape (> 40% pastures and fields) at Noxubee National Wildlife Refuge, Mississippi (2002 – 2004).

Variable	BHF	Pine	Field	F	Р
Diversity (H')	2.480±0.037	2.482±0.055	2.494±0.155	0.045	0.956
Evenness (J')	0.192±0.004	0.194±0.006	0.192±0.018	0.23	0.795
Breeding Bird Conservation Values	46.70±2.501	42.05±2.555	44.86±8.008	0.929	0.401
Wetland Dependency	22.55±1.935	18.08±1.426	17.57±6.418	2.286	0.111
Habitat Specialization	44.30±2.231	38.75±2.454	41.43±9.238	1.369	0.263
Abundance	18.00±0.932	16.65±0.938	17.86±3.231	0.685	0.509
Richness	13.15±0.519	13.15±0.662	13.14±1.994	0.044	0.957

of variation in species data. Using Monte Carlo randomization tests, neither axis 1 (F = 1.44, P = 0.190), nor axis 2 (F = 1.03, P = 0.390) was significant. Thus points within different landscape matrices did not vary significantly in overall species composition.

DISCUSSION

Avian assemblage structure and composition of bottomland hardwood forests did not differ significantly among sites within bottomland hardwood, pine-hardwood, and open-hardwood landscapes. These results support none of my predictions regarding landscape-scale influence on local assembly patterns in birds. They are also in contrast to Kilgo et al.'s (1997) findings in South Carolina in which species richness and total abundance of forest birds were higher in BHF stands surrounded by fields rather than pine forests. It should be noted that Kilgo et al. (1997) examined fragmented hardwood forests where patch size demonstrated a stronger positive relationship with avian community structure than did landscape type. Because of the contiguous nature of BHF at NNWR, and my distance to edge of habitat criteria for each point, sampled points were within areas of minimally 3.5 ha (most were ≥ 6 ha) of pure BHF, compared to the Kilgo et al.'s (1997) study in which most patches were < 2 ha. Perhaps the majority of sites I examined contained a sufficient amount of BHF to support area sensitive species, like Swainson's and Hooded warblers, which were recorded at sites within all landscapes, including those in an open-hardwood matrix.

Such differences between results of this study and Kilgo et al. (1997) are consistent with the contrasting results found in numerous landscape studies of forest birds. For example, McGarigal and McComb (1995) and Trzcinski et al. (1999) found that variation in landscape composition was the most important predictor of abundance and distribution of local forest breeding birds, while Lee et al. (2002) found only select species (e.g., interior specialists like Ovenbirds, *Seiurus aurocapillus*) to be effected significantly by variables beyond 300 m of a habitat patch. Species-specific effects of landscape metrics were not included in this study; however, such analyses may prove insightful in the future given the variability of effects and the potential influence on future conservation planning.

The results of this study may also be consistent with the findings of Atauri and de Lucio (2001) and Böhning-Gaese (1997) where both studies concluded land cover types were not as important as overall landscape heterogeneity in predicting community structure. Thus, it may be that land cover does not have a significant effect on local species, but details of inherent heterogeneity do.

Although landscape was not found to be an indicator of community structure for birds in bottomland hardwood forests at NNWR in this study, it does not necessarily imply that landscape does not affect the ability of species to successfully occupy habitat patches. Landscape metrics often have greater power when there are stronger differences among the elements that effect local habitat quality (Wiens et al. 1987). Sites used in this study rarely had non-bottomland hardwood forest habitat components exceeding the minimum requirement by more than 5% (i.e., plots were rarely within buffers comprised of > 45% pine or field). As such, I would recommend that future studies examining the effects of landscape features on bottomland hardwood forest birds consider more stringent requirements for site selection within the available landscape matrix, following a more strict stratified sampling criteria and a larger sample size to insure effects are not dismissed statistically. While reducing random selection, it will better allow investigators to consider landscape effects of habitat patches that persist as part of a larger contiguous feature.

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CHAPTER VI

CONCLUSIONS

Bottomland hardwood forests (BHF) are forested wetlands located adjacent to riverine systems and characterized by seasonal flooding and water-tolerant plants (Abernathy and Turner 1987). These heterogeneous ecosystems, which have rapidly been lost in historical times, are an important habitat for numerous migratory and nonmigratory birds of conservation concern (Hunter et al. 1993). As such, understanding variables within bottomland hardwood forests that affect avian assemblage patterns are of great interest to biologists. I examined factors influencing avian assemblage and guild patterns in bottomland hardwood forests (BHF) of Noxubee National Wildlife Refuge in east-central Mississippi. To that end, I considered the effects of greentree reservoir (GTR) management, local plant structural complexity, and landscape matrix, on several avian community metrics.

