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Breeding Ecology of Songbirds in Bottomland Hardwood Forests of Louisiana.

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**BREEDING ECOLOGY OF SONGBIRDS
IN BOTTOMLAND HARDWOOD
FORESTS OF LOUISIANA**

A Dissertation

**Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy**

in

The School of Forestry, Wildlife, and Fisheries

by

Keith Ouchley

B.S., Northeast Louisiana University, 1981

M.S., Northeast Louisiana University, 1992

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	ii
LIST OF TABLES.....	vii
LIST OF FIGURES	xii
ABSTRACT.....	xv
 CHAPTER 1. NEST SUCCESS AND PRODUCTIVITY.....	1
INTRODUCTION	1
OBJECTIVES.....	4
METHODS	5
STUDY AREAS	5
FIELD METHODS.....	8
DATA ANALYSIS.....	9
RESULTS	11
SPECIES ACCOUNTS	11
ACADIAN FLYCATCHER (<i>Empidonax virescens</i>)	11
WHITE-EYED VIREO (<i>Vireo griseus</i>)	16
RED-EYED VIREO (<i>Vireo olivaceus</i>).....	24
PROTHONOTARY WARBLER (<i>Protonotaria citrea</i>)	27
RUBY-THROATED HUMMINGBIRD (<i>Archilochus colubris</i>)	32
HOODED WARBLER (<i>Wilsonia citrina</i>).....	36
KENTUCKY WARBLER (<i>Oporonis formosus</i>).....	40
YELLOW-BILLED CUCKOO (<i>Coccyzus americanus</i>)	43
OTHER MIGRANT SPECIES	47
NORTHERN CARDINAL (<i>Cardinalis cardinalis</i>)	47
CAROLINA WREN (<i>Thryothorus ludovicianus</i>)	52
OTHER RESIDENT SPECIES	56
SPECIES GROUPS	57
FREQUENCY OF NEST CHECKS.....	68
DISCUSSION.....	69
MIGRANT SPECIES	69
SITE DIFFERENCES.....	69
TIMING OF NESTING	72
STAGES OF THE NESTING CYCLE	75
TYPES OF NESTS	75
RESIDENT SPECIES.....	78
FREQUENCY OF NESTS CHECKS	80
MANAGEMENT CONSIDERATIONS.....	81
LITERATURE CITED	86
 CHAPTER 2. ANNUAL SURVIVORSHIP	92
INTRODUCTION	92

OBJECTIVES	95
METHODS	95
STUDY AREAS	95
FIELD METHODS	96
DATA ANALYSIS	97
RESULTS	98
INDIVIDUAL SITE RATES	98
FERRIDAY.....	98
SHERBURNE.....	99
RED DIAMOND	99
TRENDS AMONG SITES	100
INDIVIDUAL SPECIES RATES AT SHERBURNE AND RED DIAMOND	100
ANNUAL RETURN DISTANCES.....	101
DISCUSSION.....	105
FACTORS AFFECTING SURVIVORSHIP ESTIMATES	105
SEX DIFFERENCES	108
SITE DIFFERENCES.....	112
MIGRANTS VS. RESIDENTS.....	114
AGE DIFFERENCES.....	115
SPECIES DIFFERENCES	117
LITERATURE CITED	118
 CHAPTER 3. NEST-SITE HABITAT.....	123
INTRODUCTION	123
OBJECTIVES	124
METHODS	125
STUDY AREAS	125
FIELD METHODS.....	127
DATA ANALYSIS.....	129
RESULTS	131
USE AND AVAILABILITY OF NEST-SITE HABITAT.....	131
ACADIAN FLYCATCHER (<i>Empidonax virescens</i>)	131
AMERICAN REDSTART (<i>Setophaga ruticilla</i>)	135
CAROLINA WREN (<i>Thryothorus ludovicianus</i>)	137
HOODED WARBLER (<i>Wilsonia citrina</i>).....	138
KENTUCKY WARBLER (<i>Oporornis formosus</i>)	139
NORTHERN CARDINAL (<i>Cardinalis cardinalis</i>)	141
NORTHERN PARULA (<i>Parula americana</i>)	144
PROTHONOTARY WARBLER (<i>Protonotaria citrea</i>)	145
RED-EYED VIREO (<i>Vireo olivaceus</i>)	147
RUBY-THROATED HUMMINGBIRD (<i>Archilochus colubris</i>)	149
WHITE-EYED VIREO (<i>Vireo griseus</i>)	150

YELLOW-BILLED CUCKOO (<i>Coccyzus americanus</i>)	153
NEST COVER	155
DISTINGUISHING NEST-SITES AND RANDOM SITES	156
NEST HEIGHT AND NEST PLANT HEIGHT	157
NEST-SITE HABITAT AND NEST SUCCESS	159
MAJOR SOURCES OF VARIABILITY	166
CLUSTER ANALYSIS	167
DISCUSSION	170
MANAGEMENT CONSIDERATIONS	175
LITERATURE CITED	178
APPENDIX A: LIST OF ABBREVIATIONS FOR BIRD SPECIES	
USED IN THIS TEXT	182
APPENDIX B: LIST OF ABBREVIATIONS FOR PLANT SPECIES	
USED IN THIS TEXT	183
VITA	184

LIST OF TABLES

1.1. Number of Acadian Flycatcher nests by year and site.....	12
1.2. Mean daily survival rates of Acadian Flycatcher nests at four sites.....	12
1.3. Fates of Acadian Flycatcher nests by site.....	14
1.4. Fates of Acadian Flycatcher nests by time of nest initiation.....	15
1.5. Mean number of Acadian Flycatcher young fledged per nest at each site.....	16
1.6. Number of White-eyed Vireo nests by year and site.....	17
1.7. Mean daily survival rates of White-eyed Vireo nests by site.....	17
1.8. Mean daily survival rates of White-eyed Vireo nests by site and time of initiation.....	20
1.9. Fates of White-eyed Vireo nests by site.....	21
1.10. Fates of White-eyed Vireo nests by time of nest initiation.....	22
1.11. Mean number of White-eyed Vireo young fledged per nest by site and time of nest initiation.....	23
1.12. Number of Red-eyed Vireo nests by year and site.....	24
1.13. Mean daily survival rate of Red-eyed Vireo nests by site.....	25
1.14. Mean daily survival rates of Red-eyed Vireo nests initiated before (early) and after (late) June 1 and during incubation and nestling stages.....	26
1.15. Fates of Red-eyed Vireo nests by site.....	26
1.16. Fates of Red-eyed Vireo nests by time of nest initiation.....	27
1.17. Number of Prothonotary Warbler nests by site and year.....	28
1.18. Mean daily survival rate of Prothonotary Warbler nests by site.....	29
1.19. Fates of Prothonotary Warbler nests by site.....	30
1.20. Fates of Prothonotary Warbler nests by time of nest initiation.....	31

1.21. Mean number of Prothonotary Warbler young fledged per nest at each site	31
1.22. Number of Ruby-throated Hummingbird nests by site and year	33
1.23. Fates of Ruby-throated Hummingbird nests by site	35
1.24. Fates of Ruby-throated Hummingbird nests by time of nest initiation.....	35
1.25. Number of Hooded Warbler nests by year and site	37
1.26. Fates of Hooded Warbler nests by site.....	39
1.27. Fates of Hooded Warbler nests by time of nest initiation.....	39
1.28. Number of Kentucky Warbler nests by site and year	41
1.29. Fates of Kentucky Warbler nests by site.....	42
1.30. Number of Yellow-billed Cuckoo nests by site and year	44
1.31. Fates of Yellow-billed Cuckoo nests by site.....	46
1.32. Mean daily survival rates for nests of eleven Neotropical migrant species by site.....	47
1.33. Number of Northern Cardinal nests by year and site.....	48
1.34. Mean daily survival rates of Northern Cardinal nests by site.....	48
1.35. Fates of Northern Cardinal nests by site	50
1.36. Fates of Northern Cardinal nests by time of nest initiation	51
1.37. Mean number of Northern Cardinal young fledged per nest at each site.....	51
1.38. Number of Carolina Wren nests by year and site	52
1.39. Mean daily survival rates of Carolina Wren nests by site.....	53
1.40. Fates of Carolina Wren nests by site.....	54
1.41. Fates of Carolina Wren nests by time of nest initiation.....	55
1.42. Mean number of Carolina Wren young fledged per nest at each site	56

1.43. Mean daily survival rates for nests of eleven resident species by site	56
1.44. Mean daily survival rates of all nests by site and type of species.....	57
1.45. Mean daily survival rates of three migrant nest types	60
1.46. Fates of nests for all migrant and resident species.....	60
1.47. Fates of nests for all migrant species by time of nest initiation.....	61
1.48. Fates of all resident species nests by time of nest initiation	62
1.49. Fates of all migrant nests by site.....	63
1.50. Fates of three migrant nest types	64
1.51. Mean number of migrant and resident young fledged per nest at each site.....	64
1.52. Mean number of migrant young fledged per nest by time of nest initiation and type of nest.....	67
1.53. Mean daily survival rates of nests checked at two and four-day intervals for eight species.....	68
2.1. Annual return rates of most commonly captured migrant and resident species at Red Diamond and Sherburne and results of Chi-square tests between sites	104
2.2. Results of comparison of Prothonotary Warbler return rates at Red Diamond and Sherburne with other common species at each site	105
2.3. Annual return rates of all migrant and resident species at Red Diamond and Sherburne and results of Chi-square tests among sites	105
3.1. Observed and expected proportions of shrub vegetation at Acadian Flycatcher nest-sites.	133
3.2. Observed and expected proportions of mid-story vegetation at Acadian Flycatcher nest-sites.	133
3.3. Observed and expected proportions of mid-story vegetation at American Redstart nest-sites.....	135
3.4. Observed and expected proportions of canopy vegetation at American Redstart nest-sites.....	136

3.5. Observed and expected proportions of shrub vegetation at Carolina Wren nest-sites	137
3.6. Observed and expected proportions of ground vegetation at Kentucky Warbler nest-sites	140
3.7. Observed and expected proportions of shrub vegetation at Kentucky Warbler nest-sites	140
3.8. Observed and expected proportions of mid-story vegetation at Kentucky Warbler nest-sites	141
3.9. Observed and expected proportions of ground vegetation at Northern Cardinal nest-sites	142
3.10. Observed and expected proportions of mid-story vegetation at Northern Cardinal nest-sites	142
3.11. Observed and expected proportions of canopy vegetation at Northern Cardinal nest-sites	143
3.12. Observed and expected proportions of ground vegetation at Prothonotary Warbler nest-sites	146
3.13. Observed and expected proportions of shrub vegetation at Prothonotary Warbler nest-sites	146
3.14. Observed and expected proportions of ground vegetation at Red-eyed Vireo nest-sites	147
3.15. Observed and expected proportions of mid-story vegetation at Red-eyed Vireo nest-sites	148
3.16. Observed and expected proportions of mid-story vegetation at Ruby-throated Hummingbird nest-sites	149
3.17. Observed and expected proportions of shrub vegetation at White-eyed Vireo nest-sites	151
3.18. Observed and expected proportions of mid-story vegetation at White-eyed Vireo nest-sites	151
3.19. Observed and expected proportions of canopy vegetation at White-eyed Vireo nest-sites	152
3.20. Nest-site habitat features chosen and avoided by 12 species	154

3.21. Nest cover measures with mean, minimum, and maximum values	155
3.22. Percent of successful classifications between nest-sites and random sites based on discriminant function analysis	156
3.23 Nest and plant heights with mean ratios for 11 species..	158
3.24. Results of MANOVA tests for differences in nest-site microhabitat variables of successful and unsuccessful nests	166
3.25. Eigenvectors of first four principal components of nest-site microhabitat variables	167
3.26. Comparison of foraging height and foliage height density with nest height and foliage density	172
3.27. Comparison of the mean number of young fledged per nest between nests in sweet gum trees and all other nest plants.....	177

LIST OF FIGURES

1.1 Nest initiation dates for Acadian Flycatchers. May 1 = day 120, June 1 = day 151, July 1 = day 181	13
1.2. Nest initiation dates for White-eyed Vireos. May 1 = day 120, June 1 = day 151, July 1 = day 181	18
1.3. Three-way interaction of site, time and stage (incubation and nestling) exhibited by mean daily survival rates of White-eyed Vireo nests.....	19
1.4. Mean daily survival rates of White-eyed Vireo nests initiated early and late at each site.....	19
1.5. Mean number of White-eyed Vireo young fledged per nest for nests initiated early and late at each site	23
1.6. Nest initiation dates for Red-eyed Vireos. May 1 = day 120, June 1 = day 151, July 1 = day 181	25
1.7. Nest initiation dates for Prothonotary Warblers. May 1 = day 120, June 1 = day 151, July 1 = day 181	29
1.8. Nest initiation dates for Ruby-throated Hummingbirds. May 1 = day 120, June 1 = day 151, July 1 = day 181	34
1.9. Nest initiation dates for Hooded Warblers. May 1 = day 120, June 1 = day 151, July 1 = day 181	38
1.10. Nest initiation dates for Kentucky Warblers. May 1 = day 120, June 1 = day 151, July 1 = day 181	42
1.11. Nest initiation dates for Yellow-billed Cuckoos. May 1 = day 120, June 1 = day 151, July 1 = day 181	45
1.12. Nest initiation dates for Northern Cardinals. May 1 = day 120, June 1 = day 151, July 1 = day 181	49
1.13. Nest initiation dates for Carolina Wrens. May 1 = day 120, June 1 = day 151, July 1 = day 181	54
1.14. Mean daily survival rates of three migrant nest types at each site.....	59
1.15. Mean number of migrant young fledged per nest at each site for nests initiated early and late	66

1.16. Mean number of young fledged per nest for three migrant nest types at each site.....	67
2.1. Return rates of male and female migrant and resident species at both Ferriday sites, Red Diamond, and Sherburne. Note: Significant differences denoted by <i>P</i> -values.....	102
2.2. Return rates of hatching year and after hatching year migrant and resident species at both Ferriday sites, Red Diamond, and Sherburne. Note: HY = Hatching year, AHY = After hatching year. Significant differences denoted by <i>P</i> -values	103
3.1 Mean values with 95 percent confidence intervals and ranges for nest-site habitat in 4 vegetation layers for 11 species (left axis). Mean nest heights are depicted by "x" marks and correspond to right axis. Bird species abbreviations are listed in Appendix A.	132
3.2. Differences in percent use and availability of nest plant species by Acadian Flycatchers. Plant species codes are given in Appendix B.	134
3.3. Differences in percent use and availability of nest plant species by American Redstarts. Plant species codes are given in Appendix B.....	136
3.4. Differences in percent use and availability of nest plant species by Carolina Wrens. Plant species codes are given in Appendix B	138
3.5. Differences in percent use and availability of nest plant species by Hooded Warblers. Plant species codes are given in Appendix B	139
3.6. Differences in percent use and availability of nest plant species by Northern Cardinals. Plant species codes are given in Appendix B.....	144
3.7. Differences in percent use and availability of nest plant species by Northern Parulas. Plant species codes are given in Appendix B	145
3.8. Differences in percent use and availability of nest plant species by Red-eyed Vireos. Plant species codes are given in Appendix B.....	148
3.9. Differences in percent use and availability of nest plant species by Ruby-throated Hummingbirds. Plant species codes are given in Appendix B	150
3.10. Differences in percent use and availability of nest plant species by White-eyed Vireos. Plant species codes are given in Appendix B	153

3.11. Differences in percent use and availability of nest plant species by Yellow-billed Cuckoos. Plant species codes are given in Appendix B	154
3.12. Variation in percent canopy closure of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.....	160
3.13. Variation in percent midstory density of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.....	161
3.14. Variation in percent shrub density of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.....	162
3.15. Variation in percent ground cover of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.....	163
3.16. Variation in percent nest cover of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.....	164
3.17. Variation in height of successful and unsuccessful nests for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.....	165
3.18. Cluster analysis dendrogram depicting species relationships based on nest-site characteristics. Bird species abbreviations are presented in Appendix A.....	169

ABSTRACT

I examined productivity, survivorship and nest-site habitat characteristics of small terrestrial landbirds breeding in bottomland hardwood forest study sites in Louisiana. Bottomland hardwood forests are the dominate ecosystem of riverine floodplains in the southeastern United States, and these forests support a diverse bird community. Over 80 percent of this forest type has been lost, primarily due to agricultural clearing, and the relative abundance of many bird species that breed in these forests has also declined.

The outcomes of 790 nests of 33 species were determined. For most species, productivity was greater in large forest tracts than in small tracts. Predation was the leading factor affecting nest success, and rates ranged from 25 percent in large (> 20,000 ha) forest tracts to 43 percent in a 4000 ha select-cut tract. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) was greater in small forest tracts than in large tracts. Rates of brood parasitism ranged from 5 percent in large tracts to 19 percent in smaller tracts. Parasitism rates of migrant species were 5 times greater than that of resident species, but there was no difference in the predation rate of migrant and resident species. Migrant nests initiated early (before 1 June) were parasitised at a significantly higher rate than nests initiated later. Predation rates of migrant nests did not differ between early and late initiation times.

Annual return rates of female migrants were less than that of male migrants at all sites. Resident females returned at the same rate as resident males at two sites and less than males at one site. Return rates of hatching year birds were less than that of after

hatching year birds at all sites. Return rates of hatching year birds in this study (7 to 9 percent) were greater than that reported in most studies.

Differences between nest-site habitat used and that available were found for most species. No difference was found between the nest-site habitat characteristics of successful and unsuccessful nests. For 6 of 8 migrant species, sweet gum was the most commonly used nest plant.

CHAPTER 1. NEST SUCCESS AND PRODUCTIVITY

INTRODUCTION

A decline in abundance of Neotropical migrant birds was first signaled in the late 1970's (Foreman et al. 1976, Galli et al. 1976, Whitcomb et al. 1977, Briggs and Criswell 1979, Robbins 1979, 1980), and further evidence of the decrease in numbers of many species has continued to mount into the 1990's (Askins et al. 1990, Terborgh 1992). The causes of this decline are yet to be fully assessed and may differ among species and locations. Forest fragmentation, especially in the once continuous stands of forest in eastern North America, is one possible explanation for abundance declines (Robbins 1980, Ambuel and Temple 1983, Askins et al. 1987). Linked with fragmentation as a contributing factor affecting breeding populations have been increased nest predation (Gates and Gysel 1978, Wilcove 1985) and increased nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) (Mayfield 1977, Whitcomb et al. 1981, Brittingham and Temple 1983). Much research has focused on the breeding grounds, but habitat loss and alteration on the wintering grounds and on stopover sites have also been considered important (Myers 1980, Hutto 1985, Moore and Kerlinger 1987, Gradwohl and Greenberg 1988, Lindstrom 1989, Terborgh 1989, Moore et al. 1990, Finch 1991). One recent change in habitat within the United States has been a dramatic loss of bottomland hardwood forests, the once-dominant ecosystem complex in the Southeast, through conversion to agricultural land. Forested wetlands covered approximately 52 million ha of the continental United States prior to European colonization (Turner et al. 1981).

Fifty-seven percent of this total was in the bottomland hardwood forests of the Southeast (Harris and Gosselink 1990). Today, over 80 percent of the Mississippi Alluvial Valley has been cleared (Tiner 1984). Abernathy and Turner (1987) believe that the loss of bottomland hardwoods is nearly five times more than the loss of any other major type of hardwood forest in the United States. The current estimate of the remaining area of bottomland hardwood forest in the Mississippi River Valley is 1.96 million ha. (Creasman et al. 1992). Although losses due to conversion to agriculture have recently decreased, natural factors still affect the remaining bottomlands, as evidenced by the thousands of hectares of forest that were heavily affected by Hurricane Andrew in 1992.

A decrease in area is not the only measure of change of bottomland hardwood habitat. Due to changes in flooding regimes and sedimentation rates, commercial timber harvesting, and other land-use practices, the age and composition of tree species differs now from pre-colonial times. The remaining bottomland hardwood forests are highly fragmented and mostly surrounded by large expanses of agriculture.

The loss of bottomland hardwoods and the fragmentation of the remaining patches has been so extensive that The Nature Conservancy in its Mississippi River Alluvial Plain Ecosystem Initiative has identified conservation of breeding bird populations through protection or improvement of habitat as a key objective (Creasman et al. 1992). Greater conservation focus on the Neotropical migratory birds of the Mississippi Valley has also been identified as one of the five highest conservation priorities in the southeastern

United States by Partners in Flight, a multipartner effort to reverse population declines in migratory birds throughout the hemisphere.

In summary, "remaining bottomland hardwoods are fragmented, have been altered by a completely different hydrologic regime, and are characterized by a plant species composition that may reflect historical silvicultural treatments more than natural conditions" (Pashley and Barrow 1993).

Bottomland hardwoods are crucial habitats for many Neotropical migrants (Dickson 1978); many of these are undergoing regional or range-wide declines (Robbins et al. 1989, Askins et al. 1990), and losses have also been noted in northeastern Louisiana (Burdick et al. 1989). Of the approximately 70 bird species known to breed in bottomland hardwood forests, 30 are Neotropical migrants. The large scale loss and alteration of these forests have likely impacted populations of Neotropical migrants as well as resident species. The effects of these changes may still be continuing. A recent analysis by Wiedenfeld et al. (unpublished data) of Breeding Bird Survey data for the Mississippi Alluvial Plain showed that 77 percent of breeding bird species declined in abundance over the last 25 years. Declining species included forest interior and edge species.

Understanding effects of habitat loss and alteration on bird species that use bottomland forests is critical in formulating management plans for these species. Data on reproductive performance and adult survivorship during the breeding season as well as information on survivorship throughout the year are needed. Unfortunately, few of these

data are available for birds in bottomland hardwood forests. I will attempt to address these issues in an effort to better understand the breeding ecology of bird species in this forest type.

OBJECTIVES

The objectives for this part of the study deal primarily with the daily survival rates and productivity of nests of migrant and resident species. Few data exists concerning these factors for birds breeding in bottomland forests of Louisiana. It is usually necessary to have some measure of reproductive performance of the species involved to make proper management plans. Factors influencing reproductive performance, either positively or negatively, should be identified. I believe that determining trends in relative abundance is only a part of the researcher's obligation. Until one understands the reproductive dynamics of a population and the factors that influence critical demographic components, management considerations are likely incomplete. Whether we will ever entirely understand the fullness of the ecological relationships of bird communities is debatable. But we must press beyond the basic survey and census data and look at deeper issues such as reproductive performance to better understand what is truly happening to bird populations in our remaining forest blocks. The work presented in this chapter is an attempt to address this issue and the specific objectives of this phase of the study are listed below.

Objective 1. Determine daily survival rate of nests for each species found breeding on the study plots and compare rates among the different habitat types. The four

habitat types to be tested are: older-growth or mature forest, mature forest recently select-cut, mid-age forests, and mid-age forest affected by Hurricane Andrew.

Objective 2. Determine productivity (number of young fledged) for nests of each species found breeding on the study plots and compare these values among the different habitat types.

Objective 3. Determine causes of nests failure for each species and compare the failure rates due to each cause among the different habitat types.

Objective 4. Formulate management objectives for species breeding in bottomland forests based on knowledge gained in this study.

METHODS

STUDY AREAS

The study was conducted in two different areas in Louisiana. Two study sites, Ferriday "Treatment" and "Control", were at the southern end of the Tensas Basin in northeastern Louisiana, and two other study sites, Red Diamond and Sherburne, were located in the Atchafalya Basin in south-central Louisiana.

The Ferriday sites are in Concordia Parish in a 4000 ha tract of bottomland hardwood forest owned by the U. S. Fish and Wildlife Service. This property was part of the Fisher Tract, so named because it was once owned by Fisher Body Division of General Motors Corporation. In the first half of the century, wooden car parts were made from timber harvested in these forests. This location contains one of the largest remaining contiguous stands of older-growth bottomland hardwood forest in existence

(Creasman et al. 1992). The majority of this tract is now included in the newly formed (1992) Bayou Cocodrie National Wildlife Refuge, approximately 13 km southwest of Ferriday, Louisiana (91°3'W, 31°3'N), in Concordia Parish. The Ferriday Control site is in an approximately 500-ha stand of older-growth forest (within the 4000-ha block) that was last lightly select-cut in the late 1920's and early 1930's. The second study site (Ferriday Treatment) is in the same forest, but in an area that was again select-cut in the early 1980's. The Ferriday Treatment site is adjacent to the Ferriday Control stand and remained part of the same uncut stand until the 1980's. In the early and mid-1980's, logging crews performed a diameter-type of select-cut in which the majority of trees above a 60 cm diameter were removed. In this type of silvicultural practice, most of the larger, mature trees in the stand are removed.

At both Ferriday sites, the forest canopy consists of the following species in decreasing order of abundance: hackberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanica*), willow oak (*Quercus phellos*), American elm (*Ulmus americana*), sweet gum (*Liquidambar styraciflua*), and Nuttall oak (*Quercus nuttallii*). Other species such as swamp red maple (*Acer rubrum drumundi*), cedar elm (*Ulmus crassifolia*), and water oak (*Quercus nigra*) occur in lesser proportions. The understory consists primarily of saplings, palmetto (*Sabal minor*), deciduous holly (*Ilex decidua*), and in the Treatment site, blackberry (*Rubus* sp.). Various vines, such as poison ivy (*Rhus radicans*), pepper vine (*Ampelopsis arborea*), muscadine, and other grapes (*Vitis* spp.), are common. A

few small patches of the native cane (*Arundinaria gigantea*), are present on the Control site.

The second field location is in the Atchafalya Basin in south-central Louisiana. One study site, Red Diamond, is in a 20,000-ha block of relatively unfragmented forest that was moderately damaged by Hurricane Andrew in August 1992. Tree damage was estimated at 35 to 40 percent at this site (Ouchley unpublished data). It is located approximately 16 km south of Ramah, Louisiana, in Iberville Parish (91°3'W,31°3'N), on property owned by Dow Chemical and Wilbert Bros. Inc. The second study site, known as Sherburne, is located in St. Martin Parish on the Atchafalya National Wildlife Refuge, 13 km southeast of Krotz Springs, LA (91°4'W,30°2'N). It is in an approximately 100,000-ha block of forest that sustained minimal (estimated less than 5 percent) hurricane damage. The forests at both of these sites are younger than at the Ferriday sites.

Principal canopy tree species in order of decreasing abundance at the Red Diamond site are swamp red maple, box elder (*Acer negundo*), sweet gum, hackberry, and green ash. Other canopy species such as American elm, bald cypress (*Taxodium distichum*), and Nuttall oak occur in lesser amounts.

Canopy dominants at the Sherburne site (in order of decreasing abundance) are box elder, hackberry, American elm, sweet gum, and swamp red maple. Bald cypress, Nuttall oak, and green ash compose a lesser proportion of the forest canopy.

The understory of both Red Diamond and Sherburne sites consists primarily of saplings, southern shield fern (*Thelypteris* sp.), deciduous holly, and at the Red Diamond site, blackberry vines. Other vine species such as poison ivy, pepper vine, and various grapes are common at both sites. Palmetto is relatively uncommon and virtually no native cane is found at these sites.

For convenience, I refer to each site in the tables and figures by the following abbreviations: Ferriday Control = FC, Ferriday Treatment = FT, Red Diamond = RD, Sherburne = SH.

Bird species names are those of the American Ornithologists' Union (1983), and plant species names are those of Kartesz and Kartesz (1980) and Tiner (1993).

FIELD METHODS

Each plot was searched for nests from daylight to around 1400 daily during each field season, that was from approximately the third week in April to the second week in August, 1992-1994. One 10-ha plot was operated in the Ferriday Control and Treatment sites in 1992. In the 1993 and 1994 field seasons, two 10-ha plots were operated at Ferriday Control, Ferriday Treatment, Red Diamond, and Sherburne. All plots were marked with a grid system with grid points located every 25 m. Each point was conspicuously marked with colored flagging. One person was assigned to a 10-ha plot daily, and workers were systematically rotated among the plots to ensure equal coverage by all persons.

Once a nest was found, its location was marked with flagging placed in a characteristic pattern near the nest. The location, species, nest number, and description were written on the flagging to aid in nest relocation for nest checks. Nests were checked at two-day intervals during the 1992 and 1993 field season. During the 1994 field season, nests were randomly assigned to either a 2- or 4-day checking interval to test for possible observer affects. Effort was made to minimize the impact on vegetation around and leading to the nests and to minimize disturbance of the birds. Lower nests were checked by direct visual inspection, and higher nests, up to 12 m, were checked with pole-mounted mirrors during the 1992 field season and with pole-mounted micro-video cameras (Ouchley et al. 1994) in the 1993 and 1994 field seasons. The fate of nests higher than 12 meters could often be determined through close observation.

Data regarding the number of eggs or young, parental attendance, parasitism, predation, band combinations of adults, and eventual fate of the nest were recorded at each visit when possible. As with other researchers (e.g., Martin and Roper 1988), I considered a nest successful when at least one young of the nest-building species fledged.

DATA ANALYSIS

I used the Mayfield method (Mayfield 1961, 1975) to calculate daily survival rates for each nest. Mayfield's daily survival rates are the probability of a nest surviving from one day to the next such that the probability of surviving the entire period is the product of these rates. The need for a better method to assess the survival probabilities of bird nests was first addressed by Mayfield in his work with the endangered Kirtland's

Warbler (*Dendroica kirtlandii*) (1960). The mathematical technique he developed accounts for the fact that nests are often found at all times throughout the nesting cycle and bases the probability of survival on the number of days the nest is exposed. I used an angular (arcsin-square root) transformation of the daily survival rates (e.g., Martin and Li 1992), which provides closer assumptions of normality and heterogeneous variances than non-transformed data, in analysis of variance (ANOVA) models and Student's t-tests to test for differences in mean daily survival rates of nests among years, sites, timing of nest initiation, incubation and nestling stages, and frequency of nest checks. I considered early nests to be those initiated before June 1 and late nests were those initiated after that date. I used the least-square means (LSMeans) procedure in SAS (SAS 1985) to make post-hoc comparisons from the ANOVA's because of unequal sample sizes. Data presented in the text, tables, and figures are the untransformed values.