Because GTR management has been shown to affect vegetation structure and composition (e.g., King 1995, King and Allen 1996, and King et al. 1998) and invertebrate diversity (Young et al. 1995), there have been concerns that these modifications may directly or indirectly affect non-game bird diversity or abundance (e.g., Christman 1987, Deller and Baldassarre 1999). I predicted that GTRs would exhibit significant decreases in species diversity, richness, and BBCV scores compared to

unimpounded BHF and that lower-level understory nesting and foraging guilds would have a decrease in richness and abundance within GTRs. At Noxubee National Wildlife Refuge, GTRs do appear to have a subtle effect on avian habitat. I found that sites within GTRs, sites in BHF adjacent to GTRs, and random BHF sites did differ in diversity, richness, and evenness of breeding birds (p < 0.05 for all variables). However, the pattern exhibited in a continuum of decreasing diversity occurring from within GTRs to random BHF sites. This gradient could indicate that GTR avian communities are within the expected range of variation of unimpounded BHF given their inherent structural variation. However, it is unclear whether GTR management indirectly affects the surrounding landscape as well. No differences were found among measures of abundance, conservation status, or habitat specialization. Within guild richness and abundance were similar among sites except for a decreasing continuum in species richness among BHF, GTR-peripheral, and GTR sites. The canopy nesting guild was the only guild found to have significantly higher richness in BHF sites, and the ground gleaning foraging guild had a significantly lower abundance in GTRs.

Previous studies have demonstrated positive effects of GTR management on waterfowl (e.g., Reinecke et al. 1998), but this was the first study to examine potential effects on wintering, non-game bird communities. Winter data indicated that neither general GTR management nor within season inundation events significantly affect general community structure, conservation rankings, or habitat specialization characteristics. While ground gleaning birds did exhibit a seasonal shift in habitat use, this change was study-wide and appears to reflect a more general movement of birds within this particular foraging guild away from the hydrologically dynamic bottomland hardwood forests and not necessarily a direct response to GTR management. The overall results appear to reflect the ubiquitous nature of many birds wintering in east-central Mississippi forests.

Thus, my results suggest that while GTR management overall may alter a variety of habitat variables, modifications are within the range of variation one might expect among bird communities within BHF systems. It would be beneficial to replicate this study at a variety of locations reflecting varying aged GTRs and locations within different physiographic areas to better understand the general applicability of theses results. Addition of GTRs of various ages could add to our knowledge of temporal effects. Furthermore, sampling local points along transects radiating away from established GTRs may clarify whether or not data from the outer periphery of GTRs reflect natural condition, allowing for conclusions such as those I have made, or if they reflect indirect alterations resulting from GTR management of adjacent sites.

Because birds rely on various vegetative and structural components to provide necessary life requirements (e.g., Hamel 1992, Pashley et al. 1992, Mauer et al. 1992), it is of interest to understand how those features directly effect local avian assemblages. In considering effects of plant structural complexity on avian communities in BHF, regression analyses demonstrated a direct positive relationship between shrub and tree structural divesity and avian assemblage structure as predicted by long standing hypotheses, such as Martin's (1993) structural vertical heterogeneity hypothesis. However, regression analyses of principal component scores derived from sixty structural descriptor metrics suggest that avian communities and guilds in bottomland hardwood forests in east-central Mississippi are more directly influenced by overall local structural complexity, especially as it relates to understory plants. This indirectly supports hypotheses, such as Southwood's spatial heterogeneity hypothesis (1996) that suggests a greater influence of local scale plant heterogeneity. Variation in abundance of species was found to increase with mature canopies, understories with increased plant diversity, and trees in a variety of health stages. Future studies might consider a finer scale of variation using within-plot sampling. Such information may better clarify effects of local spatial heterogeneity on avian assemblage patterns.

Finally, an examination of potential effects of landscape variation revealed that species diversity, species richness, abundance, conservation values, wetland dependency, and habitat specialization use did not vary among land cover categories. Similarly, detrended correspondence analysis and canonical correspondence analysis found no significant patterns of variation in species composition among land cover types. These results are in contrast to several previous studies examining fragmented BHF (e.g., Kilgo et al. 1997, Williams et al. 2002) in which "hard" edges, such as forest/field borders, exhibited pronounced effects on local species composition, primarily impacting area sensitive species. However, other work has suggested land cover effects are very much scale dependent and perhaps species specific within relatively contiguous habitats (e.g., Böhning-Gaese 1997, Atauri and de Lucio 2001). One caveat with my study is that because my point count sites were deeply embedded within a large, contiguous BHF landscape, it was not possible to get a large sample size for all land cover categories.

Thus, conclusions on effects of landscape-scale heterogeneity from this study are relatively tenuous. It would be beneficial in the future to consider similar community parameters using continuous data of all land cover types associated with point count samples. Imposing restrictions on point count locations to insure a more diverse habitat at scales of interest and an increased sample size would also be recommended. Finally, it may well be necessary to consider such landscape effects on a species-specific basis, considering both area sensitive and non area sensitive species.

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APPENDIX A

BREEDING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES

Table A.1. Conservation concern rankings, habitat specificity scores, wetland dependency scores, and guilds of species in unimpounded BHF, GTR, and GTR-peripheral sites. Conservation concern scores are Partners in Flight rankings. Habitat specificity and wetland dependency ranks follow Croonquist and Brooks (1991) and Snell-Rood and Cristol (2003) and when not available, author experience. Habitat Specificity: 1 = generalist, 3 = selection based upon general landscape features, not a single habitat type, 5 = habitat specialist. Wetland dependency: 0 = upland, 1 =occasionally uses wetlands, 3 = usually uses wetlands, 5 = found in wetlands only. Nesting guild (Ehrlich et al. 1988): 1 = ground, 2 = shrub, 3 = understory, 4 = canopy, 5 = cavity, 6 = bank, 7 = nest parasites. Foraging guild (Ehrlich et al. 1988): 1 = foliage gleaning insectivore, 2 =bark gleaning insectivore, 3 = ground gleaning insectivore, 4 = ground gleaning granivore, 5 = ground gleaning omnivore, 6 = flycatching, 7 =nectarivores, 8 = aerial divers, 9 = raptorial, 10 = stalk and strike, 11 =dabblers.

Species	Conservation Concern Scores	Habitat Specificity	Wetland Dependency	Nesting Guild	Foraging Guild
Great Blue Heron (Ardea herodius)	3	3	5	4	10
Little Blue Heron (Egretta caerulea)	3	3	5	4	10
Cattle Egret (Bubulcus ibis)	1	1	3	4	10
Yellow-crowned Night-Heron (Nyctannasa					
violacea)	3	3	5	4	10
Wood Duck (Aix sponsa)	3	5	5	5	11
Red-shouldered Hawk (Buteo lineatus)	3	3	3	4	9
Broad-winged Hawk (Buteo platypterus)	4	3	3	4	9
Wild Turkey (Meleagris gallopavo)	2	1	0	1	5
Yellow-billed Cuckoo (Coccyzus americanus)	3	1	0	4	1
Barred Owl (Strix varia)	3	3	1	5	9
Ruby-throated Hummingbird (Archilochus					
colubris)	3	1	1	4	7
Belted Kingfisher (Ceryle alcyon)	4	3	3	7	8
Red-headed Woodpecker (Melanerpes					
erythrocephalus)	3	3	1	5	2
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	3	3	1	5	2
Downy Woodpecker (Picoides pubescens)	4	1	0	5	2
Hairy Woodpecker (Picoides villosus)	4	3	0	5	2
Pileated Woodpecker (Dryocopus pileatus)	3	5	0	5	2
Eastern Wood-Pewee (Contopus virens)	3	1	0	3	6
Acadian Flycatcher (Empidonax virescens)	3	3	3	3	6
Eastern Phoebe (Sayornis phoebe)	2	3	1	2	6
Great-crested Flycacher (Myiarchus crinitus)	3	3	0	5	6

Table A.1. Continued.