I used contingency table analysis with Chi-square (χ^2) tests for homogeneity to analyze differences in causes of nest failure. I considered all test results to be significant when P -values were ≤ 0.05 , unless otherwise stated.

I used ANOVA models to test for differences in the mean number of young fledged per nest among sites and nest initiation times, I blocked on clutch size when comparisons were made among groups of species.

In all cases I attempted to follow the same general order of analysis, that included three basic parts: 1) testing for differences in mean daily survival rates of nests among sites and years, and among sites, stages, and times of initiation; 2) analysis of causes of

nest failure; 3) analysis of differences in the mean number of young fledged per nest among sites and times of initiation. Because of small sample sizes for some species, I did not always perform each test and this is mentioned where applicable.

I present the results first in a species account format. Secondly, I present the results from broader analysis performed on groups of species. I grouped species as Neotropical migrants and residents and then subdivided the migrant species into cavity nesters, open-cup high nesters, and open-cup low- to mid-height nesters. The final analysis presented in this chapter includes the results from analysis among nests checked at 2- and 4-day intervals.

RESULTS

SPECIES ACCOUNTS

Acadian Flycatcher (*Empidonax virescens*)

All Acadian Flycatcher nests (N = 221) were hanging cups in the forks of branches and were constructed primarily of Spanish moss (*Tillandsia usneoides*). Some were so sparsely constructed that the contents of the nest could be seen from below, and most had streamers of Spanish moss trailing down several centimeters below the bottom of the cup. It appeared that females alone constructed the nests, and they were often found prior to nest-building while pressing their breasts into forks of limbs as if to "try-on" the location before beginning construction. Nest building took from 2 to 5 days, with incubation and nestling stages averaging 14 days each. Females were often heard giving a soft "weep" note while sitting on the nest, and they alone incubated and brooded, but

both parents fed the nestlings. Acadian Flycatchers were often highly aggressive during nest checks. Both adults would dive at the camera and click their bills; they would sometimes strike the camera. The average nest height for all sites was 8.8 m with a range of 2.3 to 22.0 m. Further analysis of nest heights will be done in chapter 3.

The number of Acadian flycatcher nests varied by site and year (Table 1.1). I tested mean daily survival rates of nests among years and sites using a factorial ANOVA model, and found no interaction ($F = 1.77$, $df = 4$, 197 , $P = 0.13$). The mean daily survival rate of nests did not differ among years ($F = 2.19$, $df = 2$, 197 , $P = 0.11$), but the rate was different among sites ($F = 3.67$, $df = 3$, 197 , $P = 0.01$). Nests at Sherburne had a greater mean daily survival rate than nests at the three other sites (Table 1.2).

Table 1.1. Number of Acadian Flycatcher nests by year and site.

Year	FC	FT	RD	SH	Total
1992	13	9	*	*	22
1993	32	26	18	7	83
1994	30	28	28	16	102
Total	75	63	46	23	207

*No field work performed at these sites during 1992.

Table 1.2. Mean daily survival rates of Acadian Flycatcher nests at four sites

FC ^a	FT ^a	RD ^a	SH ^b
0.914	0.917	0.935	0.973
± 0.105	± 0.086	± 0.097	± 0.060
N = 75	N = 63	N = 46	N = 23

Note. Sites with similar letters are not different. ± = one standard deviation, N = sample size.

In a second factorial ANOVA model, I separated the nesting period into the incubation and nestling stages, when possible, and tested for differences in mean daily survival rates of nests among stages, sites, and times of nest initiation. I labeled nests as initiated early or late if started before or after June 1. One-hundred eight nests were initiated early and 98 nests were initiated late (Figure 1.1).

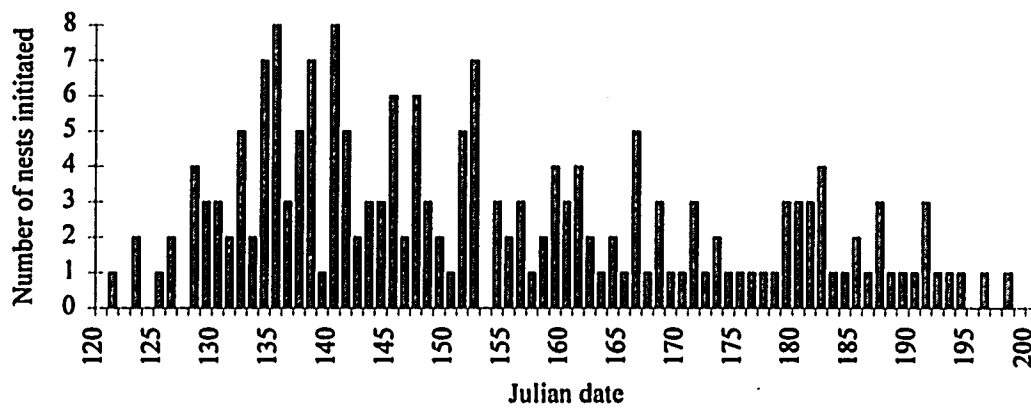


Figure 1.1. Nest initiation dates of Acadian Flycatchers. May 1 = day 120, June 1 = day 151, July 1 = day 181.

There were no significant two-way or three-way interactions between the stage, site, or time of initiation of nests. The main effect of site was again significant in this model ($F = 3.56$, $df = 3$, 265 , $P = 0.015$) with the same results as presented in Table 1.2. The mean daily survival rate of nests during the incubation stage ($.927 \pm 0.099$) was not different than during the nestling stage ($.927 \pm 0.143$) ($F = 0.29$, $df = 1$, 265 , $P = 0.588$). The mean daily survival rate of early nests (0.917 ± 0.137) did not differ ($F = 2.88$, $df = 1$, 265 , $P = 0.090$) from the mean daily survival rate of late nests (0.940 ± 0.096).

I examined 208 nests and the fates of nests varied among sites (Table 1.3). There was a significant difference in the predation rate among the sites ($\chi^2 = 12.98$, $df = 3$, $P = < 0.01$). The predation rate at Ferriday Control and Sherburne was less than expected, and at Ferriday Treatment and Red Diamond the predation rate was greater than expected. The parasitism rate was not significantly different among sites ($\chi^2 = 6.38$, $df = 3$, $P = 0.09$). Ferriday Control had the largest percentage of nests in the other/unknown category because a greater proportion of the nests there were too high to be checked with the camera and exact cause of failure sometimes could not be determined.

Table 1.3. Fates of Acadian Flycatcher nests by site.

Fate	FC N = 75	FT N = 63	RD N = 46	SH N = 24
Success	0.43	0.32	0.48	0.79
not parasitised	0.43	0.32	0.48	0.79
parasitised	0.0	0.0	0.0	0.0
Predation	0.32	0.51	0.48	0.12
not parasitised	0.28	0.44	0.48	0.12
parasitised	0.04	0.06	0.0	0.0
Parasitism	0.07	0.12	0.02	0.0
no predation	0.03	0.06	0.02	0.0
Other/Unknown failures	0.23	0.11	0.02	0.08

Note. Values are expressed as percentages of total nests for each site.

I next categorized the fates of these nests according to time of nest initiation (Table 1.4). I considered early nests those initiated before June 1 and late nests those

initiated afterwards. There was no significant difference in the predation rate of early and late nests ($\chi^2 = 0.47$, $df = 1$, $P = 0.49$). There was a difference in the parasitism rate between early and late nests ($\chi^2 = 4.06$, $df = 1$, $P = 0.04$). The parasitism rate of early nests was greater than expected, and the parasitism rate of late nests was less than expected. The parasitism rate of early nests was more than three times higher than that of late nests.

Table 1.4. Fates of Acadian Flycatcher nests by time of nest initiation.

Fate	Early N = 108	Late N = 98
Success	0.38	0.53
not parasitised	0.38	0.53
parasitised	0.0	0.0
Predation	0.42	0.37
not parasitised	0.37	0.35
parasitised	0.05	0.02
Parasitism	0.10	0.03
no predation	0.06	0.01
Other/Unknown failures	0.15	0.11

Note. Values are expressed as percentages of total nests for each time period.

I next tested for differences in mean number of young fledged per nest among sites and initiation times. The interaction term of site and time of initiation was not significant ($F = 1.95$, $df = 3$, 198 , $P = 0.123$) nor was the main effect of time of initiation ($F = 0.15$, $df = 1$, 198 , $P = 0.696$), although early nests had 0.887 young fledged and late

nests had 0.949 young fledged. The main effect of site was significant ($F = 7.13$, $df = 3$, 198 , $p = <0.01$). The mean number of young fledged per nest at Ferriday Treatment was less than any other site, and Sherburne had a greater mean number of young fledged per nest than at any other site. The mean number of young fledged per nest at Ferriday Control did not differ from that of nests at Red Diamond (Table 1.5).

Table 1.5. Mean number of Acadian Flycatcher young fledged per nest at each site.

FCA ^a	FT ^b	RD ^a	SH ^c
0.906 ± 0.727	0.524 ± 0.710	1.04 ± 0.493	1.67 ± 1.05
N = 75	N = 63	N = 46	N = 23

Note. ± = one standard deviation, N = sample size. Sites with similar letters are not different.

White-eyed Vireo (*Vireo griseus*)

The nest of the White-eyed Vireo is a tightly woven hanging cup constructed of fine strips of bark, leaves, rootlets, and moss. Most nests (N = 139) were placed in the forks of limbs in small shrubs or trees at an average height of 1.92 m with a range of 0.3 to 10.3 m. The first sign of nest construction is a tightly woven ring that forms the rim of the cup attached to small branches. The male and female both build the nest, but the female seems to perform most of the work. Nest construction takes from 3 to 6 days, with incubation and nestling stages lasting an average of 14 and 10 days respectively. The female does all incubating and brooding, and normally sits tightly on the nest. If approached with caution, she may sometimes be touched before flushing. Both adults

feed the young and will often give a continuous scold note when an observer approaches the nest, particularly during the nestling stage. The number of White-eyed Vireo nests varied by site and year (Table 1.6).

In the first ANOVA model, I tested for differences in mean daily survival rates of nests among sites and years and for the site by year interaction. The two-way interaction was not significant (site * year $F = 1.19$, $df = 4$, 129 , $P = 0.317$) and the main effect of year was not significant ($F = 1.87$, $df = 2$, 129 , $P = 0.158$). The main effect of site was significant ($F = 11.21$, $df = 3$, 129 , $P = < 0.01$), however. The mean daily survival rate for nests at Ferriday Control site was lower than at all other sites. Nests at Ferriday Treatment had a higher mean daily survival rate than nests at Ferriday Control, but it was lower than that of Red Diamond and Sherburne, where rates did not differ significantly from each other (Table 1.7).

Table 1.6. Number of White-eyed Vireo nests by year and site.

Year	FC	FT	RD	SH	Total
1992	4	3	*	*	7
1993	8	12	13	16	49
1994	13	23	18	29	83
Total	25	38	31	45	139

*No field work performed at these sites during 1992.

Table 1.7. Mean daily survival rates of White-eyed Vireo nests by site.

FC ^a	FT ^b	RD ^c	SH ^c
0.746 ± 0.277	0.868 ± 0.157	0.943 ± 0.113	0.939 ± 0.081
N = 25	N = 38	N = 31	N = 45

± = one standard deviation, N = sample size. Sites with similar letters are not different.

I next tested for differences in the mean daily survival rate of nests among stages (incubation and nestling), sites, and times of nest initiation. Seventy-two nests were initiated early (before June 1), and 67 nests were initiated late (Figure 1.2).

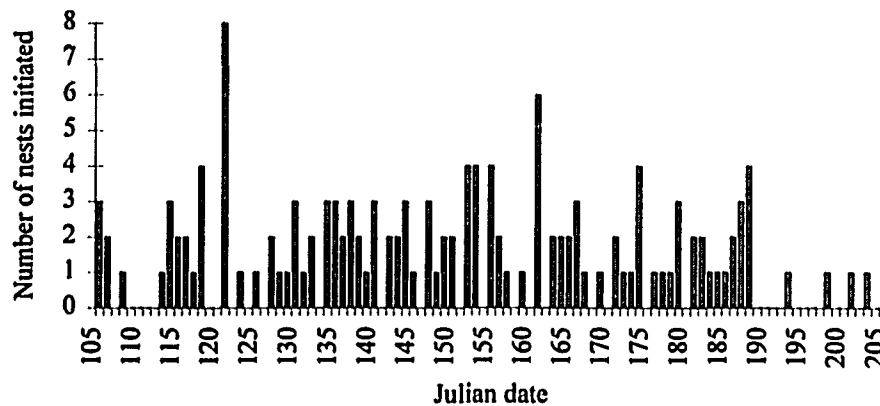


Figure 1.2. Nest initiation dates for White-eyed Vireos. May 1 = day 120, June 1 = day 151, July 1 = day 181.

The three-way interaction of site, stage, and time of initiation was significant ($F = 5.01$, $df = 3, 171$, $P = < 0.01$) (Figure 1.3) as was the two-way interaction of site and time of initiation ($F = 3.95$, $df = 3, 171$, $p = 0.01$). The large differences in mean daily survival rates among sites was a main component of these interactions as was the main effect of time of initiation. Mean daily survival rates of early nests at Ferriday Control, Ferriday Treatment, and Red Diamond were lower than the mean daily survival rate of late nests, whereas early nests at Sherburne had higher mean daily survival rates than late nests. The two-way interaction is represented in Figure 1.4 and the values are presented in Table

1.8. The stage-by-time and stage-by-site interactions were not significant (stage * time $F = 0.75$, df 1, 171, $P = 0.389$; stage * site $F = 0.91$, $df = 3$, 171, $P = 0.436$).

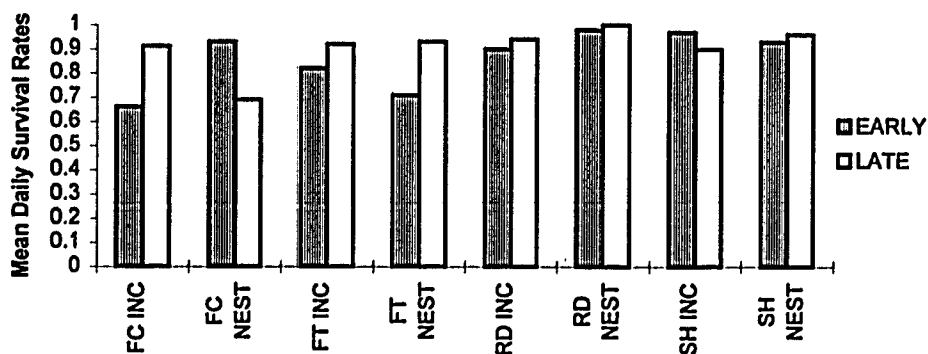


Figure 1.3. Three-way interaction of site, time and stage (incubation and nestling) exhibited by mean daily survival rates of White-eyed Vireo nests.

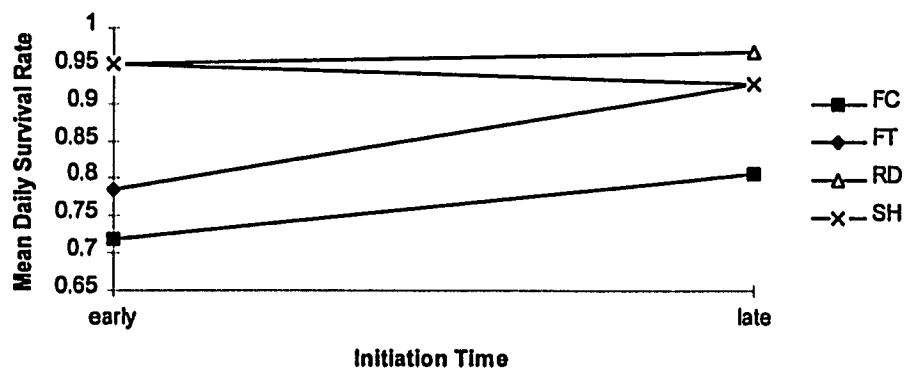


Figure 1.4. Mean daily survival rates for White-eyed Vireo nests initiated early and late at each site.

Table 1.8. Mean daily survival rates of White-eyed Vireo nests by site and time of initiation.

Time*	FC	FT	RD	SH	Mean
Early	0.718 ± 0.349	0.787 ± 0.241	0.951 ± 0.115	0.953 ± 0.103	0.876 ± 0.217
Late	0.808 ± 0.195	0.927 ± 0.150	0.968 ± 0.064	0.925 ± 0.100	0.908 ± 0.145

*Time denotes nests initiated before (early) and after (late) June 1. \pm = one standard deviation.

Although interpretation of the tests for the main effects in the ANOVA model is not clearly warranted because of the above mentioned interactions some generalizations can still be made concerning these variables. For all sites and stages combined, the mean daily survival rate of early nests was less than late nests (Table 1.8). This was true for each site except Sherburne. For all sites and both initiation times combined, the mean daily survival rate for the incubation stage (0.898 ± 0.020 , $N = 100$) was lower than the nestling stage (0.916 ± 0.023 , $N = 84$).

I next categorized the fates of nests found at each site (Table 1.9). Predation was the leading factor affecting nests, and parasitism was the second most common factor. There was a significant difference in the predation rate and that expected by chance ($\chi^2 = 8.80$, $df = 3$, $P = 0.03$). The predation rate at Ferriday Control and Ferriday Treatment was greater than expected, and the predation rate at Sherburne and Red Diamond was less than expected. There was no significant difference in the parasitism rate ($\chi^2 = 5.6$, $df = 3$, $P = 0.13$) among sites. Sherburne and Ferriday Control had the most nests in the other/unknown category that included such factors as weather and abandonment.

Table 1.9. Fates of White-eyed Vireo nests by site.

Fate	FC N = 25	FT N = 38	RD N = 31	SH N = 45
Success	0.16	0.31	0.68	0.49
not parasitised	0.12	0.26	0.61	0.47
parasitised	0.04	0.05	0.06	0.02
Predation	0.44	0.55	0.23	0.27
not parasitised	0.40	0.34	0.23	0.18
parasitised	0.04	0.21	0.0	0.09
Parasitism	0.36	0.37	0.13	0.20
no predation	0.28	0.13	0.13	0.11
Other/Unknown failures	0.12	0.03	0.03	0.16

Note. Values are expressed as percentages of total nests for each site.

These data were also categorized for nests initiated before (early) and after (late) June 1 (Table 1.10). The difference in parasitism rates of early and late nests and that expected by chance approached significance ($\chi^2 = 3.26$, $df = 1$, $P = 0.065$). Early nests were parasitised over two times as often as late nests. The predation rates of early and late nests did not differ from that expected by chance ($\chi^2 = 6.07$, $df = 1$, $P = 0.43$).

In the next ANOVA model, I tested for differences in the mean number of young fledged per nest among the four sites and both initiation times. The interaction term of site and time of initiation was significant ($F = 3.24$, $df = 3, 131$, $P = 0.024$). The mean number of young fledged from early nests at Ferriday Control and Treatment sites was less than later nests. At the Red Diamond and Sherburne sites, the mean number of young fledged per nest was greater in early nests than in late nests (Figure 1.5) (Table

1.11). Although interpretation of test statistics for the individual main effects is not recommended due to the strong interaction, the following generalizations can be made: early nests averaged slightly more young fledged per nest than later nests, and Red Diamond and Sherburne sites averaged more than one young fledged per nest; nests at Ferriday Treatment and Control fledged an average of less than one young per nest. The average number of young fledged per nest was highest at Red Diamond (1.87) and lowest at Ferriday Control (0.40).

Table 1.10. Fates of White-eyed Vireo nests by time of nest initiation.

Fate	Early N = 72	Late N = 67
Success	0.42	0.43
not parasitised	0.35	0.42
parasitised	0.07	0.01
Predation	0.43	0.30
not parasitised	0.26	0.28
parasitised	0.17	0.01
Parasitism	0.35	0.16
no predation	0.11	0.13
Other/Unknown failures	0.04	0.13

Note. Values are expressed as percentages of total nests for each time period.

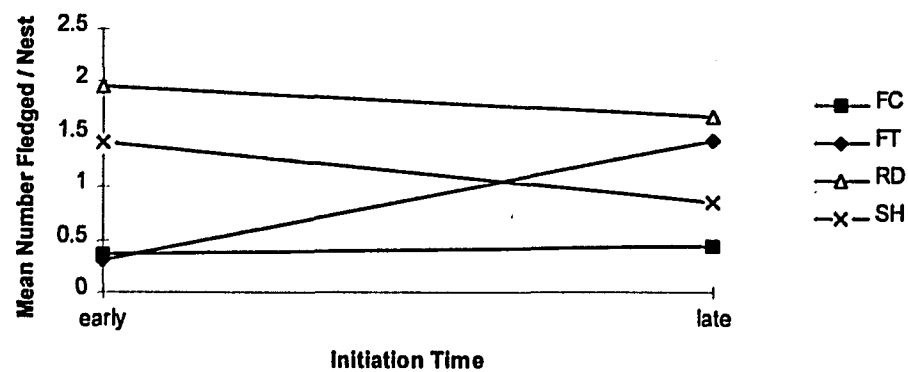


Figure 1.5. Mean number of White-eyed Vireo young fledged per nest for nests initiated early and late at each site.

Table 1.11. Mean number of White-eyed Vireo young fledged per nest by site and time of nest initiation.

Time	FC	FT	RD	SH	Mean
Early	0.36	0.30	1.95	1.42	1.11
	± 0.92	± 0.98	± 1.62	± 1.50	± 1.49
	N = 11	N = 20	N = 22	N = 19	N = 72
Late	0.43	1.44	1.67	0.85	1.03
	± 1.08	± 1.38	± 1.41	± 1.15	± 1.29
	N = 14	N = 18	N = 9	N = 26	N = 67
Mean	0.40	0.84	1.87	1.08	
	± 1.00	± 1.30	± 1.54	± 1.33	
	N = 25	N = 38	N = 31	N = 45	

Note. \pm = one standard deviation, N = sample size.

Red-eyed Vireo (*Vireo olivaceus*)

Nests of the Red-eyed Vireo are similar in construction and materials to those of the White-eyed Vireo. The hanging cups of the Red-eyed Vireo appeared to be deeper than those of the White-eyed, although I took no measurements to verify this. Nests of the Red-eyed Vireo are often placed quite high; the heights of 44 nests averaged 9.07 m with a range of 4.1 to 22.6 m. Red-eyed Vireos spend much of their time in the mid- to upper-canopy but can commonly be found during nest building gathering material at low levels in the forest. The female alone incubates and broods the young; each stage takes an average of 12 days. The male does help feed the young, and both parents can often be heard giving a soft "mew" call when the nest is approached by an observer.

Forty-four nests were found during the study, but the outcomes of only 34 could be determined definitely and only these were entered into this analysis (Table 1.12).

Table 1.12. Number of Red-eyed Vireo nests by year and site.

Year	FC	FT	RD	SH	Total
1993	*	*	6	3	9
1994	2	3	5	15	25
Total	2	3	11	18	34

* No nests found.

In the first ANOVA model, I tested for differences in mean daily survival rate of nests among years and sites. There was no two-way interaction between year and site ($F = 0.89$, $df = 1, 26$, $P = 0.355$), and the main effect of year was not significant ($F = 0.26$, df

= 1, 26, $P = 0.616$), nor was the main effect of site ($F = 0.03$, $df = 3, 26$, $P = 0.992$)

(Table 1.13).

Table 1.13. Mean daily survival rate of Red-eyed Vireo nests by site.

FC	FT	RD	SH
0.930 ± 0.098	0.943 ± 0.049	0.936 ± 0.101	0.936 ± 0.090
N = 2	N = 3	N = 11	N = 18

\pm = one standard deviation, N = sample size. No significant difference among sites was detected.

I next tested for differences in the mean daily survival rate of nests among sites, stages, and initiation times. Nineteen nests were initiated before June 1, and 13 nests were initiated afterwards (Figure 1.6).

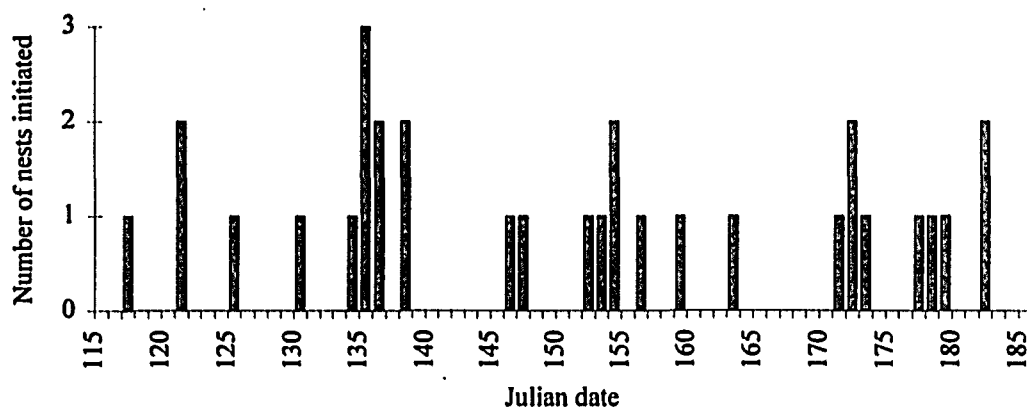


Figure 1.6. Nest initiation dates for Red-eyed Vireos. May 1 = day 120, June 1 = day 151, July 1 = day 181.

None of the two-way interactions or the three-way interaction were significant.

The site main effect was not significant ($F = 0.16$, $df = 2, 21$, $P = 0.855$), as in the

preceding model. The main effects of time of initiation and stage of nesting cycle were not significant (time $F = 0.08$, $df = 1, 21$, $P = 0.782$; stage $F = 1.44$, $df = 1, 21$, $P = 0.243$) (Table 1.14).

Table 1.14. Mean daily survival rates of Red-eyed Vireo nests initiated before (early) and after (late) June 1 and during incubation and nestling stages.

Early Nests	Late Nests	Incubation Stage	Nestling Stage
0.922 ± 0.137	0.936 ± 0.101	0.916 ± 0.109	0.942 ± 0.138
N = 19	N = 13	N = 17	N = 15

\pm = one standard deviation, N = sample size. No significant difference in time of initiation was detected.

The fates of these nests varied by location (Table 1.15). Due to small sample sizes in several categories, no tests were performed. Predation was the leading factor affecting Red-eyed Vireo nests, and it affected twice as many nests as parasitism.

Table 1.15. Fates of Red-eyed Vireo nests by site.

Fate	FC N = 2	FT N = 3	RD N = 11	SH N = 16
Success	0.50	0.33	0.54	0.50
not parasitised	0.50	0.33	0.45	0.50
parasitised	0.0	0.0	0.09	0.0
Predation	0.50	0.33	0.36	0.25
not parasitised	0.50	0.33	0.36	0.25
parasitised	0.0	0.0	0.0	0.0
Parasitism	0.0	0.33	0.09	0.19
no predation	0.0	0.33	0.09	0.19
Other/Unknown failures	0.0	0.0	0.09	0.06

Note. Values are expressed as percentages of total nests for each site.

The fates of these nests were also categorized by initiation time (Table 1.16). Although small sample size prevented statistical testing, certain differences are noted. Parasitism rates were slightly less in early nests than in late nests. Predation rates were nearly twice as great in early nests than in late nests, and other/unknown factors (primarily weather and abandonment) affected over 10 percent of late nests but no early nests.

Table 1.16. Fates of Red-eyed Vireo nests by time of nest initiation.

Fate	Early N = 15	Late N = 17
Success	0.47	0.53
not parasitised	0.47	0.47
parasitised	0.0	0.06
Predation	0.40	0.23
not parasitised	0.40	0.23
parasitised	0.0	0.0
Parasitism	0.13	0.18
no predation	0.13	0.18
Other/Unknown failures	0.0	0.12

Note. Values are expressed as percentages of total nests for each time period.

Prothonotary Warbler (*Protonotaria citrea*)

The Prothonotary Warbler is one of the two cavity-nesting migrant songbirds that regularly nest in the bottomlands of Louisiana. The only other species in this category is the Great Crested Flycatcher (*Myiarchus crinitus*). Prothonotary Warblers place their nests in a variety of cavity types and perform little of the actual cavity excavation. The

male may build several dummy nests within its territory, but the female makes the final site choice and builds the actual nest, finishing the lining with fine materials such as moss. The average height of 82 nests in this study was 3.31 m with a range of 0.4 to 11.1 m; the median height was 2.9 m. The female alone incubates and broods; these take an average of 13 and 11 days respectively, but both parents participate in feeding the young. Showing the somewhat opportunistic nature of this species, during the 1994 season one pair successfully raised a brood of four in an aluminum can-crusher fastened to a metal porch-post not more than 3 m from the front door of the busy camp house at the Red Diamond site.

Eighty-two nests were found throughout the study (Table 1.17), but the outcome of only 67 could be positively determined.

Table 1.17. Number of Prothonotary Warbler nests by site and year.

Year	FC	FT	RD	SH	Total
1992	*	2	**	**	2
1993	1	5	10	5	21
1994	6	4	22	12	44
Total	7	11	32	17	67

* No nests found. ** No field work performed at these sites in 1992.

There was no significant interaction in the ANOVA test for differences in mean daily survival rates among sites and years (year * site $F = 0.82$, $df = 3, 58$, $P = 0.486$).

There was no significant difference among years ($F = 2.11$, $df = 2, 58$, $P = 0.137$) or sites ($F = 1.16$, $df = 3, 58$, $P = 0.333$) (Table 1.18).

Table 1.18. Mean daily survival rate of Prothonotary Warbler nests by site.

FC	FT	RD	SH
0.884 ± 0.131	0.917 ± 0.117	0.959 ± 0.094	0.962 ± 0.082
N = 7	N = 11	N = 32	N = 17

Note. \pm = one standard deviation, N = sample size.

In the next model, I tested for differences in mean daily survival rate of nests among sites, incubation and nestling stages, and early and late nest initiation times. Fifty nests were initiated before June 1, and 32 were initiated after June 1 (Figure 1.7).

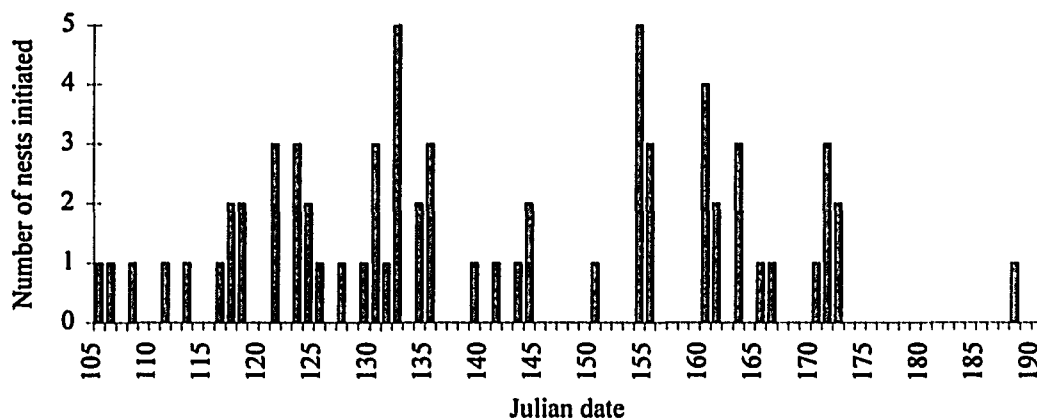


Figure 1.7. Nest initiation dates for Prothonotary Warblers. May 1 = day 120, June 1 = day 151, July 1 = day 181.

The three-way interaction and all two-way interactions were not significant. The main effect of site was not significant ($F = 0.55$, $df = 3, 66$, $P = 0.651$). The mean daily survival rate of earlier nests was $0.959 (\pm 0.086)$, and for late nests it was $0.929 (\pm 0.117)$; this difference was not significant ($F = 0.53$, $df = 1, 66$, $P = 0.470$). The main effect of

stage of nesting period was significant ($F = 5.40$, $df = 1, 66$, $P = 0.023$). The mean daily survival rate during the incubation stage (0.926 ± 0.116 , $N = 40$) was lower than during the nestling stage (0.969 ± 0.076 , $N = 42$).

I next categorized the fates of these nests for each site (Table 1.19). Predation was the leading factor affecting nests at all sites except Ferriday Control (which had the smallest sample size) where other/unknown factors were first. The predation rate was not different than that expected by chance ($\chi^2 = 0.67$, $df = 3$, $P = 0.88$). Only one nest was parasitised during the study.

Table 1.19. Fates of Prothonotary Warbler nests by site.

Fate	FC N = 7	FT N = 11	RD N = 32	SH N = 17
Success	0.43	0.54	0.69	0.70
not parasitised	0.43	0.45	0.69	0.70
parasitised	0.0	0.09	0.0	0.0
Predation	0.14	0.27	0.28	0.29
not parasitised	0.14	0.27	0.28	0.29
parasitised	0.0	0.0	0.0	0.0
Parasitism	0.0	0.09	0.0	0.0
no predation	0.0	0.09	0.0	0.0
Other/Unknown failures	0.43	0.18	0.03	0.0

Note. Values are expressed as percentages of total nests for each site.

I next categorized the fates of these nests by initiation times (Table 1.20).

Predation was the leading factor affecting both early and late nests and there was a significant difference in the predation rate between early and late nests ($\chi^2 = 4.68$, $df = 1$,

$P = 0.03$). The predation rate of late nests was almost 2.5 times greater than that of early nests. Other factors such as weather and abandonment affected early and late nests at similar rates, and the only case of nest parasitism occurred in a late nest.

Table 1.20. Fates of Prothonotary Warbler nests by time of nest initiation.

Fate	Early N = 41	Late N = 26
Success	0.73	0.50
not parasitised	0.73	0.46
parasitised	0.0	0.04
Predation	0.17	0.42
not parasitised	0.17	0.42
parasitised	0.0	0.0
Parasitism	0.0	0.04
no predation	0.0	0.04
Other/Unknown failures	0.10	0.08

Note. Values are expressed as percentages of total nests for each time period.

I next tested for differences in the mean number of young fledged per nest among the sites and times of nest initiation (early and late). The interaction of site and time of initiation was not significant ($F = 1.51$, $df = 3, 59$, $P = 0.221$), and neither of the main effects were significant (site $F = 0.44$, $df = 3, 59$, $P = 0.727$; time $F = 1.87$, $df = 1, 59$, $P = 0.177$) (Table 1.21). The average number of young fledged from early nests was 2.34 (± 1.85), and the average number of young fledged from late nests was 1.19 (± 1.49).

Table 1.21. Mean number of Prothonotary Warbler young fledged per nest at each site.

FC	FT	RD	SH
1.28 \pm 1.70	1.36 \pm 1.50	2.15 \pm 1.81	2.00 \pm 2.00
N = 7	N = 11	N = 32	N = 17

Note. \pm = one standard deviation, N = sample size.

Ruby-throated Hummingbird (*Archilochus colubris*)

The Ruby-throated Hummingbird is the smallest breeding bird in these forests, weighing an average of 3.1 g (N = 12). Consequently, nests of this species are also very small, about the size of a walnut. The female performs all nesting duties with no help from the male. The nests are constructed of fine plant fibers and spider webs with a coating of gray lichen on the exterior surfaces. I have often witnessed females adding lichens and spider webs to their nests throughout the nesting cycle. The nests are normally quite high in bottomland forests; they averaged 11.2 m for 29 nests in this study, with a range of 6 to 20.5 m. Incubation takes an average of 13 days with the nestling stage averaging 20 days. Females can be aggressive in their defense of the nest, and I have located several nests by observing the female chasing and diving at much larger birds that have approached too closely. In areas where the low-growing palmetto plant (*Sabal minor*) occurs in dense stands, Ruby-throated Hummingbirds can often be found foraging among its tall, thin, flower spikes. The spikes seem to catch or support a good supply of spider webs, and females can regularly be seen tugging at strands of web supported by the flower spikes.

Thirty nests were found during the course of the study, but the outcomes of only 21 could be definitely ascertained; only these were entered into this analysis. The distribution of those nests varied by site and year (Table 1.22).

Table 1.22. Number of Ruby-throated Hummingbird nests by site and year.

Year	FC	FT	RD	SH	Total
1992	1	1	*	*	2
1993	0	1	2	0	3
1994	7	6	1	2	16
Total	8	8	3	2	21

* No work performed at these sites in 1992.

I first tested for differences in mean daily survival rates of nests among sites and years. There was no significant interaction between site and year ($F = 1.4$, $df = 2, 12$, $P = 0.284$) and the main effects of year and site were not significant (year $F = 0.36$, $df = 2, 12$, $P = 0.701$; site $F = 0.77$, $df = 3, 12$, $P = 0.534$). The mean daily survival rates at each site are as follows: Ferriday Treatment 0.975 (± 0.047 , $N = 8$), Sherburne 0.930 (± 0.001 , $N = 2$), Ferriday Control 0.925 (± 0.124 , $N = 8$), Red Diamond 0.923 (± 0.071 , $N = 3$). Obviously, low sample sizes warrant interpretation of these results with caution.

Nine nests were initiated early (before June 1), and 11 nests were initiated later (Figure 1.8). Although the three-way interaction may have been important, sample size did not permit analysis for differences in mean daily survival rates of nests by time of initiation, site, and stage of nesting cycle (incubation and nestling) as with previous species. Because the first model results had no difference among years and sites, I chose to analyze the differences in mean daily survival rate of nests among times of initiation (early and late) and stages (incubation and nestling). The interaction term of time of initiation and stage was not significant ($F = 1.37$, $df = 1, 19$, $P = 2.56$), and the main effect of time of initiation was not significant ($F = 1.37$, $df = 1, 19$, $P = 0.256$). The mean

daily survival rate of early nests was $0.946 (\pm 0.070)$ and the mean for late nests was $0.989 (\pm 0.036)$. The main effect of stage was significant ($F = 5.56$, $df = 1, 19$, $P = 0.029$), and the mean daily survival rate during the incubation stage (0.925) was lower than the nestling stage (1.00).

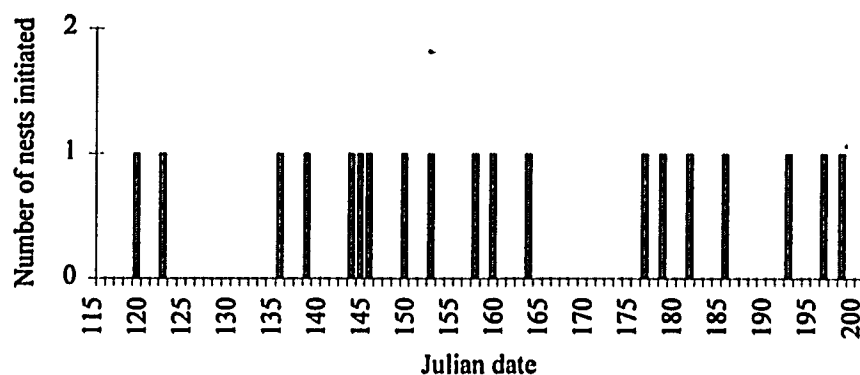


Figure 1.8. Nest initiation dates for Ruby-throated Hummingbirds. May 1 = day 120, June 1 = day 151, July 1 = day 181.

I also categorized the fates of these nests for each site (Table 1.23). Small samples in each category prevented statistical testing. I found no evidence of parasitism in Ruby-throated Hummingbird nests, but predation affected 25 percent of all nests, and other causes (abandonment) affected 15 percent.

I also categorized the fates of each nest by initiation time (Table 1.24). Small sample sizes precluded testing any of these differences and these values should be interpreted with this in mind.

Table 1.23. Fates of Ruby-throated Hummingbird nests by site.

Fate	FC N = 8	FT N = 8	RD N = 3	SH N = 1
Success	0.62	0.75	0.33	0.0
not parasitised	0.62	0.75	0.33	0.0
parasitised	0.0	0.0	0.0	0.0
Predation	0.12	0.25	0.66	0.0
not parasitised	0.12	0.25	0.66	0.0
parasitised	0.0	0.0	0.0	0.0
Parasitism	0.0	0.0	0.0	0.0
no predation	0.0	0.0	0.0	0.0
Other/Unknown failures	0.25	0.0	0.0	1.0

Note. Values are expressed as percentages of total nests for each site.

I tested for differences in the mean number of young fledged per nests among sites and nest initiation dates. The interaction of site and time of initiation was not significant ($F = 0.98$, $df = 2, 12$, $P = 0.404$), and neither of the main effects were significant (site $F = 0.35$, $df = 2, 12$, $P = 0.709$; time of initiation $F = 2.85$, $df = 1, 12$, $P = 0.117$). The mean number of young fledged per nest at Ferriday Treatment was 1.37; at Ferriday Control the mean was 0.875, and at Red Diamond the mean was 0.667. The average number young fledged per late nest was 1.40, and for early nests the average was 0.75.

Table 1.24. Fates of Ruby-throated Hummingbird nests by time of nest initiation.

Fate	Early N = 8	Late N = 11
Success	0.37	0.82
not parasitised	0.37	0.82

(table con'd.)

parasitised	0.0	0.0
Predation	0.50	0.09
not parasitised	0.50	0.09
parasitised	0.0	0.0
Parasitism	0.0	0.0
no predation	0.0	0.0
Other/Unknown failures	0.12	0.09

Note. Values are expressed as percentages of total nests for each time period.

Hooded Warbler (*Wilsonia citrina*)

The nest of the Hooded Warbler is a compact open-cup structure built by the female that is usually constructed with a base or outer layer of dead leaves and lined with fine plant fibers and soft grasses. Most are placed rather low, and the mean height of 35 nests in this study was 0.88 m with a range of 0.3 to 1.8 m. Some authors (Ehrlich et al. 1988) have indicated that both sexes incubate. I could not confirm this in my study; I observed only females performing incubation and brooding duties. The incubation period averages 12 days, and brooding averages 8 days and the young are fed by both adults. As with many species, the nest of the Hooded Warbler blends well with its surroundings and is often difficult to locate without closely following the behavior of the adults.

A total of 39 nests was found during the study (Table 1.25). Only one nest was located at the Ferriday study sites, and the analysis among sites only includes nests at Red Diamond and Sherburne.

Table 1.25. Number of Hooded Warbler nests by year and site.

Year	FC	FT	RD	SH	Total
1992	0	0	*	*	0
1993	0	1	6	6	13
1994	0	0	14	12	26
Total	0	1	20	18	39

*No field work performed at these sites during 1992.

In the first ANOVA model, I tested for differences in mean daily survival rates among years and sites. The interaction of year and site was not significant ($F = 0.07$, $df = 1, 34$, $P = 0.789$). There was no difference ($F = 0.09$, $df = 1, 34$, $P = 0.765$) in the mean daily survival rate between years. The mean daily survival rate in 1994 was $0.923 (\pm 0.105, N = 6)$ and in 1993 the mean was $0.910 (\pm 0.148, N = 13)$. The main effect of site was not significant ($F = 0.21$, $df = 1, 34$, $P = 0.652$); nests at the Sherburne site had a mean daily survival rate of $0.917 (\pm 0.095, N = 18)$, and the mean at Red Diamond was $0.916 (\pm 0.141, N = 20)$.

I also tested for differences in mean daily survival rates of nests among sites, stages (incubation and nestling), and times of nest initiation. Nineteen nests were initiated early (before June 1), and 20 nests were initiated later (Figure 1.9). The three-way interaction term and all two-way interactions were not significant. The main effect of site was not significant ($F = 0.97$, $df = 1, 44$, $P = 0.331$), as in the previous model, and the mean rate of early nests did not differ significantly from that of later nests ($F = 0.05$, $df = 1, 44$, $P = 0.822$). The mean daily survival rate of early nests was $0.944 (\pm 0.083)$ and for late nests the mean was $0.946 (\pm 0.102)$. The main effect of stage of nesting cycle

approached significance ($F = 3.81$, $df = 1, 44$, $P = 0.057$). The mean daily survival rate of nests during the nestling stage was $0.967 (\pm 0.078)$, and during the incubation stage the mean was $0.923 (\pm 0.101)$.

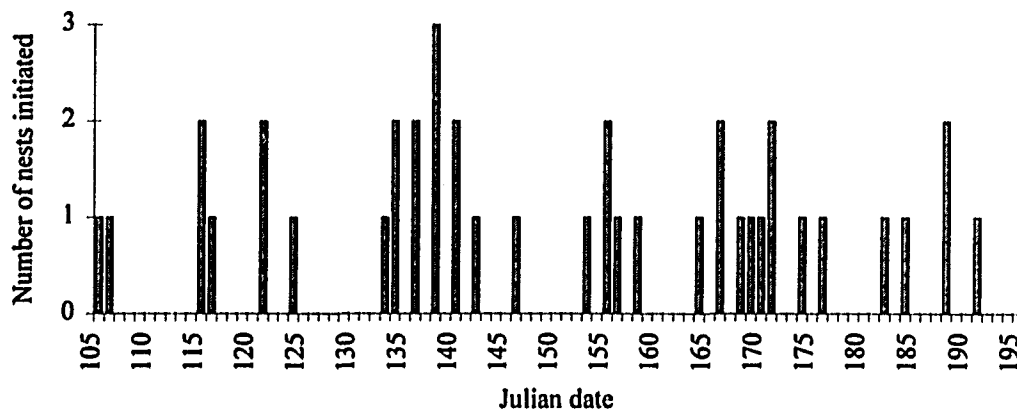


Figure 1.9. Nest initiation dates for Hooded Warblers. May 1 = day 120, June 1 = day 151, July 1 = day 181.

The fates of these nests varied among sites (Table 1.26). Predation was the main factor affecting nests overall, and it was greatest at the Red Diamond site. Considering only Red Diamond and Sherburne, predation did not differ significantly between these sites or from that expected by chance ($\chi^2 = 0.75$, $df = 1$, $P = 0.38$). Parasitism was relatively low at Red Diamond, but it was the leading factor at Sherburne where it affected nearly a quarter of all nests. The parasitism rate of these two sites was nearly significant ($\chi^2 = 3.63$, $df = 1$, $P = 0.056$). The parasitism rate at Red Diamond was less than expected, and the parasitism rate at Sherburne was greater than expected. The only Hooded Warbler nest found at Ferriday in three years was parasitised.

Table 1.26. Fates of Hooded Warbler nests by site.

Fate	FC*	FT N = 1	RD N = 20	SH N = 18
Success	-	0.0	0.65	0.44
not parasitised	-	0.0	0.60	0.44
parasitised	-	0.0	0.05	0.0
Predation	-	0.0	0.35	0.22
not parasitised	-	0.0	0.35	0.17
parasitised	-	0.0	0.0	0.05
Parasitism	-	1.0	0.05	0.28
no predation	-	1.0	0.05	0.22
Other/Unknown failures	-	0.0	0.0	0.11

Note. Values are expressed as percentages of total nests for each site. * Indicates no nests found

The fates of these nests were also categorized by early and late initiation times (Table 1.27). There was no significant difference in predation and parasitism rates of early and late nests (predation $\chi^2 = 0.06$, $df = 1$, $P = 0.79$; parasitism $\chi^2 = 0.23$, $df = 1$, $P = 0.62$). Other causes (abandonment and weather) were important in 10 percent of the early nests but were not a factor in late nests.

Table 1.27. Fates of Hooded Warbler nests by time of nest initiation.

Fate	Early N = 19	Late N = 20
Success	0.47	0.60
not parasitised	0.42	0.60
parasitised	0.05	0.0
Predation	0.26	0.30
not parasitised	0.26	0.25

(table con'd.)

parasitised	0.0	0.05
Parasitism	0.21	0.15
no predation	0.21	0.10
Other/Unknown failures	0.10	0.0

Note. Values are expressed as percentages of total nests for each time period.

I next tested for differences in the mean number of young fledged per nest among sites and times of nest initiation. The interaction of site and time was not significant ($F = 0.23$, $df = 1, 34$, $P = 0.634$), and the site main effect was not significant ($F = 1.19$, $df = 1, 34$, $P = 0.282$). The average number of young fledged per nest at Red Diamond was 1.55 (± 1.43), and Sherburne nests fledged an average of 1.05 (± 1.39) young. Early nests averaged 1.33 (± 1.65) young fledged, and late nests averaged 1.30 (± 1.22), but this difference was not significant ($F = 0.15$, $df = 1, 34$, $P = 0.828$).

Kentucky Warbler (*Oporonis formosus*)

The Kentucky Warbler is one of the few species of songbirds breeding in Louisiana that always places its nest on the ground. This seems fitting for a bird that spends most of its time skulking about the forest floor. The nest is a rather bulky structure often at the base of a small shrub or tree, where it is placed on a foundation of dead leaves 2 or 3 cm high and lined with fine strips of grass and bark. Both parents feed the young, but the female alone incubates and broods (for an average of 12 and 9 days respectively). The nests blend extremely well with their surroundings, and care must be taken not to step on them while searching for their location. I have often seen and heard the female give a series of soft chip notes as she approaches the nest; she stops making

the call when she is within a meter or two of the nest. I have been able to locate several nests using this cue.

Twenty-three nests were found during the study (Table 1.28). Because only one nest was found at Ferriday Control and Treatment sites, it was not used in the analysis among sites.

Table 1.28. Number of Kentucky Warbler nests by site and year.

Year	FC	FT	RD	SH	Totals
1993	1	0	4	4	9
1994	0	0	8	6	14
Totals	1	0	12	10	23

In the first ANOVA model, I tested for differences in mean daily survival rates among sites and years. The interaction of site by year was not significant ($F = 0.01$, $df = 1, 18$, $P = 0.909$) nor were the main effects of year ($F = 0.29$, $df = 1, 18$, $P = 0.599$) and site ($F = 2.16$, $df = 1, 18$, $P = 0.159$). The mean daily survival rate of nests at Red Diamond was $0.985 (\pm .035, N = 12)$, and the mean at Sherburne was $0.915 (\pm 0.135, N = 10)$. Again, small sample sizes require that these analyses be interpreted with caution.

Sample size did not permit analysis of mean daily survival rates among sites, times of initiation, and stages of the nesting cycle as with other species. The interaction terms may have been significant, but because of small samples, I was not able to test for them. Instead, I analyzed the differences in initiation times and nesting stages separately. Nineteen nests were initiated before June 1, and four nests were initiated afterwards (Figure 1.10). The mean daily survival rate of early nests was $0.951 (\pm 0.236)$ and the

mean of late nests was $0.970 (\pm 0.680)$; this difference was not significant ($t = -0.186$, $df = 21$, $P = 0.427$). The mean daily survival rate during the incubation stage was $0.936 (\pm 0.299, N = 10)$, and the mean of the nestling stage was $.974 (\pm 0.232, N = 19)$; this difference was not significant ($t = -1.43$, $df = 27$, $P = 0.082$).

The fates of these nests varied by site (Table 1.29). No nests were parasitised, and the predation rate at the Sherburne and Red Diamond sites did not differ from that expected by chance ($\chi^2 = 2.05$, $df = 1$, $P = 0.15$).

Twenty-six percent of the early nests (5 of 19) and 25 percent of the late nests (1 of 4) were depredated. There were no losses due to parasitism or other/unknown causes.

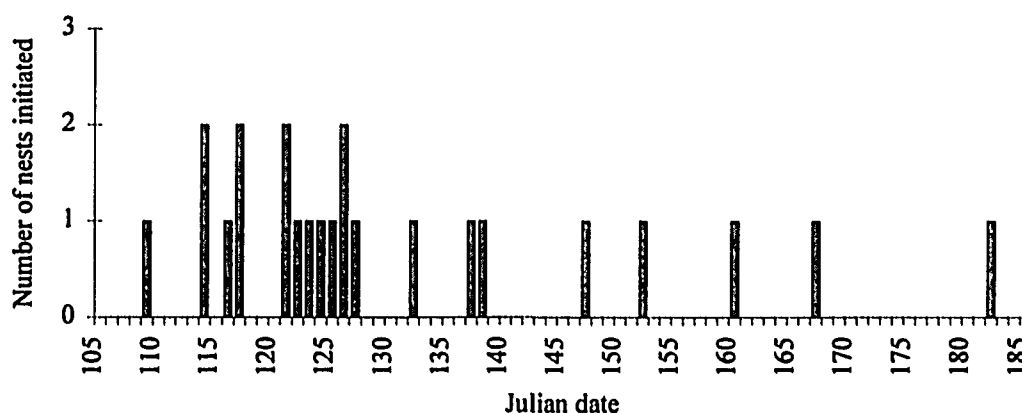


Figure 1.10. Nest initiation dates for Kentucky Warblers. May 1 = day 120, June 1 = day 151, July 1 = day 181.

Table 1.29. Fates of Kentucky Warbler nests by site.

Fate	FC N = 1	FT*	RD N = 12	SH N = 10
Success	1.0	-	0.83	0.60

(table con'd.)

not parasitised	1.0	-	0.83	0.60
parasitised	0.0	-	0.0	0.0
Predation	0.0	-	0.17	0.40
not parasitised	0.0	-	0.17	0.40
parasitised	0.0	-	0.0	0.0
Parasitism	0.0	-	0.0	0.0
no predation	0.0	-	0.0	0.0
Other/Unknown failures	0.0	-	0.0	0.0

Note. Values are expressed as percentages of total nests for each site. * Indicates no nests found at this site.

I next tested for differences in the mean number of young fledged per nest among sites and times of nest initiation. The interaction and both main effects were not significant (site * time $F = 0.55$, $df = 1, 18$, $P = 0.469$; site $F = 2.47$, $df = 1, 18$, $P = 0.134$; time $F = 0.42$, $df = 1, 18$, $P = 0.526$). Nests at Red Diamond averaged $3.41 (\pm 1.78)$ young fledged as opposed to an average of $2.20 (\pm 2.04)$ at Sherburne. Early nests averaged $3.0 (\pm 2.03)$ young fledged, and late nests averaged $2.25 \pm (1.70)$ young fledged.

Yellow-billed Cuckoo (*Coccyzus americanus*)

The nest of the Yellow-billed Cuckoo is a rather flimsily built platform of sticks and twigs containing a shallow depression lightly lined with moss and fine plant material. I have observed both adults building the nest, and once I watched as one bird passed twigs to another who then inserted them into the platform. The average height of 20 nests in this study was 8.2 m. with a range of 3 to 17.5 m. Both adults feed the young, but the female alone incubates and broods, (for an average of 10 and 8 days respectively). The habits of this bird are usually slow and deliberate as it searches among the branches, but

its flights are rather straight, swift, and direct. Although their calls can be heard for some distance, they are very quiet around the nest. Some (Bent 1940) think this bird could be a potential nest predator because it eats a variety of relatively large prey. On 8 June 1993 at the Ferriday Control site, I witnessed an adult Yellow-billed Cuckoo manipulating a blind, featherless nestling of unknown species in its beak against a tree limb, and then fly away with the young bird in its mouth. On at least 2 occasions I have seen them eating tree frogs.

Twenty nests were found during the study, but the fates of only 17 could be determined (Table 1.30).

Table 1.30. Number of Yellow-billed Cuckoo nests by site and year.

Year	FC	FT	RD	SH	Total
1992	2	0	*	*	2
1993	3	1	2	0	6
1994	3	6	0	0	9
Total	8	7	2	0	17

* No field work performed at these sites in 1992.

I first compared the mean daily survival rates of nests among sites and years. The interaction of site and year was not significant ($F = 0.12$, $df = 2, 11$, $P = 0.881$) nor were the main effects (site $F = 0.16$, $df = 2, 11$, $P = 0.855$; year $F = 0.36$, $df = 2, 11$, $P = 0.703$). The mean daily survival rates at each site were: Red Diamond $0.925 (\pm 0.021)$, Ferriday Control $0.832 (\pm 0.118)$, and Ferriday Treatment $0.807 (\pm 0.182)$.

Only four of the nests were initiated before June 1, and 11 were initiated after that date (Figure 1.11). The initiation times of two nests could not be definitely determined.

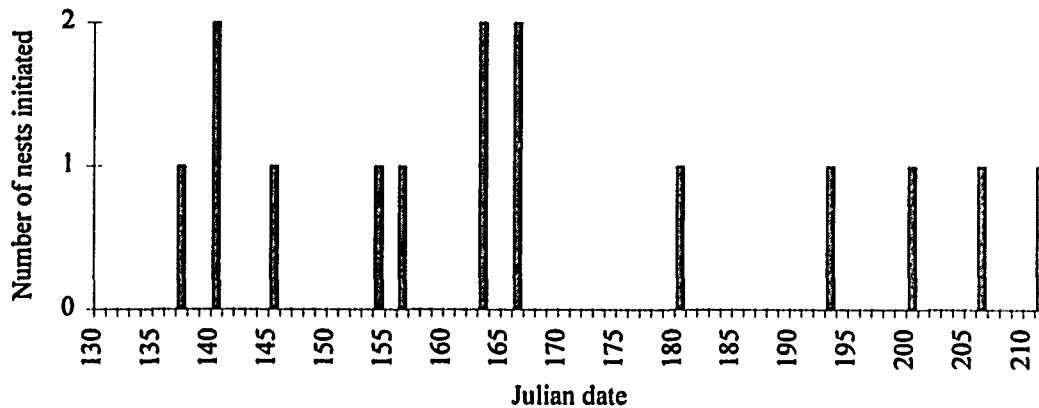


Figure 1.11. Nest initiation dates for Yellow-billed Cuckoos. May 1 = day 120, June 1 = day 151, July 1 = day 181.

Small sample sizes did not permit testing for interactions among sites, stages, and times of initiation. I tested for differences in mean daily survival rates among times of nest initiation and stages in the nesting cycle separately. There was no significant difference ($t = 0.035$, $df = 13$, $P = 0.486$) in mean daily survival rates of early and late nests. The mean daily survival rate of the early nests was $0.792 (\pm 0.375)$ and the mean of late nests was $0.825 (\pm 0.276)$. The mean daily survival rate during the incubation stage was $0.840 (\pm 0.158, N = 13)$ and the mean of the nestling stage was $0.800 (\pm 0.338, N = 7)$; this difference was not significant ($t = 0.147$, $df = 7.65$, $P = 0.443$).

The fates of 17 Yellow-billed Cuckoo nests varied among sites (Table 1.31). No tests were performed because of small sample sizes in most categories. I did not observe any parasitism at Yellow-billed Cuckoo nests, but predation was common and accounted for nearly 60 percent of all nest losses.

Table 1.31. Fates of Yellow-billed Cuckoo nests by site.

Fate	FC N = 8	FT N = 7	RD N = 2	SH*
Success	0.25	0.28	0.0	-
not parasitised	0.25	0.28	0.0	-
parasitised	0.0	0.0	0.0	-
Predation	0.75	0.43	0.50	-
not parasitised	0.75	0.43	0.50	-
parasitised	0.0	0.0	0.0	-
Parasitism	0.0	0.0	0.0	-
no predation	0.0	0.0	0.0	-
Other/Unknown failures	0.0	0.28	0.50	-

Note. Values are expressed as percentages of total nests for each site. * No nests found.

Of the four nests initiated before June 1, three were depredated. Seven of the 13 nests initiated after June 1 were depredated. Only three nests were lost to other/unknown causes and all three were late nests.