Species	Conservation Concern Scores	Habitat Specificity	Wetland Dependency	Nesting Guild	Foraging Guild
White-eyed Vireo (Vireo griseus)	3	3	3	2	1
Yellow-throated Vireo (Vireo flavifrons)	3	1	1	4	1
Red-eyed Vireo (Vireo olivaceus)	2	1	0	4	1
Blue Jay (Cyanocitta cristata)	2	0	1	4	5
American Crow (Corvus brachyrhynchos)	1	1	0	4	5
Carolina Chickadee (Poecile carolinensis)	3	1	0	4	2
Tufted Titmouse (Baeolophus bicolor)	2	3	1	4	2
White-breasted Nuthatch (Sitta carolinensis)	3	5	0	5	2
Carolina Wren (Thryothorus ludovicianus)	1	1	0	5	1
Blue-gray Gnatcatcher (Polioptila caerulea)	2	3	1	4	1
Wood Thrush (Hylocichla mustelina)	4	3	0	3	3
Gray Catbird (Dumetella carolinensis)	3	1	1	2	2
Brown Thrasher (Toxostoma rufum)	3	1	0	2	3
Northern Parula (Parula americana)	3	3	3	4	1
Kentucky Warbler (Oporornis formosus)	4	3	1	1	3
Common Yellowthroat (Geothlypis trichas)	2	2	3	2	1
Hooded Warbler (Wilsonia citrina)	3	3	3	2	1
Yellow-breasted Chat (Icteria virens)	3	3	1	2	1
Summer Tanager (Piranga rubra)	2	1	0	4	1
Eastern Towhee (Pipilo erythropthalmus)	2	1	0	1	3
Northern Cardinal (Cardinalis cardilanis)	2	1	0	2	4
Indigo Bunting (Passerina cyanea)	3	1	1	2	1
Common Grackle (Quiscalus quiscula)	1	1	0	3	3
Yellow-throated Warbler (Dendroica dominica)	3	3	3	4	1
Pine Warbler (Dendroica pinus)	3	5	0	4	1
American Redstart (Setophaga ruticilla)	3	3	1	3	3
Worm-eating Warbler (Helmintheros vermivorus)	3	5	5	1	1
Swainson's Warbler (Limnothlypis swainsonii)	4	5	5	2	3
Louisiana Waterthrush (Seiurus motacilla)	3	3	5	1	3
Brown-headed Cowbird (Molothrus ater)	1	1	0	7	5

APPENDIX B

WINTERING BIRDS OBSERVED AT NOXUBEE NATIONAL WILDLIFE REFUGE, MISSISSISSIPPI, AND ASSOCIATED POPULATION VALUES

Table B.1. Conservation concern rankings, habitat specificity scores, wetland dependency scores, and Foraging guilds of species in unimpounded BHF, GTR, and GTR-peripheral sites. Conservation concern scores are Partners in Flight rankings. Habitat specificity and wetland dependency ranks follow Croonquist and Brooks (1991) and Snell-Rood and Cristol (2003) and when not available, author experience was used. Habitat Specificity: 1 = generalist, 3 = selection based upon general landscape features, but not a single habitat type, 5 = habitat specialist. Wetland dependency: 0 = upland, 1 = occasionally uses wetlands, 3 = usually uses wetlands, 5 = found in wetlands only. Foraging guild (Ehrlich et al. 1988): 1 = foliage gleaning insectivore, 2 = bark gleaning insectivore, 3 = ground gleaning insectivore, 4 = ground gleaning granivore, 5 = ground gleaning omnivore, 6 = flycatching, 7 = nectarivores, 8 = aerial divers, 9 = raptorial, 10 = stalk and strike, 11 = dabblers.

Species	Conservation Concern Scores	Habitat Specificity	Wetland Dependency	Foraging Guild
Great Blue Heron (Ardea herodius)	3	3	5	10
Wood Duck (Aix sponsa)	3	5	5	11
Mallard (Anas platyrhynchos)	3	3	5	13
Hooded Merganser (Lophodytes cucullatus)	4	3	5	14
Sharp-shinned Hawk (Accipiter striatus)	3	3	1	11
Cooper's Hawk (Accipiter cooperi)	3	3	1	3
Red-shouldered Hawk (Buteo lineatus)	3	3	3	9
Wild Turkey (Meleagris gallopavo)	2	1	0	5
Barred Owl (Strix varia)	3	3	1	9
Belted Kingfisher (Ceryle alcyon)	4	3	3	8
Red-headed Woodpecker (Melanerpes				
erythrocephalus)	3	3	1	2
Red-bellied Woodpecker (Melanerpes carolinus)	3	3	1	2
Yellow-bellied Sapsucker (Sphyrapicus varius)	1	3	0	2
Downy Woodpecker (Picoides pubescens)	4	1	0	2
Hairy Woodpecker (Picoides villosus)	4	3	0	2
Northern Flicker (Colaptes auratus)	2	3	0	4
Pileated Woodpecker (Dryocopus pileatus)	3	5	0	2
Eastern Phoebe (Sayornis phoebe)	2	3	1	6
Blue-headed Vireo (Vireo solitarius)	2	3	1	1
Blue Jay (Cyanocitta cristata)	2	0	1	5
American Crow (Corvus brachyrhynchos)	1	1	0	5
Fish Crow (Corvus ossifragus)	3	3	3	6
Eastern Bluebird (Sialia sialis)	2	5	0	7
Hermit Thrush (Catharus guttatus)	2	3	0	4
American Robin (Turdus migratorius)	2	1	1	4

Table B.1. Continued.