I next tested for differences in the mean number of young fledged per nest among sites and initiation times. Because of small sample sizes, I was not able to test for the interaction of these variables, so I tested each separately. The mean number of young fledged per nest that were initiated early was 0.25 (± 0.50 , $N = 4$), and the mean of late nests was 0.545 (± 1.21 , $N = 11$); this difference was not significant ($t = -0.464$, $df = 13$, $P = 0.650$). Nests at Ferriday Control fledged an average of 0.50 young per nest (± 1.07 , $N = 8$) compared to an average of 0.71 young per nest (± 1.25 , $N = 7$) at Ferriday Treatment. This difference was not significant ($t = -0.357$, $df = 13$, $P = 0.726$).

Other Migrant Species

The mean daily survival rates for nests of eleven additional species of Neotropical migrants were calculated for each site (Table 1.32). Their sample sizes precluded analysis individually but they are treated in the composite analysis later in this chapter.

Table 1.32. Mean daily survival rates for nests of eleven Neotropical migrant species by site.

Species	FC	FT	RD	SH
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	*	1.0 (N=1)	*	*
Eastern Wood-Pewee (<i>Contopus virens</i>)	1.0 (N=2)	*	*	*
Wood Thrush (<i>Hylocichla mustelina</i>)	0.923 (N=1)	*	0.825 (N=2)	*
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	*	0.980 (N=3)	0.945 (N=11)	*
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	*	1.0 (N=1)	1.0 (N=1)	*
Northern Parula (<i>Parula americana</i>)	1.0 (N=1)	1.0 (N=2)	1.0 (N=4)	1.0 (N=2)
Swainson's Warbler (<i>Limnothlypis swainsonii</i>)	*	*	1.0 (N=1)	0.50 (N=1)
American Redstart (<i>Setophaga ruticilla</i>)	*	*	0.945 (N=11)	1.0 (N=2)
Yellow-breasted Chat (<i>Icteria virens</i>)	*	*	*	0.90 (N=2)
Summer Tanager (<i>Piranga rubra</i>)	0.833 (N=1)	0.885 (N=4)	0.966 (N=5)	*
Indigo Bunting (<i>Passerina cyanea</i>)	*	0.792 (N=12)	*	*

* No nests found at these sites.

Northern Cardinal (*Cardinalis cardinalis*)

Nests of this common resident species are built mostly by the females although males may provide some assistance. The nests are constructed of small twigs, bark strips, and occasional dried leaves, and are lined with finer plant materials. The average height

of 100 nests in this study was 3.9 m with a range of 0.4 to 14.0 m. I have only witnessed females incubating and brooding the young and both stages average 12 days. The male is very attentive to the female during nesting and shares the duty of feeding the young.

Northern Cardinals were a common species at most sites and 111 nests were found during the study (Table 1.33). In the first ANOVA model, I tested for differences in mean daily survival rates of nests among sites and years. The interaction of year and site was not significant ($F = 0.96$, $df = 3, 139$, $P = 0.436$) nor were the main effects (year $F = 0.36$, $df = 2, 101$, $P = 0.698$; site $F = 1.47$, $df = 3, 101$, $P = 0.228$) (Table 1.34).

Table 1.33. Number of Northern Cardinal nests by year and site.

Year	FC	FT	RD	SH	Total
1992	6	1	*	*	7
1993	11	13	13	9	46
1994	13	18	11	16	58
Total	30	32	24	25	111

* No field work performed at these sites in 1992.

Table 1.34. Mean daily survival rates of Northern Cardinal nests by site.

FC	FT	RD	SH
0.876 ± 0.118	0.919 ± 0.104	0.901 ± 0.164	0.936 ± 0.094
N = 30	N = 32	N = 24	N = 25

Note. \pm = one standard deviation, N = sample size.

I next tested for differences in mean daily survival rates of nests among sites, stages, and times of nest initiation. Forty-four nests were initiated before June 1 and 67 nests were initiated afterwards (Figure 1.12). The three-way interaction and all two-way interactions were not significant. The site main effect was not significant ($F = 1.48$, $df = 3$, 139 , $P = 0.222$). There was no difference ($F = 0.33$, $df = 1$, 139 , $P = 0.567$) in the mean daily survival rate of early nests (0.929 ± 0.128) and late nests (0.921 ± 0.116). The mean daily survival rate during the incubation stage was $0.915 (\pm 0.119)$ and the mean daily survival rate of the nestling stage was $0.937 (\pm 0.121)$; this difference was not significant ($F = 2.86$, $df = 1$, 139 , $P = 0.093$).

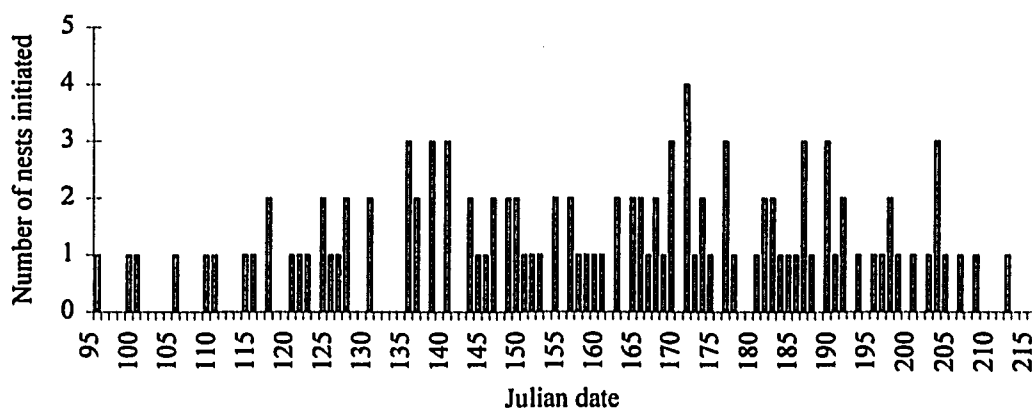


Figure 1.12. Nest initiation dates for Northern Cardinals. May 1 = day 120, June 1 = day 151, July 1 = day 181.

Predation was the main factor affecting nest success. However, there was no significant difference in the predation rate among sites ($\chi^2 = 1.32$, $df = 3$, $P = 0.71$) (Table 1.35). The second most common factor was the category of other/unknown causes.

These factors occurred most often at Ferriday Control and Sherburne, and were mostly losses due to weather and abandonment. Only three Northern Cardinal nests were parasitised; two at Ferriday Treatment and one at Ferriday Control.

There was a significant difference in the predation rates of early and late nests ($\chi^2 = 5.67$, $df = 1$, $P = 0.017$) (Table 1.36). Early nests were depredated less often than expected and late nests were depredated more often than expected. The three cases of parasitism occurred only in early nests.

Table 1.35. Fates of Northern Cardinal nests by site.

FATE	FC N = 30	FT N = 32	RD N = 24	SH N = 25
Success	0.27	0.50	0.58	0.52
not parasitised	0.27	0.50	0.58	0.52
parasitised	0.0	0.0	0.0	0.0
Predation	0.50	0.44	0.37	0.36
not parasitised	0.50	0.37	0.37	0.36
parasitised	0.0	0.06	0.0	0.0
Parasitism	0.03	0.06	0.0	0.0
no predation	0.03	0.0	0.0	0.0
Other/Unknown failures	0.20	0.06	0.04	0.12

Note. Values are expressed as percentages of total nests for each site.

Table 1.36. Fates of Northern Cardinal nests by time of nest initiation.

Fate	Early N = 44	Late N = 67
Success	0.57	0.39
not parasitised	0.57	0.39
parasitised	0.0	0.0
Predation	0.29	0.51
not parasitised	0.25	0.51
parasitised	0.04	0.0
Parasitism	0.07	0.0
no predation	0.02	0.0
Other/Unknown failures	0.11	0.10

Note. Values are expressed as percentages of total nests for each time period.

I tested for differences in the mean number of young fledged per nest among sites and times of nest initiation. The interaction of site and time was not significant ($F = 1.48$, $df = 3, 103$, $P = 0.224$). There was no difference in the average number of young fledged per nest among the four sites ($F = 1.76$, $df = 3, 103$, $P = 0.159$) (Table 1.37). Early nests averaged $1.41 (\pm 1.35)$ young fledged per nest and late nests averaged $0.940 (\pm 1.25)$ but this difference could only be considered marginally significant ($F = 3.37$, $df = 1, 103$, $P = 0.069$)

Table 1.37. Mean number of Northern Cardinal young fledged per nest at each site.

FC	FT	RD	SH
0.67 ± 1.15	1.34 ± 1.40	1.37 ± 1.28	1.16 ± 1.31
N = 30	N = 32	N = 24	N = 25

Note. Standard deviations and sample sizes (N) are in parenthesis.

Carolina Wren (*Thryothorus ludovicianus*)

The nests of this resident species can be found in a variety of situations in bottomland hardwood forests. Some were placed in natural cavities, but Carolina Wrens used a broad range of nest-sites. Nests heights ranged from 0 to 7.5 m. with an average height of 1.44 m (N = 47). The nest is a bulky structure of leaves, moss, rootlets and other small plant debris constructed by both adults with the entrance often placed on the side. The female alone incubates and broods for an average of 13 days, but the male does help feed the young. These birds are very vocal throughout the breeding season, but despite this fact, their nests can be difficult to locate, especially in heavily wooded areas. I have on several occasions watched the adults fly to the ground 15-20 m from the nest and silently approach it by hopping along the forest floor under the cover of dense vegetation such as palmetto.

Although Carolina Wrens are a common species at most sites, only 51 nests were found (Table 1.38).

Table 1.38. Number of Carolina Wren nests by year and site.

Year	FC	FT	RD	SH	Total
1992	*	4	**	**	4
1993	5	3	6	1	15
1994	8	10	7	7	32
Total	13	17	13	8	51

*No nest found. ** No field work performed at these sites in 1992.

The first ANOVA model involved testing for differences in mean daily survival rates of nests among sites and years. The interaction of site by year was not significant ($F = 1.17$, $df = 3, 42$, $P = 0.334$), and the main effect of year was not significant ($F = 0.38$, $df = 2, 42$, $P = 0.685$). The main effect of site was significant ($F = 2.89$, $df = 3, 42$, $P = 0.046$). Nests at Red Diamond had the greatest mean daily survival rate followed by nests at Sherburne, Ferriday Treatment, and Ferriday Control. The mean daily survival rate of nests was significantly lower at Ferriday Control than at Red Diamond. No other significant differences were detected (Table 1.39).

Table 1.39. Mean daily survival rates of Carolina Wren nests by site.

FC ^a	FT ^{ab}	RD ^b	SH ^{ab}
0.845 ± 0.175	0.918 ± 0.140	0.969 ± 0.092	0.926 ± 0.090
N = 13	N = 17	N = 13	N = 8

Note. Sites with similar letters are not different. \pm = one standard deviation, N = sample size.

I tested for differences in mean daily survival rates of nests among sites, times of initiation, and stages of the nesting cycle. Twenty-seven nests were initiated before June 1, and 24 were initiated afterwards (Figure 1.13). The three-way interaction and all two-way interactions were not significant. The mean daily survival rate of early nests was 0.933 (± 0.134) and the mean of late nests was 0.882 (± 0.250); this difference was not significant ($F = 0.26$, $df = 1, 55$, $P = 0.611$). The mean daily survival rate during the nestling stage was 0.913 (± 0.243) and the mean for the incubation stage was 0.902 (± 0.150) ($F = 0.56$, $df = 1, 55$, $P = 0.456$).

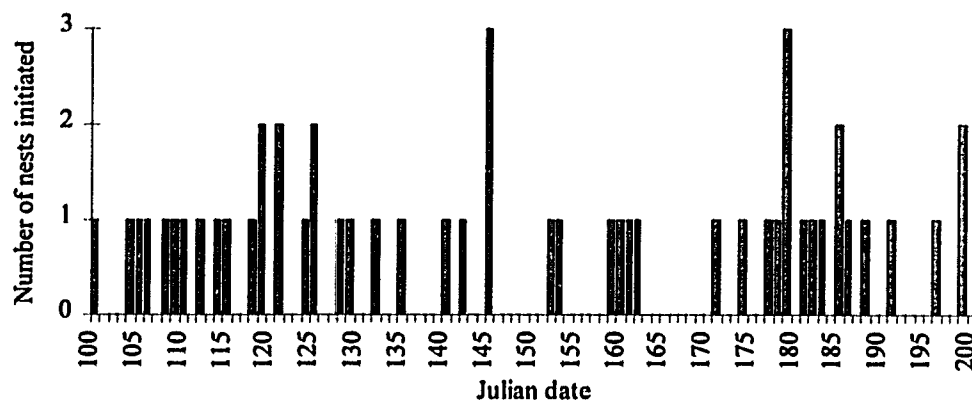


Figure 1.13. Nest initiation dates for Carolina Wrens. May 1 = day 120, June 1 = day 151, July 1 = day 181.

Parasitism was not a factor influencing nest success in Carolina Wrens. Predation was the main cause of failure and accounted for a total loss of 31 percent of all nests (Table 1.40). However, there was no significant difference in the predation rate among sites and that expected by chance ($\chi^2 = 5.10$, $df = 3$, $P = 0.16$). Other/unknown causes (primarily abandonment) affected the success of 10 percent of all nests and was most common at Ferriday Control.

Table 1.40. Fates of Carolina Wren nests by site.

Fate	FC N = 13	FT N = 17	RD N = 13	SH N = 8
Success	0.38	0.59	0.85	0.50
not parasitised	0.38	0.59	0.85	0.50
parasitised	0.0	0.0	0.0	0.0
Predation	0.38	0.35	0.08	0.50
not parasitised	0.38	0.35	0.08	0.50

(table con'd.)

parasitised	0.0	0.0	0.0	0.0
Parasitism	0.0	0.0	0.0	0.0
no predation	0.0	0.0	0.0	0.0
Other/Unknown failures	0.23	0.06	0.08	0.0

Note. Values are expressed as percentages of total nests for each site.

There was no significant difference in the predation rates of early and late nests (Table 1.41) ($\chi^2 = 0.856$, $df = 1$, $P = 0.355$). Other/unknown (primarily abandonment) causes did not affect the early nests but accounted for 21 percent of losses in late nests.

Table 1.41. Fates of Carolina Wren nests by time of nest initiation.

Fate	Early N = 27	Late N = 24
Success	0.63	0.54
not parasitised	0.63	0.54
parasitised	0.0	0.0
Predation	0.37	0.25
not parasitised	0.37	0.25
parasitised	0.0	0.0
Parasitism	0.0	0.0
no predation	0.0	0.0
Other/Unknown failures	0.0	0.21

Note. Values are expressed as percentages of total nests for each time period.

I tested for differences in the mean number of young fledged per nest among sites and times of initiation. The interaction of time of initiation and site was not significant ($F = 0.48$, $df = 3, 43$, $P = 0.695$). Early nests averaged 2.11 (± 1.82) young fledged and late nests averaged 1.67 (± 1.71); this difference was not significant ($F = 0.17$, $df = 1, 43$,

$P = 0.680$). The average number of young fledged per nest was not different among the four sites ($F = 1.95$, $df = 3, 43$, $P = 0.136$) (Table 1.42).

Table 1.42. Mean number of Carolina Wren young fledged per nest at each site.

FC	FT	RD	SH
1.15 ± 1.67	2.00 ± 1.84	2.84 ± 1.57	1.38 ± 1.59
N = 13	N = 17	N = 13	N = 8

Note. \pm = one standard deviation, N = sample size.

Other Resident Species

The mean daily survival rates for nests of five other resident species were calculated for each site (Table 1.43). Due to sample sizes, I did not perform analysis individually on the separate species but they are included in the analysis of species groups that follows.

Table 1.43. Mean daily survival rates for nests of eleven resident species by site.

Species	FC	FT	RD	SH
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	1.00 N = 5	1.00 N = 2	1.00 N = 2	*
Downy Woodpecker (<i>Picoides pubescens</i>)	1.00 N = 1	*	1.00 N = 2	*
Carolina Chickadee (<i>Parus carolinensis</i>)	1.00 N = 2	*	*	*
Tufted Titmouse (<i>Parus bicolor</i>)	1.00 N = 2	*	*	*
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	*	*	0.964 N = 2	*

* No nest found.

SPECIES GROUPS

I tested for differences in mean daily survival rates of nests among sites and types of species (migrant or resident) combining together all migrants ($N = 609$) and residents ($N = 181$). The interaction of site and type of species was not significant ($F = 0.95$, $df = 3, 782$, $P = 0.418$). There was no difference in the mean daily survival rate of migrant and resident species nests ($F = 1.02$, $df = 1, 782$, $P = 0.314$). The main effect of site was significant ($F = 8.17$, $df = 3, 782$, $P < 0.01$). For all species, nests at Ferriday Control and Ferriday Treatment had the lowest mean daily survival rates and were not different from each other. Red Diamond and Sherburne nests had the greatest mean daily survival rate, and these two sites did not differ. The mean daily survival rate of nests at the Ferriday Treatment did not differ from that of the Sherburne site (Table 1.44).

Table 1.44. Mean daily survival rates of all nests by site and type of species.

Type	FC	FT	RD	SH	Total
Migrant	0.878	0.893	0.942	0.941	0.917
	± 0.167	± 0.134	± 0.095	± 0.094	± 0.127
	$N = 131$	$N = 154$	$N = 186$	$N = 138$	$N = 609$
Resident	0.892	0.923	0.939	0.933	0.920
	± 0.133	± 0.115	± 0.136	± 0.092	± 0.122
	$N = 53$	$N = 52$	$N = 43$	$N = 33$	$N = 181$
Total	0.882 ^a	0.901 ^{ac}	0.945 ^b	0.940 ^{bc}	0.917
	± 0.157	± 0.130	± 0.103	± 0.093	± 0.035
	$N = 184$	$N = 206$	$N = 229$	$N = 171$	$N = 790$

Note. Sites with similar letters are not different. \pm = one standard deviation, N = sample size.

I categorized all migrant species by types and heights of nests (cavity, low- to mid-height open-cup, high open-cup) and used a factorial ANOVA model to test for differences in mean daily survival rates among types, sites, stages of the nesting cycle (incubation and nestling), and times of initiation. This analysis only included migrant species. Cavity nesting species were the Prothonotary Warbler and Great Crested Flycatcher. High open-cup species were the Acadian Flycatcher, American Redstart, Blue-gray Gnatcatcher, Eastern Wood-Pewee, Northern Parula, Red-eyed Vireo, Ruby-throated Hummingbird, Summer Tanager, and Yellow-throated Vireo. Low- to mid-height open-cup species were the Hooded Warbler, Indigo Bunting, Kentucky Warbler, Swainson's Warbler, White-eyed Vireo, Yellow-breasted Chat, Wood Thrush, and Yellow-billed Cuckoo.

The four-way interaction and all three-way interactions were not significant. All two-way interactions except site by type ($F = 3.39$, $df = 6, 725$, $P = 0.002$) were not significant. To explore the site by nest type relationship, I plotted the mean daily survival rates of the three nest types at each site (Figure 1.14). Low to mid-height open-cup nests had a much lower mean daily survival rate at Ferriday Control and Treatment sites than did cavity and high open-cup nests. At Red Diamond, the mean daily survival rate of low to mid-height open-cup nests was intermediate to cavity and high open-cup nests, and at Sherburne it was again lower than the other two types.

Three of the four main effects in this model (site, stage, and type) were significant, but these results should be interpreted with some caution due to the presence

of a significant interaction. The differences in mean daily survival rates among sites was significant ($F = 12.78$, $df = 3$, 725 , $P = 0.01$). The mean rates for each site were analogous to those presented in Table 1.44. Ferriday Treatment and Control sites did not differ from each other, but both were less than Red Diamond and Sherburne, and Red Diamond and Sherburne did not differ. Again, these results are presented with the above mentioned interaction in mind. The incubation stage had a lower ($F = 9.46$, $df = 1$, 725 , $P = 0.022$) mean daily survival rate (0.909 ± 0.137) than the nestling stage (0.930 ± 0.155). A difference ($F = 9.27$, $df = 2$, 725 , $P = 0.01$) was also detected among the different types of nests. Low to mid-height open-cup nests had a lower mean daily survival rate than cavity and high open-cup nests, which were not different from each other (Table 1.45).

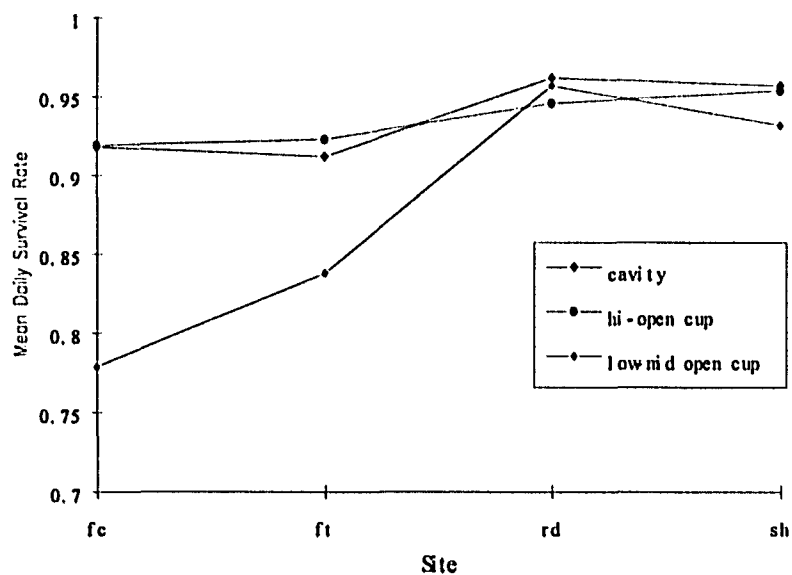


Figure 1.14. Mean daily survival rates of three migrant nest types at each site.

Table 1.45. Mean daily survival rates of three migrant nest types.

Cavity ^a	High Open-cup ^a	Low to Mid-Height Open-cup ^b
0.949 ± 0.099	0.933 ± 0.115	0.894 ± 0.183
N = 83	N = 384	N = 311

Note. Types with similar letters are not different. \pm = one standard deviation, N = sample size.

The fourth main effect, time of nest initiation, was not significant ($F = 1.17$, $df = 1$, 725, $P = 0.281$). Early nests (N = 412) had a mean daily survival rate of 0.915 (± 0.156), and late nests had a mean daily survival rate of 0.924 (± 0.134 , N = 361).

I next categorized the fates of all resident and migrant species (Table 1.46) and tested for differences from expected values for predation and parasitism rates. There was no significant difference in the predation rate of migrant and resident species from that expected by chance ($\chi^2 = 0.61$, $df = 1$, $P = 0.43$). There was a significant difference in the parasitism rate of migrant and resident species and that expected by chance ($\chi^2 = 15.18$, $df = 1$, $P < 0.01$). Migrant species were parasitised more often than expected and resident species were parasitised less often than expected.

I next analyzed the fates of migrant and resident nests based on time of initiation. Because of differences in the migratory nature of each group, I chose to analyze each separately for differences in predation and parasitism rates.

Table 1.46. Fates of nest for all migrant and resident species.

Fate	Migrants N = 509	Residents N = 181
Success	0.50	0.55

(table con'd.)

not parasitised	0.48	0.55
parasitised	0.015	0.0
Predation	0.33	0.35
not parasitised	0.29	0.34
parasitised	0.04	0.01
Parasitism	0.11	0.02
no predation	0.08	0.01
Other/Unknown failures	0.11	0.10

Three-hundred migrant nests were initiated early and 285 were initiated late (after June 1) (Table 1.47). Predation rates of early and late migrant nests did not differ significantly ($\chi^2 = 0.13$, $df = 1$, $P = 0.71$). Early nests were parasitised more often than expected and late nests were parasitised less often than expected ($\chi^2 = 5.52$, $df = 1$, $P = 0.018$).

Eighty-three resident nests were initiated early and 97 were initiated late (Table 1.48). Predation was the biggest factor contributing to nest loss and there was a significant difference in the predation rate of early and late ($\chi^2 = 4.023$, $df = 1$, $P = 0.04$). The predation rate of early nests was less than expected and the predation rate of late nests was greater than expected. Only three resident nests were parasitised and all were early nests.

Table 1.47. Fates of nests for all migrant species by time of nest initiation.

Fate	Early N = 319	Late N = 285
Success	0.49	0.51
not parasitised	0.47	0.50

(table con'd)

parasitised	0.02	0.01
Predation	0.34	0.32
not parasitised	0.29	0.30
parasitised	0.05	0.02
Parasitism	0.15	0.08
no predation	0.09	0.06
Other/Unknown failures	0.09	0.12

Table 1.48. Fates of all resident species nests by time of nest initiation.

Fate	Early N = 83	Late N = 97
Success	0.65	0.45
not parasitised	0.65	0.45
parasitised	0.0	0.0
Predation	0.28	0.41
not parasitised	0.25	0.41
parasitised	0.02	0.0
Parasitism	0.04	0.0
no predation	0.01	0.0
Other/Unknown failures	0.06	0.13

Note. Values are expressed as percentages of total nests for each time.

Predation was the number one cause of nest loss of migrants at all sites (Table 1.49) and rates differed among all sites ($\chi^2 = 8.68$, $df = 3$, $P = 0.033$). Predation rates were greater than expected at Ferriday Control and Treatment and less than expected at Sherburne and Red Diamond. The parasitism rate differed among sites ($\chi^2 = 15.35$, $df = 3$, $p = < 0.01$). Parasitism rates were greater than expected at Ferriday Treatment and Sherburne and less than expected at Ferriday Control and Red Diamond.

I next categorized the fates of all migrant nests by type of nest and nest height (cavity nests, low- to mid-height open-cup nests, and high open-cup nests) (Table 1.50). Predation caused the largest amount of nest loss, but predation rates did not differ significantly among the three nest types or from that expected by chance ($\chi^2 = 1.25$, $df = 2$, $P = 0.53$). High open-cup and cavity nests were parasitised less often than expected and low- to mid-height open cup nests were parasitised more often than expected ($\chi^2 = 24.85$, $df = 2$, $P < 0.01$).

Table 1.49. Fates of all migrant nests by site.

Fate	FC N = 131	FT N = 154	RD N = 186	SH N = 138
Success	0.39	0.38	0.62	0.58
not parasitised	0.38	0.36	0.60	0.57
parasitised	0.01	0.02	0.02	0.01
Predation	0.34	0.43	0.30	0.25
not parasitised	0.31	0.34	0.30	0.21
parasitised	0.03	0.09	0.00	0.04
Parasitism	0.10	0.19	0.05	0.12
no predation	0.07	0.10	0.05	0.08
Other/Unknown failures	0.20	0.11	0.05	0.09

Note. Values are expressed as percentages of total nests for each site.

I used a factorial ANOVA model to test for differences in the mean number of young fledged per nest among migrant and resident species and all sites, blocking on clutch size. The interaction of site by species type (migrant or resident) was not significant ($F = 1.84$, $df = 3, 651$, $P = 0.138$). Migrants fledged an average of 1.19 ± 1.42

young per nests and residents an average of 1.41 ± 1.45 but this difference was not significant ($F = 1.24$, $df = 3, 651$, $P = 0.267$). The main effect of site was significant ($F = 6.05$, $df = 3, 651$, $P < 0.01$). Nests at Ferriday Control, Ferriday Treatment, and Sherburne all averaged fewer young fledged per nest than Red Diamond, but none of the three differed from each other (Table 1.51.)

Table 1.50. Fates of three migrant nest types.

Fate	High open-cup N = 304	Low- Mid- height open- cup N = 237	Cavity N = 68
Success	0.51	0.45	0.65
not parasitised	0.50	0.42	0.63
parasitised	0.003	0.03	0.01
Predation	0.32	0.36	0.26
not parasitised	0.30	0.29	0.26
parasitised	0.02	0.07	0.0
Parasitism	0.07	0.20	0.01
no predation	0.05	0.13	0.01
Other/Unknown failures	0.13	0.09	0.09

Note. Values are expressed as percentages of total nests for each type.

Table 1.51. Mean number of migrant and resident young fledged per nest at each site.

Type	FC	FT	RD	SH	All Sites
Migrants	0.81	0.77	1.67	1.39	1.19
	± 1.16	± 1.13	± 1.58	± 1.48	± 1.42
	N = 131	N = 154	N = 186	N = 138	N = 609

(table con'd)

Residents	1.02 ± 1.32 N = 53	1.59 ± 1.55 N = 52	1.81 ± 1.47 N = 43	1.21 ± 1.36 N = 33	1.41 ± 1.45 N = 181
All Nests	0.87 ^a ± 1.21 N = 184	0.98 ^a ± 1.29 N = 206	1.69 ^b ± 1.56 N = 229	1.35 ^a ± 1.46 N = 171	

Note. Sites with similar letters are not significantly different. \pm = one standard deviation, N = sample size.

I categorized the migrant species by height and nest type (cavity, high open-cup, low- to mid-height open-cup), and used a factorial ANOVA model to test for differences in the mean number of young fledged per nest among types, sites, and times of nest initiation, blocking on clutch size. Only the two-way interaction of site and time of nest initiation was significant ($F = 3.83$, $df = 3, 437$, $P = 0.010$). To evaluate this interaction, I plotted the values for each site against each time of nest initiation (Figure 1.15). Early nests averaged more young fledged per nest than late nests at Ferriday Control, Red Diamond, and Sherburne. At Ferriday Treatment, late nests fledged an average of more young than early nests. The two-way interaction of type of nest by site approached significance ($F = 2.04$, $df = 6, 437$, $P = 0.059$), and I plotted the values for each type against each site to help interpret this relationship (Figure 1.16). Cavity and high open-cup nests had the largest mean number of young fledged per nest at Ferriday Control and Sherburne. At Ferriday Treatment and Red Diamond, the mean number fledged per nest in low- to mid-height open-cup nests was intermediate to the other types.

Interpretation of the main effects should be approached with caution because of the strong interactions. The main effect of type approached significance ($F = 2.92$, $df = 2, 437$, $P = 0.055$). Cavity nests had the greatest mean number of young fledged, followed

by low- to mid-height open-cup nests and high open-cup nests (Table 1.52). The main effect of time of initiation was not significant ($F = 1.63$, $df = 1, 437$, $P = 0.203$), but the main effect of site was significant ($F = 3.73$, $df = 3, 437$, $P = 0.011$). Values for each site are analogous to those presented in Table 1.51.

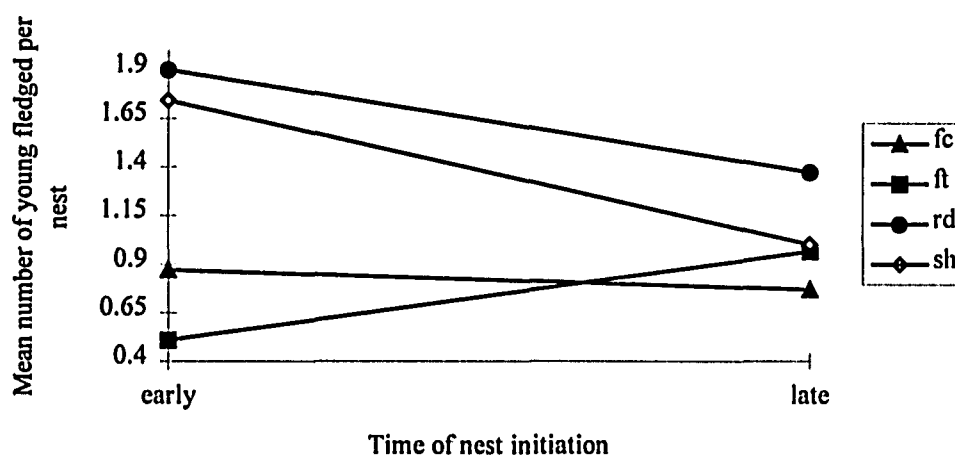


Figure 1.15. Mean number of migrant young fledged per nest at each site for nests initiated early and late.

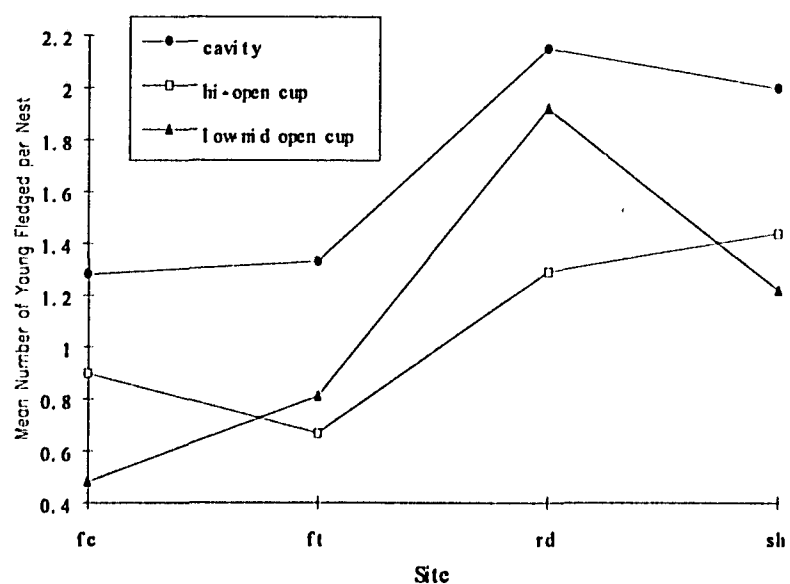


Figure 1.16. Mean number of young fledged per nest for three migrant nest types at each site.

Table 1.52. Mean number of migrant young fledged per nest by time of nest initiation and type of nest.

Variable	Mean, S.D., N
Early Initiation	1.35 ± 1.59 N = 314
Late Initiation	1.04 ± 1.19 N = 290
Cavity	1.88 ± 1.79 N = 68
High Open-cup	1.02 ± 1.17 N = 304
Low-Mid-Height Open-cup	1.21 ± 1.53 N = 237

FREQUENCY OF NEST CHECKS

I tested for differences in the mean daily survival rates of nests that were checked at 2 and 4-day intervals. For all species combined, there was no difference in the mean daily survival rate of nests checked at two (0.923 ± 0.117 , $N = 241$) or four-day (0.933 ± 0.103 , $N = 213$) intervals ($t = 0.725$, $df = 452$, $P = 0.498$).

Additionally, no species had a significant difference in mean daily survival rates between nests checked at two or four-day intervals (Table 1.53).

Table 1.53. Mean daily survival rates of nests checked at two and four-day intervals for eight species.

Species	Two-day Checking Interval	Four-day Checking Interval	<i>T</i> -test value, <i>P</i> value, degrees of freedom,
Acadian Flycatcher	0.891 ± 0.099 $N = 51$	0.900 ± 0.096 $N = 44$	$t = 1.03$ $P = 0.302$ $df = 93$
White-eyed Vireo	0.911 ± 0.121 $N = 46$	0.901 ± 0.136 $N = 37$	$t = -0.292$ $P = 0.771$ $df = 81$
Red-eyed Vireo	0.945 ± 0.096 $N = 12$	0.908 ± 0.095 $N = 13$	$t = -1.108$ $P = 0.297$ $df = 23$
Prothonotary Warbler	0.932 ± 0.139 $N = 19$	0.952 ± 0.074 $N = 25$	$t = 0.003$ $P = 0.997$ $df = 42$
Kentucky Warbler	1.00 ± 0.000 $N = 4$	0.958 ± 0.105 $N = 10$	$t = -0.867$ $P = 0.403$ $df = 12$
			(table con'd.)

Hooded Warbler	0.892 ± 0.109 N = 12	0.943 ± 0.097 N = 14	t = 1.489 P = 0.149 df = 24
Northern Cardinal	0.904 ± 0.129 N = 34	0.901 ± 0.122 N = 24	t = -0.127 P = 0.899 df = 56
Carolina Wren	0.937 ± 0.125 N = 20	0.896 ± 0.127 N = 12	t = -1.068 P = 0.294 df = 30

Note. ± = one standard deviation, N = sample size.

DISCUSSION

MIGRANT SPECIES

Site Differences

Six of eight migrant species examined had highest mean daily nest survival rates at either the Sherburne or Red Diamond site. Red Diamond had the highest rates for Yellow-billed Cuckoo, White-eyed Vireo, and Kentucky Warbler. Sherburne had the highest rates for Acadian Flycatcher, Prothonotary Warbler, and Hooded Warbler. For all species except Ruby-throated Hummingbird and Yellow-billed Cuckoo, Sherburne or Red Diamond had the second highest rates. Ferriday Treatment had the greatest mean daily nest survival rates for two species, Red-eyed Vireos and Ruby-throated Hummingbirds, but ranked third or last for all other species. The probability of nest survival was lowest at Ferriday Control for Acadian Flycatchers, White-eyed Vireos, Prothonotary Warblers, and Red-eyed Vireos. At Ferriday Control, the survival rate of Yellow-billed Cuckoo nests was second highest and for Ruby-throated Hummingbirds it was third highest. For all migrant species combined the highest daily survival rates

occurred at Red Diamond (0.942) and Sherburne (0.941) and the lowest rates occurred at Ferriday Treatment (0.893) followed by Ferriday Control (0.878).

These differences among sites tend to conform to a general pattern. Most species have a higher probability of producing a successful nest in the larger contiguous tracts of the Atchafalya Basin (Sherburne and Red Diamond) than in the smaller, more fragmented Bayou Cocodrie forests (Ferriday). Although this study was not specifically designed to test for differences from a landscape-scale perspective, it seems quite likely that factors operating at this level are responsible for the noted contrasts. In other areas of the country, larger blocks of forest have been shown to have lower rates of both predation and parasitism than smaller blocks (Wilcove 1985, Terborgh 1992). This is also the case in this study where both Ferriday sites had higher predation and parasitism rates than either Red Diamond or Sherburne. That the forest of the Ferriday Control plots remains in a fairly pristine condition (for modern-day bottomland hardwoods) cannot overcome the problems of being surrounded by a highly fragmented, primarily agricultural landscape. That the large contiguous Red Diamond forests were recently affected by one of the strongest hurricanes of this century did not seem to alter its function as a productive breeding ground for most migrant songbirds (when compared to a similar unimpacted area, Sherburne).

Why do migrant nests at the recently logged (mid-1980's) Ferriday Treatment site have higher daily survival rates than the un-cut Ferriday Control site? How can Ferriday Treatment have higher parasitism and predation rates and still have, on average, higher

daily survival rates than Ferriday Control? The answer lies in the types of nest failure. Nearly twice as many migrant nests were parasitised at Ferriday Treatment than at Ferriday Control, and in all cases I did not consider a parasitised nest lost until the host eggs or chicks were dead or missing. This increased the exposure days for these nests and led to higher Mayfield estimates of daily survival rates. The nests simply went a longer time before they failed.

The percent nest success was actually higher at Ferriday Control than at Ferriday Treatment and, as stated above, predation and parasitism rates were lower at Ferriday Control. I attribute these findings to the effects of logging on the Ferriday Treatment site. Logging roads, loader-sets (small clearings where log-trucks were loaded), and tree gaps (caused by removal of trees) all created openings in the forest that caused the site to become fragmented. Such fragmentation increases the amount of edge habitat and hence the edge-to-interior ratio. As forests become more fragmented and the ratio of edge-to-interior increases, rates of nest predation and parasitism are known to increase elsewhere (Temple 1986, Temple and Cary 1988). Thus, logging may have been detrimental to the nest success of most migrant species at the Ferriday Treatment site. That two species, Ruby-throated Hummingbird and Red-eyed Vireo, had highest daily nest survival rates at Ferriday Treatment was most likely a function of their low sample size.

To say that logging in general is detrimental to breeding birds in bottomland forests would be premature since I compared the effects of only one particular logging regime to a similar un-cut forest. The inferences from my study can only be applied to

forests cut in a similar manner as the Ferriday Treatment site. In this case, a diameter cut in which the largest trees are removed increases the amount of forest openings or gaps. These gaps, along with logging roads and loader-sets, alter vegetation structure and species composition. Differences in structure can lead to changes in bird species composition (e.g. Johnston and Odum 1956). This is exemplified by the fact that 12 Indigo Bunting nests were found on the Ferriday Treatment plots whereas none were found on the Control plots. But 33 percent of those nests were parasitised. This type of logging may increase structure favored by certain edge species, but it also adds the risk of increased predation and parasitism.

Timing of Nesting

Most migrant species breeding in these forests arrive at least by April or early May (some may come much earlier) and with little delay begin mate selection and nesting. It is apparent from the nest initiation dates that most individuals attempt two broods; an almost equal number of nests are initiated before and after June 1. This is likely due to the longer season afforded by our southern latitude. The breeding season for most migrant species in Louisiana could last for three to four months.

Because most individuals attempt two broods, is there a difference in the success rates of early and late broods and what factors are affecting this success? In seven of the eight species examined, the mean daily survival rate of early nests was lower than for late nests, the exception being the only cavity nester in the group, the Prothonotary Warbler. Early nests experienced higher rates of both predation and parasitism. I think that higher

parasitism rates earlier in the nesting season are due to timing of the reproductive biology of the Brown-headed Cowbird. Cowbirds typically lay one egg per day for an average of 30 to 40 eggs per season (Bent 1958, Scott and Ankney 1980, Holford and Roby 1993), and I have found them in host nests as early as April. With a 30 to 40 day laying period, most cowbirds finish laying by mid- to late May. There are fewer cowbirds in reproductive condition after June 1, and parasitism rates decline after this time. Of course, parasitism did not have a major affect on Prothonotary Warblers because they were seldom parasitised, and this is one reason their early nests had higher survival rates.

For example, the White-eyed Vireo, a species that I found to be a frequent host of the Brown-headed Cowbird, 28 percent of early nests were parasitised whereas only 15 percent of late nests were parasitised. Thus, in areas having problems producing enough young to sustain the population, late nests could be determining the fate of the population. At Ferriday Treatment, where parasitism rates of the White-eyed Vireo were highest, early nests fledged an average of only 0.30 young whereas late nests fledged an average of 1.44.

One species in particular, the Kentucky Warbler, does not seem to produce second clutches as regularly as most other species. Nineteen nests were initiated before June 1, whereas only four nests were initiated afterwards. This could be just an anomaly in the data if a large portion of the late Kentucky Warbler nests simply went unnoticed. I do not believe this to be the case because in most instances the ability to find the nests is linked to the birds' behavior and activities (Martin and Geupel 1993, personal observation). For

example, Kentucky Warblers were still present in June and July, and we continued to follow the birds throughout the plots looking for their nests, but in most instances the birds did not exhibit any nesting behaviors such as carrying nesting material or food, which were obvious and easily recognizable earlier in the season.

That the Kentucky Warbler typically attempts only one early clutch in bottomland hardwoods provokes several questions concerning the adaptive nature of this life history trait. The Kentucky Warbler is one of the few migrant species occurring in the bottomland forests that is an obligate ground nester. The Black-and-white Warbler (*Mniotilta varia*), the Louisiana Waterthrush (*Seiurus motacilla*), and the Worm-eating Warbler (*Helmitheros vermivorus*) are other examples of ground-nesting songbirds that breed in the state (Lowery 1974), but these species do not regularly nest in bottomland forests (J. V. Remsen pers. communication). I did not find these birds on my study sites until near the end of the breeding season, and I think that those birds were post-breeding dispersers or early fall migrants.

None of the Kentucky Warbler nests in my study were parasitised, and the predation rate was only 26 percent. These factors coupled with a larger clutch size than most species made it the most productive nester on my plots. One possible reason this species typically attempts only one clutch a year is that it may put so much energy into the first brood that it does not have the reserves for a second attempt. The cost of a first brood may be high, but the success rate makes it beneficial. If the success rate of first broods was low, then it would not be adaptive for the species to put all its resources into

one attempt and not be able to renest. The species' ground-nesting habit apparently gives it the freedom from parasitism and the higher rates of predation seen in other. It has evolved a life history strategy that works well for a ground nester but would likely not be adaptive for an above-ground, open-cup nester such as a White-eyed Vireo that suffers higher rates of parasitism and predation.

Stages of the Nesting Cycle

Seven of the eight species had lower daily nest survival rates during the incubation stage than during the nestling stage, the only exception being the Yellow-billed Cuckoo. This differential mortality suggests that either predators are more better at finding nests during incubation or that the nests are more vulnerable during this time. From my experience, adults tend to defend a nest with young more adamantly than a nest with eggs; thus, perhaps this increased nest defense increases daily survival rates at least during the nestling stage. Although I was unable to test for a difference, most nest failures during incubation occurred near the end of the stage, close to the time of hatching. Predators could have been using noises made by the young prior to hatching as cues to locate nests.

Types of Nests

Cavity nesters averaged more young fledged per nest at each site than either high or low to mid-height open-cup nesters (Figure 1.13). The daily survival rate of cavity nests was highest at each site except Ferriday Treatment, where the daily survival rate of high open-cup nests was slightly greater (Figure 1.12). At Ferriday Treatment, high

open-cup nests fledged on average the fewest young of the three groups. This contradiction concerning high open-cup nests at Ferriday Treatment (highest daily nest survival rates but lowest mean number of young fledged per nest) is again likely a function of the way daily survival rates were calculated when nests were parasitised. I did not consider the nest failed until all host eggs or chicks were dead or missing. This simply prolonged the exposure days of parasitised nests leading to higher Mayfield estimates of daily survival. Despite this fact, when considered over all sites (some with high and some with low rates of parasitism), cavity nests had the highest mean daily survival rate followed by high open-cup nests and lastly, low- to mid-height open-cup nests.

The prime factor responsible for this difference is brood parasitism. Only one cavity nest (0.012 percent) was lost to parasitism, whereas seven percent of high open-cup nests and nearly 18 percent of low- to mid-height open-cup nests were lost to parasitism (Table 1.50). Thus, Brown-headed Cowbirds are not a major factor influencing nest success of migrant cavity nesting species in these forests. Blem and Blem (1991) noted that only two of 110 Prothonotary Warbler nests were parasitised in their study in a Virginia swamp, and Petit (1989) found similar results in the first year of her study of Prothonotary Warblers in a riverine woodland in Tennessee. The size of the cavity opening can determine Brown-headed Cowbird use. Prothonotary Warblers in particular are smaller than cowbirds, and most nest-cavity openings examined seemed to

be small enough to prevent cowbirds from entering, although I have made no direct measurements to verify this.

Predation was the largest single factor affecting all nest types and was greatest in low- to mid-height open-cup nests. I think that low to mid-height nests are more vulnerable to a wider array of predators than are high nests because many high nests are placed at the distal end of small branches. These precarious nest-sites are nearly inaccessible to predators such as the raccoon (*Procyon lotor*), the Virginia opossum (*Didelphis marsupialis*), and even snakes. Cavity nesters are thought to be better protected from certain forms of predation (Ricklefs 1969) but they suffered the second highest predation rate in my study.

This study was not designed to identify nest predators, but I will attempt to speculate on probable culprits. Species noted in other studies (Roth and Johnson 1993, Patonde and White 1992) such as Raccoon, Eastern Gray Squirrel (*Sciurus carolinensis*), and various species of snakes were common on all sites. The Blue Jay (*Cyanocitta cristata*) has long been implicated as a nest predator (Lowery 1974), but this species was either not present or extremely rare at my sites. In three complete summers at both Ferriday sites, I heard or saw Blue Jays only three times. The American Crow (*Corvus brachyrhynchos*) is a known nest predator (Lowery 1974) and was fairly abundant on most sites. Although I have not found their nests at any of my study sites, I have recorded on several occasions adults feeding young that seemed to be not long out of the nest. I have found their nests in other areas of the state in March and early April, prior to

the start of my field seasons. The Red-bellied Woodpecker is also a nest predator (Conner 1974, Watt 1980, Neill and Harper 1990), and this species was the most common woodpecker on my sites (unpublished data).

Various species of rodents are suspected as potential nest predators (Blem and Blem 1991), and species such as *Peromyscus leucopus*, *P. gossypinus*, and *Neotoma floridana* were common, at least at the Red Diamond site (O'Neil 1995). Once at Ferriday Control site, I observed predation by a Wood Rat (*Neotoma floridana*) on a Carolina Wren nest that contained four 2-day-old nestlings. To what extent this occurs in bottomland forests I do not know.

RESIDENT SPECIES

Nests of resident species had higher mean daily survival rates at both Atchafalya sites than at either Ferriday site, a situation similar to that observed with migrant species. But the differences between the two Atchafalya sites and the two Ferriday sites were not as great as that seen in migrant species; this suggests that residents are not as sensitive to fragmentation effects as are migrants.

Overall, the mean daily survival rate of resident nests was higher than migrant nests. The major factor contributing to the difference among the two groups was the extent of brood parasitism. Only 1.5 percent of resident nests, all Northern Cardinals, were parasitised, whereas 11 percent of all migrant nests were parasitised. Although the rates of parasitism may vary, this difference between migrants and residents is consistent with similar studies. For example, Robinson (1992) found that the average parasitism

rate of all migrant species breeding in highly fragmented Illinois forests was 76 percent but that the parasitism rate of Northern Cardinals and Rufous-sided Towhee to be only 55 and 50 percent respectively.

Why should some species be poorer hosts than others? Ehrlich et al. (1988) suggest that some species may attack female cowbirds, or destroy or eject the foreign cowbird eggs in their nests, or they may abandon their nest when parasitised. Other researchers (e.g. Robinson 1992) have suggested that some species hide their nests better than others and are thus less vulnerable. The majority of nests of residents in my study were of two species, Northern Cardinal and Carolina Wren. Both are heavier than most migrants, and I have found that each can be aggressive in their defense of the nest. Carolina Wren nests were particularly difficult to locate, and the entrance to many was often placed on the side, giving the nest a small, domed shape that may limit access by cowbirds.

In contrast to migrant species, early nests of residents were more successful than late nests. The predation rate decreased by one percent from early to late migrant nests, but predation of nests of residents increased by 14 percent from the early to late time period. Why should migrants show practically no change in predation rates over time, but resident predation rates increase significantly ($\chi^2 = 4.24$, $df = 1$, $P = 0.04$) later in the season? Best and Stauffer (1980) also found that predation increased throughout the season in their study of riparian bird communities in central Iowa, but they did not

separate migrants from residents. Further investigation is needed to understand this observed pattern of predation.

FREQUENCY OF NESTS CHECKS

Although every effort was made to reduce disturbance near nests, no technique can claim to be 100 percent effective. Nevertheless, for each species examined, mean daily survival rates of nests checked at two- or four-day intervals did not differ significantly. Any effects caused by observers would have been the same throughout years, sites, times, etc., because similar procedures (and in most cases the same observers) were used throughout the study. Species-specific differences may have occurred, and this could have been a source of bias when comparisons among species were concerned. I would have expected this to be the case with such species as the Kentucky Warbler, a ground nester, but Kentucky Warbler had one of the highest nest survival rates of all species. It is difficult not to cause a disturbance to surrounding vegetation when checking these ground nests on a routine basis, but apparently this disturbance had little effect.

Several researchers (Schaub et al. 1992, Martin and Roper 1988, Nichols et al. 1984) have presented similar results as this study for a variety of species and different nest checking schemes. Data from these studies as well as this one indicate that with careful planning and procedure, the impact of researchers on nesting songbirds can be minimized.

MANAGEMENT CONSIDERATIONS

All species have evolved with a certain amount of predation and each species has evolved adaptive strategies that have allowed them to persist in the face of predation pressures (Endler 1991). In Ricklefs' (1969) review that included a broad range of species, he surmised that predation was the most important mortality factor affecting nests of small land birds. One can expect a certain amount of "background" predation to occur in any woodland bird community. The problem arises when, through some perturbation, the ecological balance is shifted in favor of the predators (Klopffer 1962). This seems to be the case in fragmented blocks of bottomland hardwoods.

To understand better the important predator/prey relationship, I think that a closer study of the predator community is necessary. The objective of the study should be to determine as closely as possible the identity of the predator species and the relative frequency of predation events for each species. Only when this information is determined should a decision to control the numbers of the predators be made. Indiscriminate persecution of potential predators is unwarranted and biologically unsound (Bailey 1984). If predator control is initiated, the effects on avian species should be closely monitored to determine the effectiveness of the control measures. Predator/prey relationships are often more complicated than they appear (Robinson and Bolen 1984), and any control program should be aware of potential "ripple effects" that could occur throughout the food web.

The control of the parasitic Brown-headed Cowbirds has been used to help sustain populations of certain species such as Kirtland's Warbler, Black-capped Vireo (*Vireo atricapillus*), and Least Bell's Vireo (*Vireo bellii pusillus*) (DeCapita 1993, Hayden et al. 1993, Griffith and Griffith 1993). The breeding range of each of these species is fairly restricted, and cowbird control has been focused on localized areas during the nesting season only. Technicians use bait and decoys to live-trap cowbirds, which are then euthanized. The technique has been reported to be successful in reducing the incidence of parasitism in the host species mentioned above. Hayden et al. (1993) stated that the rate of parasitism of Black-capped Vireo nests on Fort Hood Texas, was 90.9 percent in 1987 prior to trapping, and this rate decreased to 29.2 percent after three years of trapping effort. Seventy percent of the Kirtland's Warbler nests found between 1966 and 1971 were parasitised, but during the trapping period of 1972 to 1977 only 6.3 percent of all nests were parasitised (DeCapita 1993).

I do not think that this localized scale of cowbird control during the breeding season could be efficient or productive in the bottomlands of the lower Mississippi Valley. Trapping enough cowbirds to make an appreciable difference within the numerous fragments remaining in Louisiana alone would be expensive and labor intensive. I do advocate control of cowbirds on large winter roosts such as those that occur near Pine Prairie, Louisiana (Ortego 1988). This is certainly a more efficient method of control, but the effects on any given patch of forest the following season are rather diffuse. I see the potential overall advantages as significant, however. Consider

the effects of killing two million cowbirds on a winter roost, small numbers compared to some roost estimates (e.g. 20 million at Pine Prairie in 1987; Ortego 1988). In this example we will say that one half of the birds killed are females (1,000,000) and that only half of these (500,000) would have survived to breed next season. If each of these were to lay an average of only 20 eggs per season, a staggering 10,000,000 songbird nests could be affected. Even if these conservative estimates of female cowbird survival and productivity are halved, 2,500,000 nests would still likely be lost. In light of the impact this type program can have, I believe control on the winter roosts is warranted and should be pursued.

This study is the first to document landscape-scale effects that directly effect measurable values of the breeding success of migrant species in bottomland hardwood forests of the lower Mississippi River Alluvial Valley in Louisiana. What is known for other regions of the country is now verified for the bottomland hardwoods examined in this study; larger blocks of forest are better breeding sites than smaller blocks. Although it may provide some relief for nesting songbirds, cowbird and predator control address only the symptoms of a fragmented forest system and do not alleviate the main cause. The question still presents itself, "how big does a forest block have to be to ameliorate the problems associated with reduction of forest area and fragmentation?" For the highly fragmented landscape of the lower Mississippi bottomlands, I can answer that 4000 ha (roughly the size of Bayou Cocodrie N.W.R.) may not be enough, based on the high rates of predation and parasitism found at the Ferriday sites. This fact may seem somewhat

disconcerting because a recent survey (C. Loesch, unpublished data) shows that the bottomland hardwoods of Louisiana are fragmented into over 12,300 blocks, with an average block size of only 111 ha. The same study shows that for the entire Mississippi River Alluvial Valley, bottomland forest is fragmented into over 35000 blocks with the average block size being only 58 ha. If predation and parasitism rates are high in a 4000 ha block, one can predict that conditions are likely worse in an average size block of 50 to 100 ha.

I advocate preserving the larger remaining blocks and augmenting the size and shape of smaller blocks through reforestation. Existing reforestation plans, such as the Conservation Reserve Program and the Wetlands Reserve Program, should be enlisted in a comprehensive strategy aimed at restoring the size of smaller blocks. Because the vast majority of land in the lower Mississippi Valley is not publicly owned, education and assistance of private landowners must also be a priority. The functions of an intact forested wetland go far beyond that of a breeding ground for migrant bird species and as a source of income through timber harvests. Forested wetlands promote ground water recharge, act as storm buffers, perform vital nutrient cycling, enhance erosion control, and support a biologically diverse community of plant and animal species that are all a part of the natural heritage of the region (Gosselink and Lee 1989, Creasman et al. 1992).

The qualitative characteristics of the stand as well as the absolute quantity of forest must also be considered in a management scheme for migrant songbirds (Finch 1991). The case involving the older growth Ferriday Control site, which had lower

predation and parasitism rates than portions of the same forest that were selectively logged (Ferriday Treatment), is a prime example of this issue. Cutting practices that cause an inordinate number of forest gaps through excess tree removal and logging operations (roads and clearings) should not be used.

It is not reasonable to think no-cutting can be, or should be achieved. Due to the economic reasoning driving the decisions in today's world (and in our past as well), no-cutting is not an option even on most wildlife refuges. If a no-cut policy cannot be accepted, then I advocate maintaining a certain amount of core area in each forest block as a no-cut zone. These core areas should be as large as possible and be surrounded with forest blocks staggered in a long rotation cutting regime and managed with a single tree selection-cut, which more closely mimics natural disturbance factors like windthrows (Pashley and Barrow 1993). A proportion of older trees and snags should be left for the benefit of cavity-nesting species (Hamel 1992). Tree death due to old-age is a natural occurrence and should not be viewed simply as lost income.

Logging operations should be conducted after August 1 to prevent interruption of the breeding season. In any given forest tract, it is obvious that large numbers of nests will be directly destroyed or abandoned when logging activity occurs during the breeding season. We protect the populations of most all game species by not allowing harvest or harassment during their birthing or nesting seasons, and so the same logic should apply to non-game species such as songbirds. Although this proposition may not be feasible for large commercial operations, it should be instated on most refuges and wildlife

management areas, where annual timber cutting allotments are usually not large. The woods are typically driest during the months of August, September, and October, and this time period provides little conflict with existing hunting seasons.

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CHAPTER 2. ANNUAL SURVIVORSHIP

INTRODUCTION

Much research has focused recently on the decline in populations of Neotropical migrant songbirds (Robbins et al. 1989, Finch 1991, Rappole and McDonald 1994). Many studies target productivity or nest success as a measure of the viability of local populations (e.g., Robinson 1992, Sherry and Holmes 1992, Hoover et al. 1995). This demographic component is critical for understanding changes in population size and structure but is only part of the information needed to assess fully the dynamics of a population. In conjunction with productivity, estimates of survival rates are also needed to evaluate population status properly and to construct population models. Productivity measures are useful for certain purposes but do not address the concerns of complete life history patterns (Martin 1995). For example, if a high measure of productivity is obtained for a particular population, then intuitively we tend to think that the population is stable or increasing. But in reality, if the survival rates of the adults and young are sufficiently low, then the population could be decreasing. The opposite of this situation, low productivity coupled with high survivorship, can and does exist in some populations. It is the changes in the relative values of these key demographic components that determine whether populations are increasing, decreasing, or remaining stable. Productivity data are useful and needed information, but for a more complete understanding of the factors affecting populations, data on survivorship must also be included.

Obtaining accurate estimates of survival rates for migratory birds is difficult. Most methods employ some type of mark and recapture techniques. These methods first require that a relatively large sample be captured and marked. This may not be an easy task in the case of canopy-dwelling songbirds, although several methods have been described for capturing species that frequent higher levels of vegetation within the forest (Ouchley et al., in press). Estimates of survival are made by comparing the proportion of returns of marked birds to the total number of birds marked. Problems can arise in obtaining a sufficient sample of return rates if recapture data alone are used. To counter this problem, some researchers use a unique color-marking system so that individuals only have to be resighted and not recaptured to be identified (Holmes and Sherry 1992a). A tendency for some individuals (particularly young birds) to disperse and a lack of site fidelity also hamper efforts to obtain reasonable estimates of some population segments. Several sophisticated statistical models have been developed to obtain a more accurate estimation of survival rates (Jolly 1965, Seber 1965, Brownie et al. 1985). Most models require rather large sample sizes, and this often hinders their use in studies of local songbird populations.