Species	Conservation Concern Scores	Habitat Specificity	Wetland Dependency	Foraging Guild
Carolina Chickadee (Poecile carolinensis)	3	1	0	2
Tufted Titmouse (Baeolophus bicolor)	2	3	1	2
Brown Creeper (Certhia americana)	3	5	0	3
White-breasted Nuthatch (Sitta carolinensis)	3	5	0	2
Red-breasted Nuthatch (Sitta canadensis)	2	5	0	3
Carolina Wren (Thryothorus ludovicianus)	1	1	0	1
Winter Wren (Troglodytes troglodytes)	2	3	1	4
Golden-crowned Kinglet (Regulus satrapa)	2	1	0	1
Ruby-crowned Kinglet (Regulus calendula)	2	1	0	1
Brown Thrasher (<i>Toxostoma rufum</i>)	3	1	0	3
Yellow-rumped Warbler (Dendroica magnolia)	2	1	0	1
Pine Warbler (<i>Dendroica pinus</i>)	3	5	0	1
Common Yellowthroat (Geothlypis trichas)	2	2	3	1
Eastern Towhee (Pipilo erythropthalmus)	2	1	0	3
Song Sparrow (Melospiza melodia)	2	3	1	4
White-crowned Sparrow (Zonotrichia leucophrys)	1	3	1	4
White-throated Sparrow (Zonotrichia albicollis)	2	3	1	4
Dark-eyed Junco (Junco hyemalis)	2	1	0	5
Northern Cardinal (Cardinalis cardilanis)	2	1	0	4
Red-winged Blackbird (Agelaius phoeniceus)	2	1	3	4
Common Grackle (Quiscalus quiscula)	1	1	0	3
Brown-headed Cowbird (Molothrus ater)	1	1	0	5
Purple Finch (Carpodacus purpureus)	2	1	0	5
American Goldfinch (Carduelis tristis)	2	1	0	1

APPENDIX C

VEGETATION VARIABLES MEASURED AT NOXUBEE NATIONAL WILDLIFE

REFUGE, MISSISSISSIPPI

Tree canopy diversity Tree understory diversity Tree sapling diversity Canopy coverage Mean canopy height Mean understory height Number of small (<10 cm diameter) logs on ground in plot Number of large (>10 cm diameter) logs on ground in plot Number of stumps (< 1.5 m ht) in plot Distance to nearest canopy gap (m) Total number of woody plants between 1-1.5m, 1.5 - 2.0 m, 2-2.5 m, and >2.5 mTotal number of canopy trees in plot Total number of understory trees in plot Total number of sapling trees in plot Mean diameter at breast height (DBH) of Canopy trees Mean DBH of understory trees Mean DBH of sapling trees Average canopy tree health (state; scale1-5) Average understory tree health Average sapling tree health Number of woody stems terminating at 0-0.3 m, 0.3-1m, 1-2m, and > 2mNumber of oak stems terminating at 0-0.3 m, 0.3-1m, 1-2m, and > 2mNumber of herbaceous stems terminating at 0-0.3 m, 0.3-1m, 1-2m, and > 2mNumber of cane stems terminating at 0-0.3 m, 0.3-1m, 1-2m, and > 2mNumber of ferns terminating at 0-0.3 m, 0.3-1m, 1-2m, and > 2m% cover of woody plants between 0-0.3 m, 0.3-1m, 1-2m, and > 2m% cover of herbaceous plants between 0-0.3 m, 0.3-1m, 1-2m, and > 2m% cover of cane between 0-0.3 m, 0.3-1m, 1-2m, and > 2m% cover of ferns between 0-0.3 m, 0.3-1m, 1-2m, and > 2m% cover of vines between 0-0.3 m, 0.3-1m, 1-2m, and > 2m% Ground Covered by bare ground % Ground Covered by leaf litter % Ground Covered by grass % Ground Covered by water % Ground Covered by roots % Ground Covered by moss % Ground Covered by cypress knees % Ground Covered by fungi

Table C.1. Vegetation variables measured at each point count station in bottomland hardwood forest stands of Noxubee National Wildlife Refuge, Mississippi.