Information detailing the survivorship in local songbird populations has received thorough treatment in several studies (e.g. Nice 1937, 1943, Lack 1966, Thompson and Nolan 1973, Nolan 1978) although most deal with only single species, not communities. A synthesis of survival rates for many species from different regions of the country has

recently been performed (Martin 1995), but most studies cited in this work dealt with individual species and did not address the avian community of a particular region.

A goal for this phase of this study was to estimate minimum survivorship for a large number of the breeding songbird species in avian communities of bottomland hardwood forests. Few data on survivorship are available for breeding songbirds in this habitat that was once the dominate ecosystem of riverine floodplains throughout the southeastern United States. Over 80 percent of the 21 million acres of pre-settlement bottomland hardwood forest in the Mississippi River Alluvial Valley have been cleared, mostly for agricultural purposes (Tiner 1984). As the area of forest area has decreased, populations of many songbird species that use bottomland hardwoods as breeding habitat have also decreased (Burdick et al. 1989). In a recent analysis by Wiedenfeld et al. (unpublished data) of Breeding Bird Survey data for the Mississippi Alluvial Plain, 77 percent of breeding bird species declined in abundance over the last 25 years. Declining species included both forest interior and edge species.

Ideally, we would like some knowledge of the values of key demographic components, such as productivity and survivorship, in these forests prior to settlement by Europeans (or at some other time in the past) in order to compare present-day values. But unfortunately, these data do not exist. This work will establish a baseline of data for future studies in these or other bottomland hardwood sites or other habitat types.

OBJECTIVES

The objectives for this phase of the study were:

- 1) Estimate "minimum survivorship" for birds breeding in selected bottomland hardwood forest study sites.
- 2) Compare estimates of minimum survivorship among different ages, sexes, sites, and residency groups (resident and migrant).
- 3) Determine dispersal distances of returning birds and compare the average distances among sexes and residency groups (residents and migrants).

METHODS

STUDY AREAS

The study was conducted at three separate field sites in Louisiana. One site, Ferriday, was in Concordia Parish at the southern end of the Tensas River Basin in northeast Louisiana. The Ferriday site is an approximately 4000-ha block of relatively mature bottomland hardwood forest. This block was formerly part of a once more extensive holding known as the Fisher Tract and is now part of the U. S. Fish and Wildlife Service's Bayou Cocodrie National Wildlife Refuge. It is approximately 13 km southwest of the town of Ferriday Louisiana, and 8 km west of the Mississippi River (91°3'W,31°3'N). Two other field sites were in bottomland hardwood forests in the Atchafalya River Basin in south-central Louisiana. The Red Diamond site is located approximately 16 km south of Ramah, Iberville Parish, Louisiana (91°3'W,31°3'N), on property owned by Dow Chemical. This site is an approximately 20,000-ha block of

relatively un-fragmented forest. An estimated 30 to 40 percent of the trees at this site were damaged by Hurricane Andrew in August of 1992 (Ouchley unpublished data). The second site in the Atchafalaya River Basin, Sherburne, is in St. Martin Parish on the Atchafalaya National Wildlife Refuge, 13 km south of Krotz Springs Louisiana (91°4'W,30°2'N). It is in an approximately 100,000 ha-block of forest that sustained minimal (estimated less than 10 percent) damage in the 1992 hurricane.

FIELD METHODS

Two 10-ha plots were established at the Ferriday site in spring 1992, and two additional 10-ha plots were added in spring 1993. Two 10 ha-plots were established at both Red Diamond and Sherburne in spring 1993. The locations of the plots were randomly chosen within the study sites, and all plots were 250 by 400 m. Each plot was marked in a 50-meter-square grid pattern. Field work was conducted at the Ferriday site during spring and summer 1992-1994 and at Red Diamond and Sherburne during spring and summer 1993-1994.

Mist-nets were used to capture birds for banding and for determining age and sex. Netting started at the beginning of each field season (around the third week in April) and continued daily until the first week of August. Nets were 12 m long, and an even number of 30- and 36-mm-mesh nets were used at each plot. Nets were opened shortly after daylight and were normally closed by 1400.

On half of each 10-ha plot, 10 mist-nets were deployed in every other 50-m-square block. After 3 to 4 days netting, nets were moved to the other half of the 10-ha

plot and deployed in a similar manner. The nets were moved back after 3 to 4 days, but were then placed in 50-m blocks that were not covered the first time. This "checkerboard" rotation of nets was continued throughout the field season at each site. Within each 50-m block, nets were placed in the best position to capture birds (i.e. shade, cover, etc.) and were not placed at random. Tape play-backs and decoys of mounted birds were occasionally used.

Birds were banded with aluminum U.S. Fish and Wildlife Service bands and with plastic color bands in a scheme unique to each individual. The sex and age of all birds were determined when possible; the date, location of capture, bird weight, wing chord, and any other pertinent information (e.g. brood patch, cloacal protuberance) were also recorded.

In addition to daily netting, field workers systematically searched each plot daily and recorded sightings of banded birds. One worker was assigned to half of a 10-ha plot each day, and workers were rotated through the plots to ensure equal coverage by all persons. Data concerning the species, sex, location, and activity (e.g. carrying nesting material, feeding young) of banded birds were recorded.

DATA ANALYSIS

The number of banded birds that were re-sighted or recaptured the following year was tallied for each site. I refer to the percentage of recaptured and re-sighted birds as the return rate. I used the Chi-square test of homogeneity to test for significant differences in the return rates of: 1) migrant and resident species; 2) males and females; 3) hatching

year (HY) and after hatching year (AHY) birds at each site. I tested for differences in return rates among individual species at the Red Diamond and Sherburne sites. Due to small sample sizes at Ferriday, I was unable to test for differences among individual species.

For individuals recaptured or resighted in successive years, the distance between the original point of capture and the point of recapture or resighting the following year was calculated. I used the smallest distance when an individual had multiple recaptures or resightings at different points. I used t-tests to compare the average annual movement distances among all migrant and all resident species. I also used t-tests to compare the average annual movement distances among all males and all females.

RESULTS

INDIVIDUAL SITE RATES

Ferriday

Data from both Ferriday sites were combined because of small sample sizes. The return rate of resident and migrant species averaged 0.16 but did not differ between groups (Figure 2.1). The return rate of resident females and males was 0.28 and resident females returned at twice the rate of migrant females. Migrant males also returned at twice the rate of migrant females; resident and migrant males returned at the same rate.

The return rate of after hatching year (AHY) birds at Ferriday was over twice as great as that of hatching year (HY) birds (Figure 2.2). The return rate of migrant and resident HY birds averaged 0.05 but the difference was not significant. The return rate of

resident and migrant AHY birds averaged 0.15 and the difference between groups only approached significance ($P = 0.06$). The return rate of resident AHY birds was 2.6 times greater than the rate of resident HY birds, and migrant AHY birds returned at a 5 time greater rate than migrant HY birds.

Sherburne

Resident species at Sherburne returned at almost the same rate as migrant species (Figure 2.1). There was no difference in the return rate of resident males and females and there was no difference in the return rate of resident and migrant females or resident and migrant males. However, the return rate of migrant males was over twice as great as that of migrant females.

The return rate of AHY birds at Sherburne was almost 4 times as great as the rate of HY birds (Figure 2.2). The return rate of migrant AHY birds was over 3 times greater than the rate of migrant HY birds and the return rate of resident AHY birds was 5.5 time greater than that of resident HY birds. There was no difference in the return rate of resident and migrant HY birds or resident and migrant AHY birds.

Red Diamond

Migrant birds at Red Diamond returned almost twice as often as resident birds. Resident males and females returned at a rate of 0.15. The return rate of migrant males (0.33) was greater than the rate of migrant females (0.22). Resident and migrant females returned at an average rate of 0.185 and there was a difference between the groups. The return rate of migrant males was over twice that of resident males.

AHY birds returned twice as often as HY birds (Figure 2.2). Resident and migrant HY birds returned at equal rates but migrant AHY birds returned over twice as often as resident AHY birds. There was no difference in the return rate of HY residents and AHY residents but AHY migrants returned 2.6 times more often than HY migrants.

TRENDS AMONG SITES

Migrant species return rates were similar to those of residents at Ferriday and Sherburne, but residents at Red Diamond returned significantly less often than migrants. Resident females and males returned at similar rates at all three sites, but migrant females returned at significantly lower rates than migrant males at all three sites (Figure 2.1).

Return rates for HY birds were lower than for AHY birds at all sites. There was no difference in the return rates of HY migrant and HY resident species at all three sites. The difference in AHY migrant and resident return rates varied at all three sites. At Ferriday, AHY residents returned at a higher rate than migrants, at Red Diamond, AHY residents returned at a lower rate than migrants, and at Sherburne the rates were equal (Figure 2.2).

INDIVIDUAL SPECIES RATES AT SHERBURNE AND RED DIAMOND

I tested for differences in return rates between the Red Diamond and Sherburne sites for the most commonly captured species. There were no differences in the return rates of any migrant species between the Red Diamond and Sherburne sites (Table 2.1). Return rates ranged from a low of 0.028 for American Redstarts at Red Diamond to a high of 0.357 for Prothonotary Warblers at Red Diamond. Return rates of the two resident species, Carolina Wren and Northern Cardinal, were both lower at the Red

Diamond site. The return rate for Carolina Wrens at Sherburne was twice as high as that of Red Diamond. The Northern Cardinal return rate at Sherburne was over four times greater than that of Red Diamond.

The return rate of Prothonotary Warblers at Red Diamond was greater than the rate of all other species at Red Diamond except Hooded Warblers (Tables 2.1 and 2.2). The return rate of Prothonotary Warblers at Sherburne did not differ from the rates of any other species at Sherburne except for Kentucky Warblers. Prothonotary Warblers returned at almost twice the rate of Kentucky Warblers.

For all migrant species combined, the return rate at Sherburne and Red Diamond did not differ (Table 2.3). The combined return rate for all resident species at Red Diamond was over twice as great as the rate at Red Diamond.

ANNUAL RETURN DISTANCES

Migrants (including males, females, and birds of unknown sex) returned to an average distance of 111.4 m ($N = 20$) from the location where captured the previous year. Residents (including males, females, and birds of unknown sex) returned at an average distance of 179.8 m ($N = 30$) from the previous year. The difference between residency groups only approached significance ($t = -1.47$, $df = 45.8$, $P = 0.07$). Female and male residents averaged a return to within 167 m (female average = 138.7 m $N = 12$, male average = 195.1 m, $N = 8$) This difference was not significant ($t = -0.44$, $df = 7.7$, $P = 0.33$). Male migrants averaged 93.3 m ($N = 12$) and females averaged 234.2 m ($N = 3$) but tests were not performed because of a small sample size of returning females.

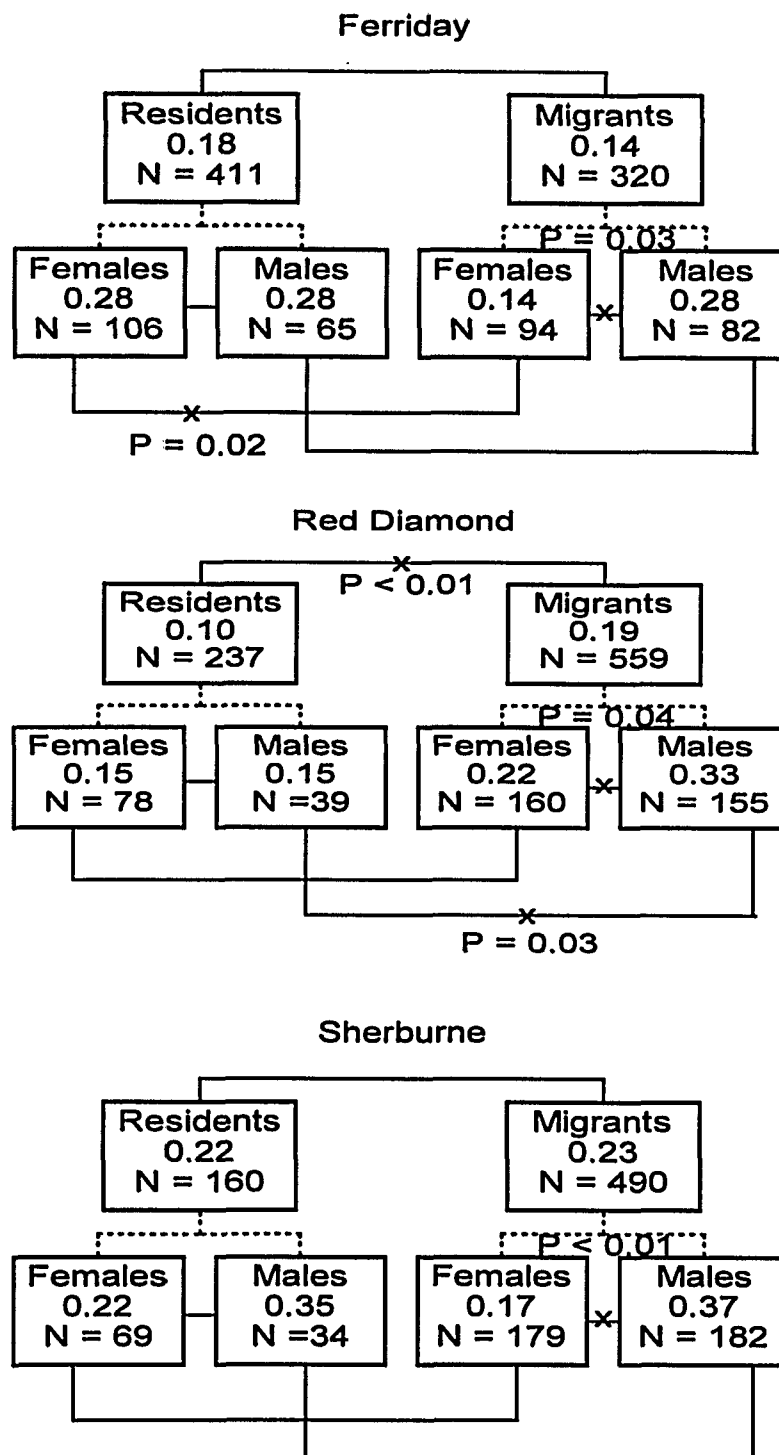


Figure 2.1. Return rates of male and female migrant and resident species at both Ferriday sites, Red Diamond, and Sherburne. Note: Significant differences denoted by *P*-values.

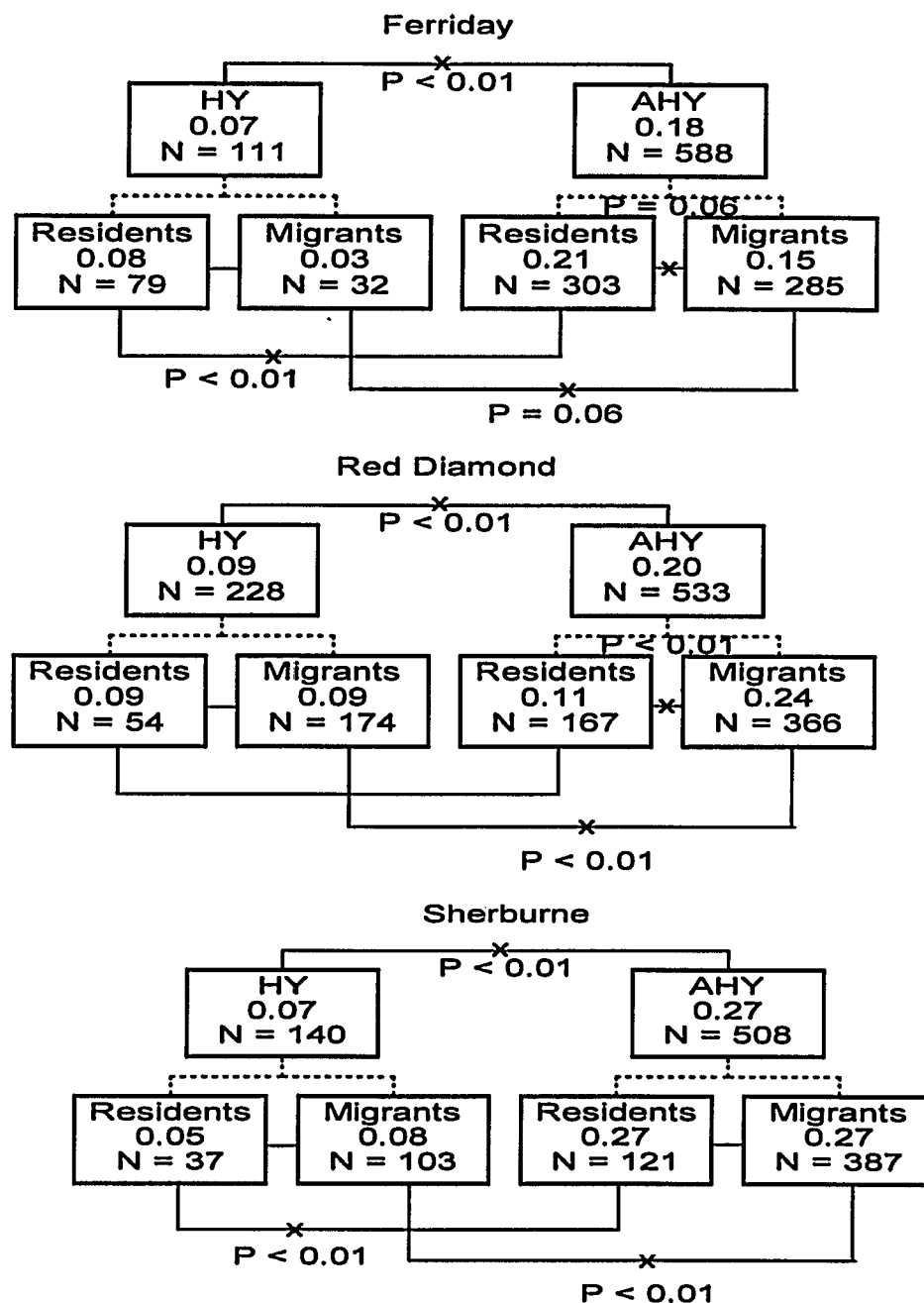


Figure 2.2. Return rates of hatching year and after hatching year migrant and resident species at both Ferriday sites, Red Diamond, and Sherburne. Note: HY = Hatching year, AHY = After hatching year. Significant differences denoted by *P*-values.

Table 2.1. Annual return rates of most commonly captured migrant and resident species at Red Diamond and Sherburne and results of Chi-square tests between sites.

Species	Red Diamond	Sherburne	¹ Chi-square, <i>P</i> -value
Acadian Flycatcher	0.148 N = 53	0.235 N = 49	1.29 0.26
American Redstart	0.028 N = 35	*	*
Hooded Warbler	0.225 N = 77	0.241 N = 56	0.05 0.82
Kentucky Warbler	0.095 N = 91	0.168 N = 87	2.20 0.14
Prothonotary Warbler	0.357 N = 97	0.303 N = 66	0.52 0.47
Red-eyed Vireo	0.149 N = 93	0.253 N = 88	3.11 0.08
White-eyed Vireo	0.194 N = 71	0.273 N = 86	1.34 0.25
Carolina Wren	0.108 N = 130	0.206 N = 96	4.30 0.04
Tufted Titmouse	0.107 N = 28	*	*
Northern Cardinal	0.073 N = 67	0.307 N = 38	10.17 <0.01

¹ All Chi-square tests have one degree of freedom. * Indicates no tests made due to small sample sizes.

Table 2.2. Results of comparison of Prothonotary Warbler return rates at Red Diamond and Sherburne with other common species at each site.

	<u>Red Diamond</u>		<u>Sherburne</u>	
	χ^2	<i>P</i>	χ^2	<i>P</i>
Acadian Flycatcher	7.49	< 0.01	0.28	0.41
American Redstart	14.10	< 0.01	*	*
Carolina Wren	20.67	< 0.01	2.05	0.15
Hooded Warbler	3.67	0.055	0.59	0.44
Kentucky Warbler	18.87	< 0.01	3.92	0.04
Northern Cardinal	17.65	< 0.01	0.01	0.96
Red-eyed Vireo	10.94	< 0.01	0.49	0.48
Tufted Titmouse	6.46	0.01	*	*
White-eyed Vireo	5.35	0.02	0.17	0.68

Note: All Chi-square tests have one degree of freedom. Sample sizes included in previous table. * Indicates no tests made.

Table 2.3. Annual return rates of all migrant and resident species at Red Diamond and Sherburne and results of Chi-square tests among sites.

Type of Species	Red Diamond	Sherburne	¹ Chi-square, <i>P</i> -value
Migrant	0.185 N = 559	0.220 N = 490	2.04 0.15
Resident	0.096 N = 237	0.221 N = 160	12.64 < 0.01

¹ All Chi-square tests have one degree of freedom.

DISCUSSION

FACTORS AFFECTING SURVIVORSHIP ESTIMATES

The annual survival rate of small landbirds is generally reported to be between 20 and 60 percent (e.g. Ricklefs 1973, Gill 1992, Holmes and Sherry 1992a). Rates in this study were characteristically low and ranged from 9.5 to 35.7 percent. At least three

factors may have contributed to these low rates. 1.) The birds returned to the study sites but were simply not recaptured or resighted. 2.) The birds survived but did not return to the study sites, i.e. they dispersed. 3.) The annual mortality of birds breeding at these sites is higher than other previously reported sites.

I do not believe the first factor greatly affected the estimation of survivorship. The location of most nests were known as well as the identity (or at least banded status) of the parents. The majority of nests were found during the early stages of the nesting cycle. No doubt certain nests and individuals escaped detection, but from the amount of observer and net coverage given to each 50 m block, I believe that these were only a small part of the overall population.

The second factor, dispersal, may have played a larger role in the ability to estimate survivorship. The search and netting efforts were confined totally to the 10 ha study plots. If an individual returned but stayed just off the plots, then it would not have been recorded. This is highly likely for individuals that had territories the previous year just inside the plot edge. However, the probability of dispersing in any direction may be equal. It should also be stressed that the dispersal distances reported in this study are only for individuals that returned to the plots and the size of the plots limits the maximum distance a dispersal event can be recorded. Because of this, it is the patterns of return rates and distances that should be stressed and not the absolute values reported.

Other workers have attempted to document annual dispersal events. Nolan (1978), working with the Prairie Warbler (*Dendroica discolor*), showed that territory

centers of returning birds tended to shift from year to year. Twenty-seven percent of the returning males in his study relocated to a new territory an average distance of 710 m from the previous years' territory. Holmes and Sherry (1992a) showed that the territory centers of returning male American Redstarts and Black-throated Blue Warblers (*Dendroica caerulescens*) may move as much as 617 and 501 m, respectively. In this study, for all migrant species combined, the average return distance from the previous year's location was 111.4 m; for all resident species combined, the average distance was 179.8 m. In both Nolan's (1978) and Holmes and Sherry's (1992a) studies, the annual dispersal distance of females was greater than males. The same pattern was also true for migrant species in this study, but in resident species, the average annual dispersal distance of females was less than males. Based on these findings, the survival estimates may also be biased among the sexes. In essence, just because an individual isn't recorded the following season doesn't necessarily mean it has died. In light of this, the estimates in this study (and most others) should be viewed as "minimum survivorship." I advocate systematic searches within a fixed zone outside the perimeter of the study area to facilitate re-sightings of marked birds that have dispersed. Radio telemetry could greatly enhance the ability to locate dispersed birds, but the current level of technology is such that the size of these instruments precludes their use on small songbirds for any extended period of time.

The third factor, higher annual mortality rates for birds use these study sites than those reported in other areas of the country, is more difficult to assess. Assuming that the

majority of the problems associated with factors 1 and 2 could be adequately addressed, such issues as differential survival on the wintering grounds or during migration would come in to play. Do the migrant species breeding in bottomland forests of the Lower Mississippi River Valley in Louisiana winter in different areas than other populations of the same species? Remarkably little is known concerning this matter. As Holmes and Sherry (1992a) stated "There is essentially no information on how breeding populations for any migratory species settle in winter areas and vice versa." We know broad regions where a species may overwinter (e.g. Pashley 1988, Ehrlich et al. 1988) but data on local populations is unavailable. Until this question can be answered, we will not be able to fully understand the year-round ecology of these species.

In this study, survivorship varied among individual species, groups of species (migrants and residents), sites, ages, and sexes, but in many cases certain patterns were evident. In the following sections, I will discuss the results pertaining to these categories.

SEX DIFFERENCES

Female migrants returned at a significantly lower rate than male migrants at all three sites (see Figure 2.1). Values for males ranged from 37 to 28 percent and for females from 22 to 14 percent. These findings are similar to those of other studies. In New Hampshire, 30 percent of all color-banded male American Redstarts returned as opposed to 19 percent of the females (Holmes and Sherry 1992a). In the same study, 39 percent of the male Black-throated Blue Warblers and 35 percent of the females returned. Walkinshaw (1953) found that 50 percent of the male and 20 percent of the female

Prothonotary Warblers returned to his sites in Michigan. In Nolan's (1978) classic study of the Prairie Warbler in southern Indiana, 60 percent of the males and 19 percent of the females returned. Berger and Radabaugh (1968) reported the return rate for male and female Kirtland's Warblers was 53 and 31 percent, respectively. Eleven percent of the male and none of the female Yellow-breasted Chats (*Icteria virens*) returned in Thompson and Nolan's (1973) study.

Differences in return rates of male and female resident species were not as evident. Resident females returned at the same rate as males at two sites and less than males at one site. Values for females ranged from 15 to 28 percent and for males from 15 to 35 percent. Researchers have found higher female mortality in bird species, although the literature concerning sex differences for resident North American passerines is scant. Cody (1971) stated that female House Sparrows (*Passer domesticus*) suffered higher mortality than males. Perrins (in Ricklefs 1973) found that female Great Tits (*Parus major*) (in Britain) had a higher mortality rate than males.

Several explanations have been given for differences in survival rates of males and females, most relating to the greater energetic cost and exposure incurred by females during reproduction. Ricklefs (1973) stated that survivorship of females is usually lower "because of the strain imposed by reproductive activities." Indications of this added strain can be found throughout the nesting cycle. For example, females in this study perform all or most of nest construction, clearly an energetically taxing duty. The energetic cost of producing eggs is certainly greater than that required to produce sperm

(Clutton-Brock and Godfray 1978). The energetic costs of egg care are relegated almost entirely to females. The amount of heat transfer required during incubation ranges from 10 to 30 percent of the basal metabolic rate in passerines (Ricklefs 1974). During incubation, females usually forage less often than males (Gill 1992), although I have witnessed supplemental feedings of nesting females by their mates, usually during later stages of incubation. Brooding is typically done by the female but feeding of the young was shared by both adults for all species in this study. The energetic cost of providing food for nestlings can be as high as four times the adult basal metabolic rate (Clutton-Brock and Godfray 1978), and this energetic cost is added to those previously experienced by females.

Increased exposure to predators during nesting is another idea advanced to explain higher female mortality (Gill 1992). Females are more closely allied to the nest than males during incubation and brooding and this is thought to make them more susceptible to predators. The mortality of nesting females is well documented in some waterfowl species (Belrose 1976), but little information is available for most passerines.

Countering this idea, Ricklefs (1973) stated that "In many dimorphic species, the easier role of the male in reproduction appears to be more than offset by his greater conspicuousness to predators (and hunters), and perhaps to deaths either directly or indirectly related to aggressive encounters with other males".

Both of these ideas concerning predation of nesting birds have merit. Further insight should be gained by continuing studies of marked populations. The hazards

incurred during migration have been often discussed (Bent 1953, Moore and Kerlinger, 1987), but little is known concerning mortality of adult North American passerines during the breeding season.

The observed difference in return rates of males and females could also be affected by a greater propensity for females to disperse (Greenwood and Harvey 1982, Jackson et al. 1989). Saturation of local habitat may influence this decision. This concept is based on the idea that males are more constrained than females because they are primarily responsible for establishing a territory, and familiarity with a given area could enhance the ability of a male to defend his territory. Drilling and Thompson (1988) stated that it is presumably easier and more advantageous for males to reestablish previous territories than to obtain new territories, so they are more site-faithful. Also, females may have a greater probability of dispersing between years because they are more likely to find a new site with an unpaired male (Jackson et al. 1989). Furthering these ideas, Greenwood (1980) proposed that because most birds have a resource-based mating system, males should exhibit greater site-fidelity because males typically defend a fixed resource, such as a territory or a nest site. Drilling and Thompson (1988) added that females, in contrast, "do not defend a fixed resource and have the flexibility to move and find the best mate or nest site, or both." Further discussion on the dispersal differences of males and females is continued in the next section with particular emphasis given to prior nesting success. The information contained in that section is equally applicable to this one.

Differences in the over-winter survival of males and females could also explain the differences in breeding season return rates. Both sexes of many species may hold winter territories (Greenberg 1986, Morton et al. 1987, Morse 1989), and segregation of the sexes based on habitat has been documented. Lynch et al. (1985) found that wintering female Hooded Warblers in the Yucatan Peninsula of Mexico occupied open, low vegetation areas, whereas males occupied closed-canopy forests. Woods (1975) reported that wintering female Black-throated Blue Warblers in Haiti were most abundant in montane areas, whereas males were most abundant in lowland forests. In Puerto Rico, Wunderle (1992) found that female Black-throated Blue Warblers were most common in the shrub-sapling stage forests at high altitudes, whereas males were most common in the older and taller forests at lower elevations. If males out-compete females for optimum wintering habitat (better food resources and protection from predators), differential winter mortality could affect annual return rates on the breeding grounds. Whether these winter habitat segregations actually confer higher over-winter survival is yet to be determined.

SITE DIFFERENCES

In a study similar to this one, Robinson (1992) evaluated the nesting success and survivorship of birds breeding in fragmented bottomland hardwoods in southern Illinois. He reported the following percent returns for migrant species nesting in small forest blocks: Great Crested Flycatcher 9.5, Acadian Flycatcher 16.7, Red-eyed Vireo 0.0, Kentucky Warbler 18.2, Wood Thrush 19.2. For the eleven most common migrant species combined, the average return rate was 15 percent.

The most fragmented site in this study, Ferriday, had a return rate for all migrant species of 14 percent; this was similar to Robinsons' (1992) study. In the larger, contiguous forest blocks, Sherburne and Red Diamond, the return rates for all migrant species combined were 23 and 19 percent, respectively.

Several possibilities could explain the differences in return rates found in these study sites. First, survival of the adults could be lower in smaller blocks due to increased predation rates. Fragmentation and increased edge favor a higher concentration of predators (Wilcove 1985, Finch 1991). Not only do these predators prey on nests, but many are skilled at taking adult birds as well. Another possible explanation for higher return rates in larger blocks could be the relationship of nest success and site fidelity. Nest predation and parasitism were highest at the Ferriday site and lowest at Red Diamond and Sherburne. One line of current thought is that successful breeders are more likely to return to the same location the following year (Greenwood and Harvey 1982, Morse 1989). Several studies have examined return rates in relation to the previous year's nesting success but results have varied among species and among sexes of the same species. Holmes and Sherry (1992a) found no difference in the return rates of successful and unsuccessful male or female American Redstarts or Black-throated Blue Warblers. Payne and Payne (1993) found that unsuccessful male Indigo Buntings were more likely to move their territories the following year than were successful males. However, successful female Indigo Buntings were just as likely to disperse as unsuccessful females. Forty-seven percent of the successful female Prairie Warblers returned in Nolan's study

(1978) as compared to only 17 percent of the unsuccessful females. The return rates of successful and unsuccessful male Prairie Warblers did not differ. Darley et al. (1977) reported that the return rate of successful male Gray Catbirds (*Dumetella carolinensis*) was greater than that of unsuccessful males, but there was no difference in the return rate of females. Drilling and Thompson (1988) found there was no significant difference in the proportions of male or female House Wrens (*Troglodytes aedon*) returning when analyzed according to the previous years nesting success.

Increased predation in smaller blocks and increased site fidelity of successful nesters are interrelated and could be possible explanations for the differences in survivorship among sites. Further research is required to test these ideas in bottomland forests.

MIGRANTS VS. RESIDENTS

At Red Diamond, the return rate of migrants was greater than that of residents, but the rates did not differ at Sherburne. At the Ferriday site, residents had a higher return rate than migrants (Figure 2.1).

Greenberg (1980) analyzed the differences in return rates of migrant and resident species from data compiled in 34 studies. He found that "the migrant group had a significantly greater adult survivorship than the resident group." Martin (1995) compared survival rates among residents, short-distance migrants, and Neotropical migrants and found a "lack of differences" in survival rates among migratory classifications. He

concluded that more intensive color-banding studies are needed to understand demographic differences among migratory classifications.

Migrants returned at similar rates at Red Diamond and Sherburne, but the return rate of residents at Red Diamond was lower than at Sherburne (Table 2.3). It is possible that the difference in resident species return rates was caused by the hurricane that affected Red Diamond in August 1992. Banding began in spring of 1993, and returns rates were based on birds recaptured or resighted the following year. This implies a delayed reaction of the resident bird community to the hurricane. Cumulative changes in the habitat structure, a decrease in over-winter food supply, or increased over-winter predation may have caused greater dispersal and increased mortality of residents at Red Diamond. The migrant community would not have been subjected to the winter season changes brought about by the hurricane. The similarity of migrant return rates at the damaged and undamaged sites supports the idea of over-winter problems (i.e. decreased quality of habitat or food) incurred by resident species.

AGE DIFFERENCES

HY birds returned at a lower rate than AHY birds at all three sites. This trend was significant ($P < 0.05$) for both migrants and residents at all sites except Red Diamond (Figure 2.2). I was unable to determine accurately the sex of most HY birds, and therefore no data are available for comparisons among sexes and ages.

A low return rate of nestling songbirds to their natal site (philopatry) is consistent with the general pattern noted in other studies. However, the return rate of 7 to 9 percent

in this study was higher than that at most other studies. Walkinshaw (1953) banded 138 nestling Prothonotary Warblers, of which only two (1 percent) were found in subsequent years. Thompson and Nolan (1973) banded 39 nestling and 15 juvenile Yellow-breasted Chats, and none returned to their Illinois study site. Payne and Payne (1990, 1993) banded "more than 2600 nestlings (Indigo Buntings) that survived to fledge", and 138 (\approx 5 percent) returned to their study sites in Michigan. In Nolan's (1978) Prairie Warbler study, 10 of 272 (3.7 percent) young that left the nest returned to his study sites. Drilling and Thompson (1988) banded 6299 House Wren nestlings in Illinois, and only 176 (2.8 percent) returned. In Roth and Johnson's (1993) 10-year study of a Wood Thrush population in Delaware, five percent of all banded fledglings returned. None of the fledgling Acadian Flycatchers banded in Mumford's (1964) or Walkinshaw's (1966) studies in Michigan returned. Over a 5-year period, only 1 of the 161 (0.6 percent) banded nestling American Redstarts returned to Holmes and Sherry's (1992b) study area in New Hampshire.

The reason birds banded as nestlings in this study returned at higher rates than those reported in other studies is unclear. The higher return rates could be due to differences in methodologies, although most studies listed above employed similar methods, such as individual color-marking. All of the above studies were conducted in more northern areas of the country than this one. It is possible that a latitudinal gradient in philopatry exists; however, little evidence is currently available to support this idea.

None of the above studies were conducted in bottomland hardwood forests and the differences could be habitat related.

SPECIES DIFFERENCES

Return rates varied among species at each site and among different sites. One notable case involved the return rates of Hooded Warbler and Prothonotary Warbler at the Red Diamond and Sherburne sites. The return rates of most all species except Prothonotary and Hooded warblers were lower at Red Diamond than at Sherburne. I attribute this to the damage caused by Hurricane Andrew at the Red Diamond site. Prothonotary and Hooded Warblers were not as affected or actually benefited by the alteration of habitat at Red Diamond. Numerous hollow trees and limbs were broken off in the storm, creating an increase in potential cavity sites for Prothonotary Warblers. Several authors (Blem and Blem 1991, Petit 1989, Martin 1992) have indicated that one of the prime factors limiting this species during breeding season may be the availability of natural cavities. Hooded Warblers are known to frequent fallen tree tops and the increased vegetation associated with tree-fall gaps for both foraging and nesting (Rappole and Warner 1980, Mossman and Lange 1982, Barrow 1990). This quantity of this type of habitat was increased due to the storm damage. Changes in forest structure may have been detrimental for some species and beneficial to others. The different response of Prothonotary and Hooded Warblers from most other species at Red Diamond and the lack of difference at Sherburne seems to support this idea. The return rates of Prothonotary and Hooded warblers were not abnormally high, but the return rates of most other species

were low. Storm damage likely decreased or limited the breeding habitat of some species and they did not return.

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CHAPTER 3. NEST-SITE HABITAT

INTRODUCTION

Studies involving habitat selection have played a major role in expanding the ecological, behavioral, and physiological knowledge of bird species (Cody 1985). Researchers have long recognized that species tend to segregate into different habitats. As advancements in study methods progressed, the understanding of species-habitat relationships followed. MacArthur and MacArthur (1961) showed that bird species diversity and habitat structure are linearly related. Their work demonstrated the importance of structure to habitat selection of birds. Later work by other researchers (James 1971, Anderson and Shugart 1974, Willson 1974, Whitmore 1975) demonstrated the use of multiple habitat variables in defining the structural characteristics related to species use and occurrence.

Structure or physiognomy is a key element in habitat selection of birds but this concept can also be expanded to include a floristic component. It is well known that some bird species select certain plant species as key components in their habitat. In North America, the Red-cockaded Woodpecker (*Picoides borealis*) is dependent on, and apparently can only survive in, mature stands of pine (Ligon 1970, Chamberlain 1974). Breeding Kirtland's Warblers (*Dendroica kirtlandii*) are known to be almost entirely dependent on young stands of jack pine (*Pinus banksiana*) (Mayfield 1960). In the new world tropics, several species of hummingbirds are closely coadapted to specific nectar-producing plant species (Cody 1985). Thus, it is important that structure and floristics

both be considered when attempting to understand the patterns of avian habitat use and selection.

Breeding habitat, the focus of this study, can be described at different scales and according to different uses. Researchers have focused on habitat characteristics of territories (e.g., Conner et al. 1986, Steele 1992), nest patches (habitat within 5 to 10 m of the nest) (e.g., MacKenzie and Sealy 1981, Clark et al. 1983), and nest-sites (habitat within 1 to 2 m of the nest) (e.g., Martin and Roper 1988, Martin 1993, 1995). In this study, I have examined the habitat characteristics at nest-sites of birds breeding in bottomland hardwood forests of Louisiana. Habitat at the nest-site can serve to protect the adult and eggs or young from predation, shield the nest from the view of brood parasites such as the Brown-headed Cowbird (*Molothrus ater*), and provide a micro-climate favorable to adults, eggs, and nestlings (Cody 1985, Martin 1992, Hoover et al. 1995). Few quantitative data have been presented on the habitat characteristics at nest-sites in this forest type. It is hoped that the results from this study may be used to formulate habitat management plans for these species.

OBJECTIVES

The objectives for this phase of the study involved determining if the birds selected for particular aspects of their nest-site habitat. This was done by comparing habitat at nest-sites for each of the most common avian species with sites chosen at random.

The specific objectives were to:

- 1). Document nest-site microhabitat characteristics for each of the most common avian species.
- 2). Determine if differences existed in nest-site microhabitat characteristics and sites chosen at random.
- 3). Determine if there was a difference in nest plant species chosen and those available.
- 4). Determine if there was a difference in nest-site microhabitat characteristics of successful and unsuccessful nests.

METHODS

STUDY AREAS

Four study sites were examined in two major study areas, all were in bottomland hardwood forest of the Lower Mississippi River Valley (LMRV) in Louisiana. The other two study sites, Ferriday Control and Ferriday Treatment, were located in northeast Louisiana at the southern end of the Tensas River Basin in Concordia Parish. Two study sites, Red Diamond and Sherburne were located in the Atchafalaya River Basin in south-central Louisiana.

Both Ferriday sites are located in a 4000 ha block of forest that is now included in the Bayou Cocodrie National Wildlife Refuge. These sites are 13 km southwest of the town of Ferriday, Louisiana, and 8 km west of the Mississippi River (91°3'W, 31°3'N). The Ferriday Control site is in an approximately 500 ha stand of older-growth forest (within the 4000 ha block) that was last lightly select-cut in the late 1920's and early

1930's. The Ferriday Treatment site is in the same forest, but in an area that was again select-cut in the early 1980's. The Ferriday Treatment site is adjacent to the Ferriday Control site and remained part of the same uncut stand until the 1980's. In the early and mid-1980's, logging crews performed a diameter type of select-cut in which the majority of trees above a 60 cm diameter were removed. This type of silvicultural practice removed many of the larger, mature trees from the stand.

The Red Diamond site is located approximately 16 km south of Ramah, Louisiana, in Iberville Parish (91°3'W, 31°3'N) on property owned by Dow Chemical. This site is in an approximately 20000 ha block of relatively un-fragmented forest. An estimated 30 to 40 percent of the trees at this site were damaged by Hurricane Andrew in August of 1992 (K. Ouchley unpublished data). The second site in the Atchafalaya River Basin, Sherburne, is located in St. Martin Parish on the Atchafalaya National Wildlife Refuge, 13 km south of Krotz Springs, Louisiana, (91°4'W, 30°2'N). It is in an approximately 100,000 ha block of forest that sustained minimal (estimated less than 10 percent) damage in the 1992 hurricane.

Two 10-ha study plots were selected at random at each study site. All plots were 250 x 400 m and each plot was marked with a 25 m grid system.

The top five tree and shrub species in descending order of relative abundance (as determined from random samples) at both Ferriday sites were deciduous holly (*Ilex decidua*), sugarberry (*Celtis laevigata*) (known in this region as hackberry - the name used in this study), green ash (*Fraxinus pennsylvanica*), willow oak (*Quercus phellos*),

and American elm (*Ulmus americana*). The first four species each comprised between 10 and 13 percent of the total sample and American elm comprised 9 percent of the total sample. At the Sherburne site, box elder (*Acer negundo*), hackberry, deciduous holly, American elm, and sweet gum (*Liquidambar styraciflua*) were the five most abundant species. Box elder and hackberry each comprised between 25 and 30 percent of the total sample. Deciduous holly and American elm each comprised 10 percent of the total sample and sweet gum made up 6 percent of the total. Red maple (*Acer rubrum*), box elder, sweet gum, deciduous holly, and hackberry were the most abundant species at the Red Diamond site. Red maple and box elder comprised 22 percent each, sweet gum comprised 17 percent, deciduous holly comprised 13 percent and hackberry made up 7 percent of the total sample.

FIELD METHODS

Field workers searched for nests each day at each site from the third week in April to the first week in August. Once a nest was found, its location was marked with flagging placed in a specific pattern near the nest. The location, species, nest number, and description were written on the flagging. Nests were visited periodically (2 to 4 days) to determine the outcome. I considered a nest successful if at least one young of the host species fledged (Martin and Li 1992).

I measured microhabitat variables associated with nests at all sites during the 1993 and 1994 field seasons. To avoid disturbing the nesting birds, I only made measurements immediately after the nests had fledged or failed. I was able to visit most

nests within 1 week of the fledge/fail date, but in a few instances, the nests were totally missing due to predation or weather, and no measurements were taken.

Microhabitat variables that I measured at each nest, when applicable were: plant species -- species of plant supporting the nest; plant height -- height of supporting plant; plant d.b.h. -- diameter at breast height of supporting plant; nest height -- height of nest above ground; nest direction -- compass bearing of the nest from the main stem of the supporting plant; nest cover -- average percent foliage density within 1 m of the nest measured in four cardinal directions and above and below the nest; canopy closure -- percent canopy closure directly over nest; ground litter -- percent of ground area covered with vegetative litter within a 2-m radius circle centered on the nest; ground cover -- percent of area from ground to 1 m high covered by vegetation within a 2-m radius cylinder centered on the nest; shrub density -- density of foliage measured at 2 m above ground in a 2-m radius cylinder centered on the nest; mid-story density -- density of foliage measured at 6 m above ground in a 2 m radius cylinder centered on the nest.

Plant height and nest height were measured with a range finder or a surveyor's rod. Plant d.b.h was measured with a forestry diameter-tape. Canopy closure, ground cover, and ground litter were measured with a James and Shugart ocular tube (James and Shugart 1970). Shrub and mid-story density were measured using a 0.5 m square MacArthur board (MacArthur and MacArthur 1961, Gysel and Lyon 1980, Conner et al. 1986) marked with 10-cm-square blocks. Nest cover was measured with the MacArthur board where possible, otherwise visual estimates were made.

I also measured the same microhabitat variables (except nest height, nest direction, and nest cover) at a random point from each nest. The direction and distance to the random point were determined by computer-generated tables of random degrees and paces.

Bird species names follow those of the American Ornithologists' Union (1983) and plant species names follow those of Kartesz and Kartesz (1980) and Tiner (1993). Abbreviations of plant and bird species names used in some of the figures and tables are listed in Appendices A and B.

DATA ANALYSIS

I used Chi-square analysis to compare differences in cover and density estimates at nest-sites to those from *all possible* random points. I used the method of Neu et al. (1974) to calculate simultaneous confidence intervals, also called Bonferroni intervals (Byers et al. 1984), for each category in the Chi-square tests. In the simultaneous intervals, the number of categories or comparisons are accounted for by adjustments in the alpha level. I also compared the nest plant species used to those available. I used discriminant function analysis to verify classification of samples as nest-sites or random sites.

I calculated the mean nest heights and nest plant heights for those species with the largest sample sizes. To explore the relationship of these measures, I calculated the ratio of nest height and nest plant height.

I tested for differences in percent canopy closure, midstory density, shrub density, ground cover, nest cover, and nest height between successful and unsuccessful nests. I used an angular (arcsin square root) transformation of the percent values in these analyses (Dowdy and Wearden 1991). For species with large sample sizes, I used multivariate analysis of variance (MANOVA); for species with smaller sample sizes, I tested each variable separately with t-tests.

I used principal components analysis to determine the major sources of variability within the data set. In this analysis, I combined data on nests from all sites and all species.

I used an agglomerative, hierarchical, cluster analysis (Johnson and Wichern 1992, Morrison et al. 1992) to determine groups of species with similar measures of nest-site microhabitat variables. Since similarity or distance between groups can be measured in many different ways (i.e., the mean distance or the shortest distance may be used) often resulting in different groupings (Johnson and Wichern 1992), I used three linkage procedures (single, average, and complete) and compared the results among each procedure. Little difference was noted among the procedures and the results of the complete linkage procedure only are presented.

RESULTS

USE AND AVAILABILITY OF NEST-SITE HABITAT

I grouped the canopy closure, midstory density, shrub density, and ground cover measures into five categories to maintain expected values over five (Dowdy and Wearden 1991, Freund and Wilson 1993). The five categories are: 0-19, 20-39, 40-59, 60-79, and 80-100 percent. Due to small sample sizes for some species, certain measures were occasionally grouped into four categories. I have discussed results only where significant differences occurred. Values for each of the above mentioned variables are depicted in Figure 3.1. The results are presented by species for those with the largest sample sizes.

Acadian Flycatcher (*Empidonax virescens*)

Shrub density at nest-sites differed from that expected by chance ($\chi^2 = 33.01$, $df = 4$, $P < 0.01$). Shrub density in the range of 0 to 19 percent was used more often than expected and shrub density in the ranges of 20 to 79 percent was used less often than expected (Table 3.1). Only two nests were found to have shrub density measures over 80 percent. The average shrub density at 221 nest-sites used in this analysis was 14.4 percent (± 18.5).

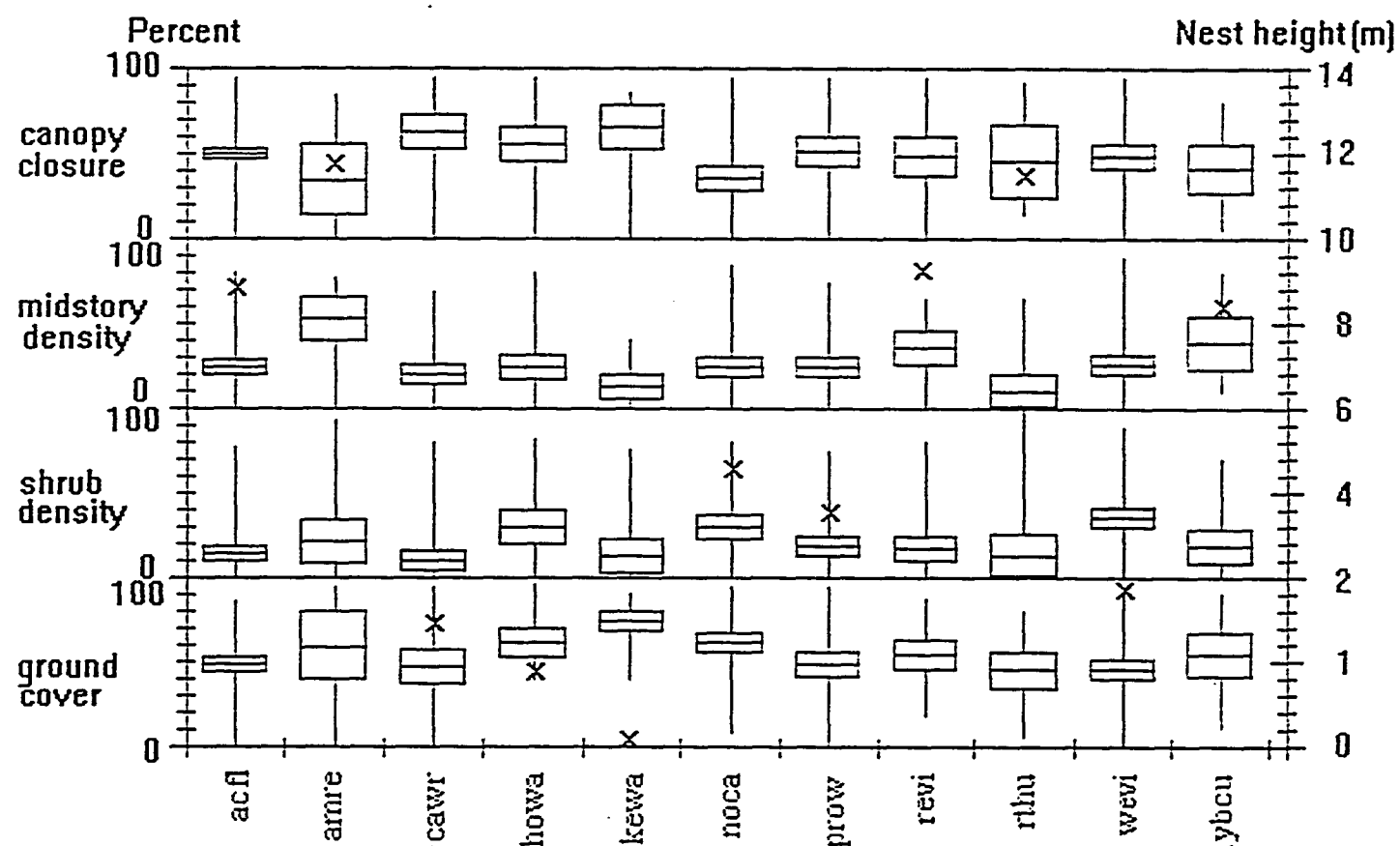


Figure 3.1. Mean values with 95 percent confidence intervals and ranges for nest-site habitat in 4 vegetation layers for 11 species (left axis). Mean nest heights are depicted by "x" marks and correspond to right axis. Bird species abbreviations are listed in Appendix A.

Table 3.1. Observed and expected proportions of shrub vegetation at Acadian Flycatcher nest-sites.

Percent Shrub Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.712	0.521	$0.633 \leq P_o \leq 0.790$ *
20-39	0.155	0.229	$0.092 \leq P_o \leq 0.217$ *
40-59	0.082	0.143	$0.034 \leq P_o \leq 0.129$ *
60-79	0.041	0.088	$0.006 \leq P_o \leq 0.075$ *
80-100	0.010	0.019	$-0.007 \leq P_o \leq 0.025$

* Indicates significant difference at $\alpha = 0.05$.

The midstory density at nest-sites differed from that expected by chance ($\chi^2 = 10.01$, $df = 4$, $P = 0.04$). The average mid-story density at 221 nest-sites was 24.6 percent (± 20.9). Acadian Flycatchers chose nest-sites with midstory density in the range of 60 to 79 percent less often than expected (Table 3.2). Only 3 nests were found to have mid-story densities over 80 percent.

Table 3.2. Observed and expected proportions of mid-story vegetation at Acadian Flycatcher nest-sites.

Percent Mid-story Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.443	0.423	$0.357 \leq P_o \leq 0.528$
20-39	0.289	0.230	$0.210 \leq P_o \leq 0.367$
40-59	0.167	0.177	$0.102 \leq P_o \leq 0.231$
60-79	0.086	0.140	$0.036 \leq P_o \leq 0.133$ *
80-100	0.013	0.028	$-0.006 \leq P_o \leq 0.032$

* Indicates significant difference at $\alpha = 0.05$.

The nest plant selected most often by Acadian Flycatchers was sweet gum; 60 of 221 nests (27 percent) were found in this tree species. The greatest difference between plant species use and availability also occurred with sweet gum (Figure 3.2). Sweet gum was used 15.1 percent more often than expected by chance. The plant species used second most often was Nuttall oak (*Quercus nuttallii*) with 22 nests (10.3 percent); it was used 7.8 percent more often than expected by chance. The third most commonly used nest plants were box elder and hackberry. Nineteen nests (8.9 percent) were found in each of these tree species. However, box elder was used 8.5 percent less often than expected by chance and hackberry was used 5.6 percent less often than expected by chance (Figure 3.2).

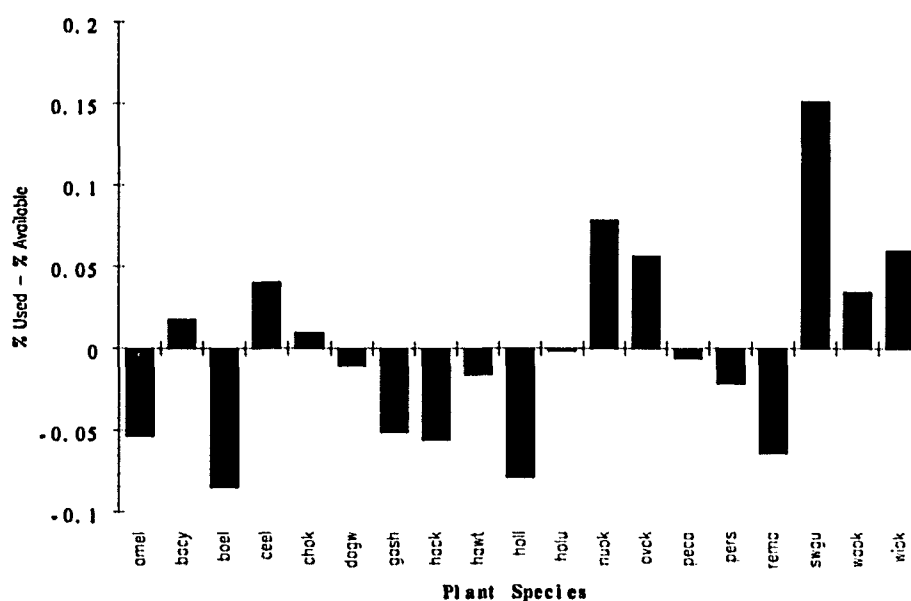


Figure 3.2. Differences in percent use and availability of nest plant species by Acadian Flycatchers. Plant species codes are given in Appendix B.

American Redstart (*Setophaga ruticilla*)

The percent mid-story density at American Redstart nest-sites was different than that expected by chance ($\chi^2 = 24.9$, $df = 4$, $P < 0.01$). Redstarts used mid-story density in the range of 0 to 19 percent less often than expected by chance (Table 3.3). The average mid-story density at the 16 nest-sites used in this analysis was 52.5 percent (± 22.6).

Table 3.3. Observed and expected proportions of mid-story vegetation at American Redstart nest-sites.

Percent Mid-story Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.062	0.421	$-0.093 \leq P_o \leq 0.217$ *
20-39	0.187	0.216	$-0.063 \leq P_o \leq 0.437$
40-59	0.250	0.197	$-0.028 \leq P_o \leq 0.528$
60-79	0.312	0.139	$0.014 \leq P_o \leq 0.609$
80-100	0.187	0.025	$-0.063 \leq P_o \leq 0.437$

* Indicates significant difference at $\alpha = 0.05$.

The percent canopy closure at American Redstart nest-sites differed from that expected by chance (Chi-square = 18.24, $p = < 0.01$). Canopy closure in the range of 0 to 19 percent was used more often than expected by chance (Table 3.4). The average canopy closure at 16 nest-sites was 30.9 percent (± 25.4).

The nest plant species used most often by American Redstarts was sweet gum. Seven of 14 (50 percent) nests were found in sweet gum trees and sweet gums were used 33.1 percent more often than expected by chance (Figure 3.3). Box elder was the second most often selected nest plant with 5 of 14 (35.7 percent) nests. Box elders were used

13.4 percent more often than expected by chance. One of 14 (7.1 percent) nests was in red maple and this species was used 15.1 percent less often than expected by chance.

Table 3.4. Observed and expected proportions of canopy vegetation at American Redstart nest-sites.

Percent Canopy Closure	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.466	0.120	$0.134 \leq P_o \leq 0.797$ *
20-39	0.200	0.168	$-0.065 \leq P_o \leq 0.465$
40-59	0.133	0.194	$-0.092 \leq P_o \leq 0.358$
60-79	0.133	0.260	$-0.092 \leq P_o \leq 0.358$
80-100	0.060	0.256	$-0.098 \leq P_o \leq 0.230$

* Indicates significant difference at alpha = 0.05.

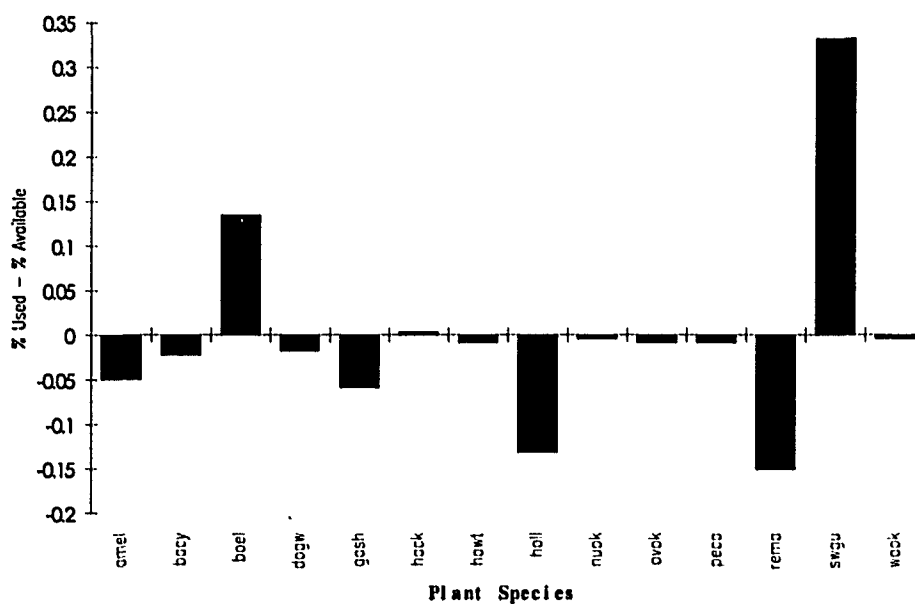


Figure 3.3. Differences in percent use and availability of nest plant species by American Redstarts. Plant species codes are given in Appendix B.

Carolina Wren (*Thryothorus ludovicianus*)

The percent shrub density at Carolina Wren nest-sites differed from that expected by chance (Chi-square = 10.52, $p = 0.01$). Carolina Wrens used shrub densities in the 0 to 19 percent range more often than expected by chance and they used shrub densities in the 60 to 100 percent range less often than expected by chance (Table 3.5). The average shrub density of the 48 nest-sites used in this analysis was 13.8 (± 17.1) percent.

Table 3.5. Observed and expected proportions of shrub vegetation at Carolina Wren nest-sites.

Percent Shrub Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.744	0.521	$0.584 \leq P_o \leq 0.903$ *
20-39	0.170	0.229	$0.033 \leq P_o \leq 0.306$
40-59	0.063	0.143	$-0.025 \leq P_o \leq 0.151$
60-100	0.021	0.108	$-0.031 \leq P_o \leq 0.073$ *

* Indicates significant difference at $\alpha = 0.05$.

Carolina Wrens commonly nested in dead snags (15 of 47 nests or 31.9 percent) but were also found to use a variety of plant species. Eight of 47 nests (17.0 percent) were found in palmetto (*Sabal minor*); it was used 10.0 percent more often than expected by chance (Figure 3.4). Seven nests (14.8 percent) were found in American elm; this species was used 8.3 percent more often than expected by chance. Two species used less often than expected by chance were box elder and hackberry, only one nest was found in each species. Box elder was used 11.8 percent less often than expected and hackberry was used 9.5 percent less often than expected by chance.

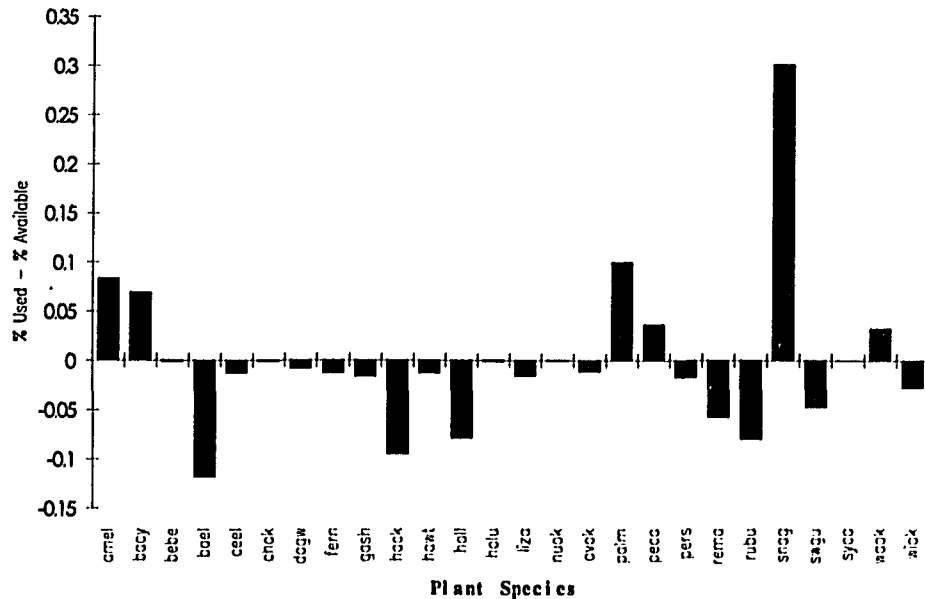


Figure 3.4. Differences in percent use and availability of nest plant species by Carolina Wrens. Plant species codes are given in Appendix B.

Hooded Warbler (*Wilsonia citrina*)

Twenty-eight nest-sites were measured, and no differences in canopy closure, midstory density, shrub density, and ground cover at Hooded Warbler nest-sites and random sites were detected.

The nest plant used most often by Hooded Warblers was *Rubus* sp. Fifty percent (14 of 28) of Hooded Warbler nests were found in *Rubus* sp. and this plant was used 38.9 percent more often than expected by chance (Figure 3.5). Four nests (14.2 percent) were found in box elder and it was used 7.4 percent less often than expected by chance. Red

maple was the third most often nest plant used (2 of 28 nests or 7.1 percent) but it was used 6.2 percent less often than expected.

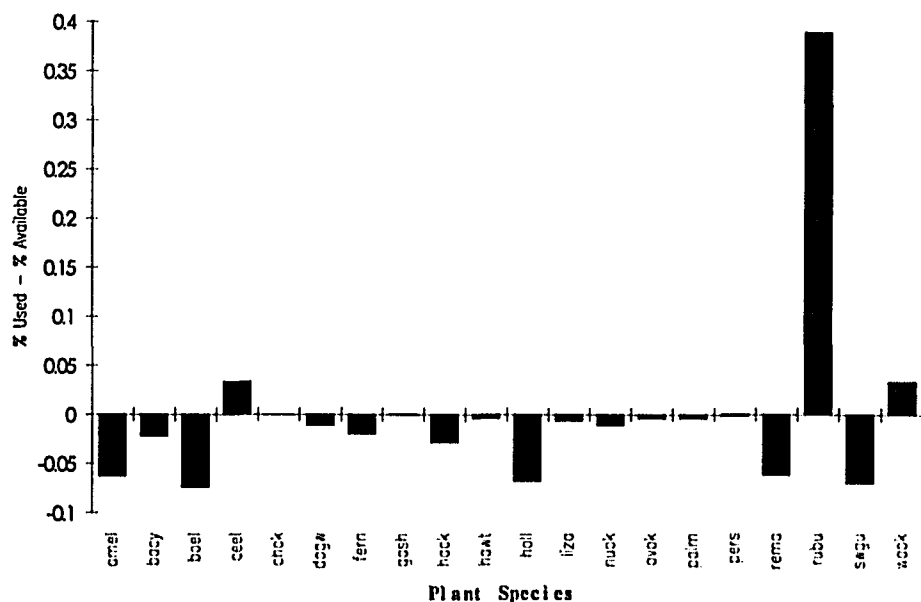


Figure 3.5. Differences in percent use and availability of nest plant species by Hooded Warblers. Plant species codes are given in Appendix B.

Kentucky Warbler (*Oporornis formosus*)

Percent ground cover at Kentucky Warbler nest-sites differed from that expected by chance ($\chi^2 = 16.1$, $df = 2$, $P < 0.01$). Kentucky Warblers chose nest-sites with ground cover in the 0 to 60 percent range less often than expected, and they chose nest-sites with ground cover in the 80 to 100 percent range more often than expected (Table 3.6). The average percent ground cover at 21 nest-sites used in this analysis was $74.5 (\pm 14.0)$.

Table 3.6. Observed and expected proportions of ground vegetation at Kentucky Warbler nest-sites.

Percent Ground Cover	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-59	0.095	0.501	$-0.258 \leq P_o \leq 0.248$ *
60-79	0.380	0.274	$0.125 \leq P_o \leq 0.634$
80-100	0.523	0.224	$0.261 \leq P_o \leq 0.784$ *

* Indicates significant difference at $\alpha = 0.05$.

Percent shrub density at Kentucky Warbler nest-sites differed from that expected by chance ($\chi^2 = 12.39$, $df = 3$, $P < 0.01$). Kentucky Warblers chose sites with shrub density in the 0 to 19 percent range more often than expected and they chose sites with shrub density in the 20 to 59 percent range less often than expected (Table 3.7). The average shrub density at 21 nest-sites was 14.2 percent (± 21.2) and only two nests were found with shrub density measures over 60 percent.

Table 3.7. Observed and expected proportions of shrub vegetation at Kentucky Warbler nest-sites.

Percent Shrub Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.809	0.434	$0.594 \leq P_o \leq 1.023$ *
20-39	0.047	0.228	$-0.068 \leq P_o \leq 0.162$ *
40-59	0.047	0.181	$-0.068 \leq P_o \leq 0.162$ *
60-100	0.095	0.155	$-0.064 \leq P_o \leq 0.254$

* Indicates significant difference at $\alpha = 0.05$.

Kentucky Warbler nest-sites differed in percentage of mid-story density from that expected by chance ($\chi^2 = 10.95$, $df = 2$, $P < 0.01$). More Kentucky Warbler nest-sites had

mid-story density in the 0 to 19 percent range than expected by chance, and there were less sites in the 50 to 100 percent range than expected by chance (Table 3.8). The average mid-story density at 21 nest-sites was 12.6 percent (± 12.9).

Table 3.8. Observed and expected proportions of mid-story vegetation at Kentucky Warbler nest-sites.

Percent mid-story density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.714	0.412	$0.477 \leq P_o \leq .950$ *
20-49	0.238	0.203	$0.014 \leq P_o \leq 0.461$
50-100	0.047	0.384	$-0.063 \leq P_o \leq 0.157$ *

* Indicates significant difference at $\alpha = 0.05$.

Northern Cardinal (*Cardinalis cardinalis*)

Percent ground cover measured for 100 nest-sites differed from that expected by chance ($\chi^2 = 11.03$, $df = 4$, $P = 0.02$). There were fewer nests-sites with ground cover in the 40 to 59 percent range than expected (Table 3.9). The average ground cover at 100 Northern Cardinal nest-sites was 57.4 percent (± 25.0).

The percent mid-story density at Northern Cardinal nest-sites was different from that expected by chance ($\chi^2 = 10.91$, $df = 4$, $P = 0.02$). Northern Cardinals chose nests sites with mid-story density in the 60 to 79 percent range more often than expected by chance (Table 3.10). The average mid-story density at 100 nest-sites was 28.4 percent (± 26.9).

Table 3.9. Observed and expected proportions of ground vegetation at Northern Cardinal nest-sites.

Percent Ground Cover	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.050	0.104	$-0.006 \leq P_o \leq 0.106$
20-39	0.230	0.196	$0.121 \leq P_o \leq 0.338$
40-59	0.130	0.218	$0.043 \leq P_o \leq 0.216$ *
60-79	0.310	0.288	$0.191 \leq P_o \leq 0.428$
80-100	0.280	0.192	$0.164 \leq P_o \leq 0.395$

* Indicates significant difference at $\alpha = 0.05$.

Table 3.10. Observed and expected proportions of mid-story vegetation at Northern Cardinal nest-sites.

Percent Mid-story Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.470	0.423	$0.341 \leq P_o \leq 0.598$
20-39	0.160	0.230	$0.065 \leq P_o \leq 0.254$
40-59	0.110	0.177	$0.029 \leq P_o \leq 0.190$
60-79	0.230	0.140	$0.151 \leq P_o \leq 0.338$ *
80-100	0.030	0.028	$-0.013 \leq P_o \leq 0.073$

* Indicates significant difference at $\alpha = 0.05$.

The percent canopy closure at Northern Cardinal nest-sites was different than expected by chance ($\chi^2 = 44.73$, $df = 4$, $P < 0.01$). There were more Northern Cardinal nest-sites in the 0 to 19 percent range than expected and fewer nest-sites in the 80 to 100

percent range than expected (Table 3.11). The average canopy closure at 100 nest-sites was 39.6 percent (± 31.2).

Table 3.11. Observed and expected proportions of canopy vegetation at Northern Cardinal nest-sites.

Percent Canopy Closure	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.290	0.109	$0.173 \leq P_o \leq 0.406 *$
20-39	0.220	0.135	$0.113 \leq P_o \leq 0.326$
40-59	0.140	0.182	$0.050 \leq P_o \leq 0.229$
60-79	0.180	0.274	$0.081 \leq P_o \leq 0.278$
80-100	0.170	0.298	$0.073 \leq P_o \leq 0.266 *$

* Indicates significant difference at $\alpha = 0.05$.

Deciduous holly was the most common nest plant used by Northern Cardinals; 19 of 96 (19.8 percent) nests were found in this species and it was used 9.5 percent more often than expected by chance (Figure 3.6). Palmetto (11 of 96 nests or 11.4 percent), box elder (10 of 96 nests or 10.4 percent), and sweet gum (8 of 96 nests or 8.3 percent) were the next most often used nest plants. Palmetto was used 4.3 percent more often than expected, box elder was used 3.8 percent less often than expected, and sweet gum was used 0.8 percent less often than expected by chance (Figure 3.5).

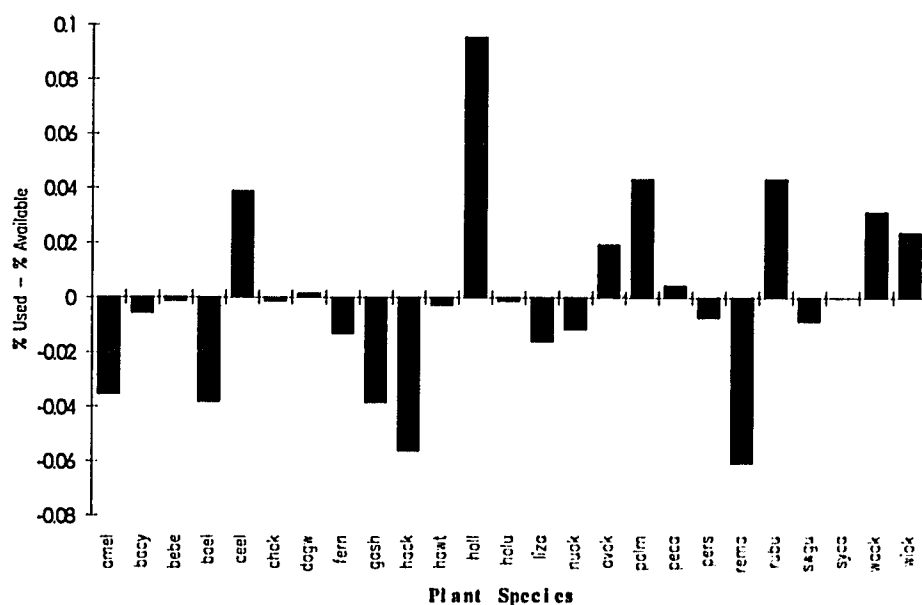


Figure 3.6. Differences in percent use and availability of nest plant species by Northern Cardinals. Plant species codes are given in Appendix B.

Northern Parula (*Parula americana*)

There were no differences in the percent ground cover, shrub density, midstory density, and canopy cover at the 21 Northern Parula nest-sites measured and that expected by chance.

The most commonly used nest plant by Northern Parulas was cedar elm (*Ulmus crassifolia*) (5 of 21 nests or 23.8 percent), it was used 22.1 percent more often than expected by chance (Figure 3.7). The second most often used nest plant was red maple; four (19.0 percent) nests were found in this plant and it was used 6.4 percent more often than expected by chance. Three nests (14.2 percent) were found in green ash and it was

used 7.7 percent more often than expected. No nests were found in hackberry or sweet gum.

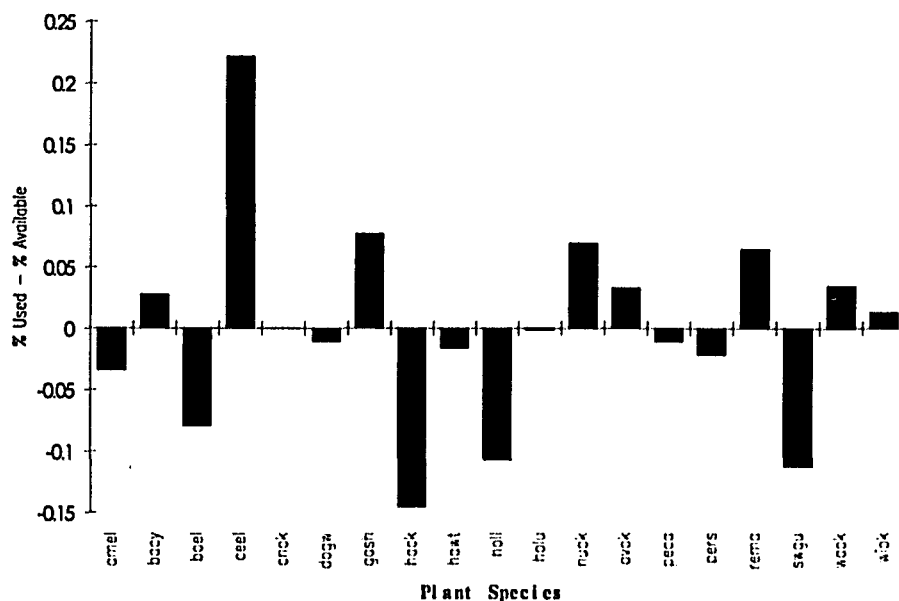


Figure 3.7. Differences in percent use and availability of nest plant species by Northern Parulas. Plant species codes are given in Appendix B.

Prothonotary Warbler (*Protonotaria citrea*)

The percent ground cover at Prothonotary Warbler nest-sites was different than expected by chance ($\chi^2 = 9.28$, $df = 4$, $P < 0.01$). Prothonotary Warblers chose nest-sites with ground cover in the range of 20 to 39 percent more often than expected by chance (Table 3.12). The average ground cover for 82 nest-sites that I measured was 41.5 percent (± 26.5).

Table 3.12. Observed and expected proportions of ground vegetation at Prothonotary Warbler nest-sites.

Percent Ground Cover	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.182	0.104	$0.072 \leq P_o \leq 0.291$
20-39	0.329	0.196	$0.198 \leq P_o \leq 0.462$ *
40-59	0.170	0.218	$0.063 \leq P_o \leq 0.276$
60-79	0.195	0.288	$0.082 \leq P_o \leq 0.307$
80-100	0.121	0.192	$0.028 \leq P_o \leq 0.213$

* Indicates significant difference at $\alpha = 0.05$.

The percent shrub density at Prothonotary Warbler nest-sites was different than that expected by chance ($\chi^2 = 11.58$, $df = 3$, $P < 0.01$). There were more nest-sites with shrub density in the 0 to 19 percent range than expected by chance and fewer nest-sites with shrub density in the 60 to 100 percent range than expected by chance (Table 3.13).

The average shrub density at 82 nest-sites was 17.9 percent (± 17.9).

Table 3.13. Observed and expected proportions of shrub vegetation at Prothonotary Warbler nest-sites.

Percent Shrub Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.701	0.521	$0.578 \leq P_o \leq 0.823$ *
20-39	0.137	0.229	$0.045 \leq P_o \leq 0.230$
40-59	0.126	0.143	$0.037 \leq P_o \leq 0.214$
60-100	0.034	0.088	$-0.014 \leq P_o \leq 0.082$ *

* Indicates significant difference at $\alpha = 0.05$.

Red-eyed Vireo (*Vireo olivaceus*)

The percent ground cover at Red-eyed Vireo nest-sites was different from that expected ($\chi^2 = 10.16$, $df = 4$, $P = 0.03$). More Red-eyed Vireo nest-sites had ground cover in the 40 to 59 percent range than expected by chance (Table 3.14). The average ground cover at 44 nest-sites was 50.6 percent (± 20.1).

Table 3.14. Observed and expected proportions of ground vegetation at Red-eyed Vireo nest-sites.

Percent Ground Cover	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.045	0.104	$-0.035 \leq P_o \leq 0.125$
20-39	0.181	0.196	$0.031 \leq P_o \leq 0.330$
40-59	0.409	0.218	$0.219 \leq P_o \leq 0.599$ *
60-79	0.227	0.288	$0.064 \leq P_o \leq 0.389$
80-100	0.136	0.192	$0.003 \leq P_o \leq 0.268$

* Indicates significant difference at $\alpha = 0.05$.

The percent mid-story density at nest-sites was different than that expected by chance ($\chi^2 = 14.2$, $df = 3$, $P < 0.01$). Red-eyed Vireos chose sites with mid-story density in the range of 40 to 59 percent more often than expected (Table 3.15). The average mid-story density at 44 nest-sites was 35.6 percent (± 22.0).

Thirty-three percent (15 of 45) of all Red-eyed Vireo nests were found in box elder. This plant was used 15.8 percent more often than expected by chance (Figure 3.8). The second most often used nest plant was sweet gum (8 of 45 nests or 17.7 percent) and it was used 6.5 percent more often than expected by chance. Six nests were found in both

Nuttall oak and red maple. Nuttall oak was used 10.7 percent more often than expected and red maple was used 0.7 percent more often than expected by chance. No nests were found in green ash or deciduous holly.

Table 3.15. Observed and expected proportions of mid-story vegetation at Red-eyed Vireo nest-sites.

Percent Mid-story Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.272	0.423	$0.104 \leq P_o \leq 0.439$
20-39	0.159	0.230	$0.021 \leq P_o \leq 0.296$
40-59	0.386	0.177	$0.202 \leq P_o \leq 0.569$ *
60-100	0.181	0.168	$0.035 \leq P_o \leq 0.326$

* Indicates significant difference at $\alpha = 0.05$.

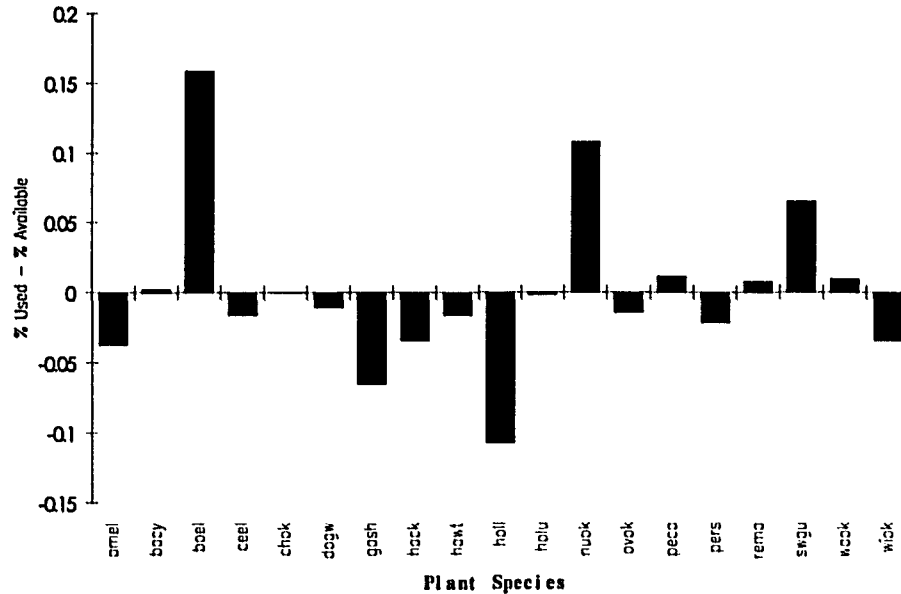


Figure 3.8. Differences in percent use and availability of nest plant species by Red-eyed Vireos. Plant species codes are given in Appendix B.

Ruby-throated Hummingbird (*Archilochus colubris*)

The percent mid-story density at nest-sites was different from that expected by chance ($\chi^2 = 13.98$, $df = 3$, $P < 0.01$). Hummingbirds chose nests sites with mid-story density in the range of 0 to 19 percent more often than expected, and they chose nest-sites with mid-story density in the range of 60 to 99 percent less often than expected by chance (Table 3.16). The average mid-story density at 30 nest-sites was 10.3 percent (± 16.1).

Table 3.16. Observed and expected proportions of mid-story vegetation at Ruby-throated Hummingbird nest-sites.

Percent Mid-story Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.766	0.431	$0.572 \leq P_o \leq 0.959$ *
20-39	0.133	0.247	$-0.021 \leq P_o \leq 0.287$
40-59	0.066	0.172	$-0.047 \leq P_o \leq 0.179$
60-100	0.033	0.147	$-0.048 \leq P_o \leq 0.114$ *

* Indicates significant difference at $\alpha = 0.05$.

Sweet gum was the most commonly used nest plant by Ruby-throated Hummingbirds; 8 of 30 (26.7 percent) nests were found in this plant. Sweet gum was used 13.3 percent more often than expected by chance (Figure 3.9). The second most often used nest plant was American elm (5 of 30 nests or 16.7 percent) and it was used 9.4 percent more often than expected by chance. Three nests (10.0 percent) were found in both cedar elm and overcup oak (*Quercus lyrata*). Cedar elm and overcup oak were both used 7.9 percent more often than expected.

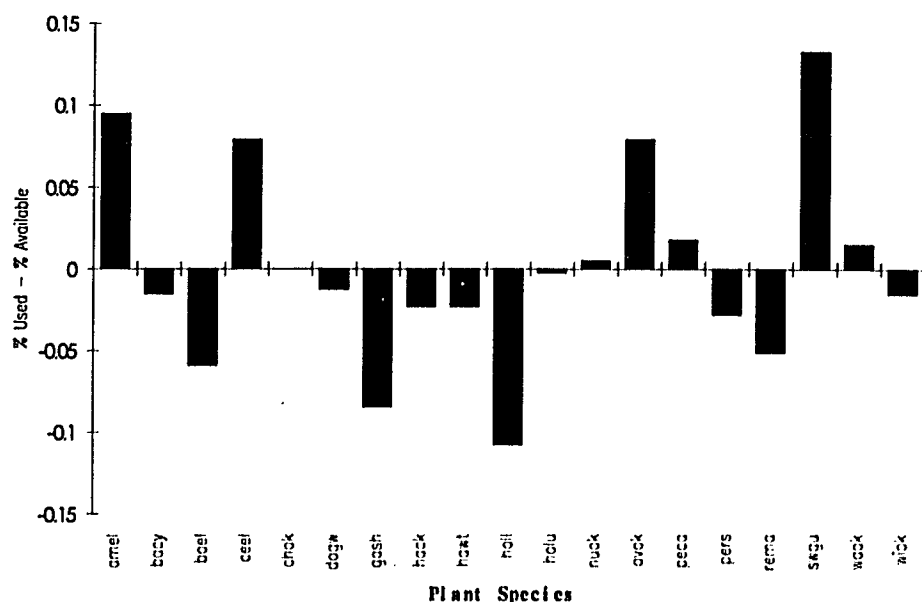


Figure 3.9. Differences in percent use and availability of nest plant species by Ruby-throated Hummingbirds. Plant species codes are given in Appendix B.

White-eyed Vireo (*Vireo griseus*)

The percent shrub density at nest-sites differed from that expected by chance ($\chi^2 = 81.73$, $df = 4$, $P < 0.01$). White-eyed Vireos chose nest-sites with shrub density in the 0 to 19 percent range less often than expected by chance. They chose nest-sites with shrub density in range of 60 to 100 percent more often than expected by chance (Table 3.17). The average shrub density at 143 nest-sites was 37.0 percent (± 26.7).

The percent mid-story density at White-eyed Vireo nest-sites was different from that expected by chance ($\chi^2 = 10.86$, $df = 4$, $P = 0.02$). White-eyed Vireos chose nest-sites with mid-story density in the range of 20 to 39 percent less often than expected by

chance (Table 3.18). The average mid-story density at 143 nest-sites was 26.7 percent (\pm 26.8).

Table 3.17. Observed and expected proportions of shrub vegetation at White-eyed Vireo nest-sites.

Percent Shrub Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.300	0.521	$0.201 \leq P_O \leq 0.398$ *
20-39	0.216	0.229	$0.127 \leq P_O \leq 0.304$
40-59	0.202	0.143	$0.115 \leq P_O \leq 0.283$
60-79	0.174	0.088	$0.095 \leq P_O \leq 0.260$ *
80-100	0.104	0.019	$0.038 \leq P_O \leq 0.169$ *

* Indicates significant difference at $\alpha = 0.05$.

Table 3.18. Observed and expected proportions of mid-story vegetation at White-eyed Vireo nest-sites.

Percent Mid-story Density	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.489	0.423	$0.381 \leq P_O \leq 0.596$
20-39	0.146	0.230	$0.070 \leq P_O \leq 0.221$ *
40-59	0.195	0.177	$0.109 \leq P_O \leq 0.280$
60-79	0.111	0.140	$0.043 \leq P_O \leq 0.178$
80-100	0.055	0.028	$0.006 \leq P_O \leq 0.103$

* Indicates significant difference at $\alpha = 0.05$.

The percent canopy closure at nest-sites was different from that expected by chance ($\chi^2 = 16.76$, $df = 4$, $P < 0.01$). White-eyed Vireos chose nest-sites with canopy closure in the 0 to 19 percent range more often than expected by chance (Table 3.19).

The average canopy closure at 143 nest-sites was 49.6 percent (± 31.4).

Table 3.19. Observed and expected proportions of canopy vegetation at White-eyed Vireo nest-sites.

Percent Canopy Closure	Observed Proportion of Usage	Expected Proportion of Usage	Bonferroni Intervals for Observed Proportion of Usage
0-19	0.209	0.109	$0.121 \leq P_o \leq 0.296$ *
20-39	0.153	0.135	$0.075 \leq P_o \leq 0.230$
40-59	0.139	0.182	$0.064 \leq P_o \leq 0.213$
60-79	0.216	0.274	$0.127 \leq P_o \leq 0.304$
80-100	0.279	0.298	$0.182 \leq P_o \leq 0.375$

* Indicates significant difference at $\alpha = 0.05$.

Sweet gum was the nest plant most often used by White-eyed Vireos. Twenty-two of 136 nests (16.1 percent) were found in sweet gum and it was used 6.9 percent more often than expected by chance (Figure 3.10). Red maple was the second most often used nest plant (18 of 136 nests or 13.2 percent) and it was used 2.9 percent more often than expected. Water oak (*Quercus nigra*) and American beautyberry (*Callicarpa americana*) were the fifth and sixth most often used species but water oak was used 4.8 percent more often than expected and American beautyberry was used 4.2 percent more often than expected by chance (Figure 3.10).

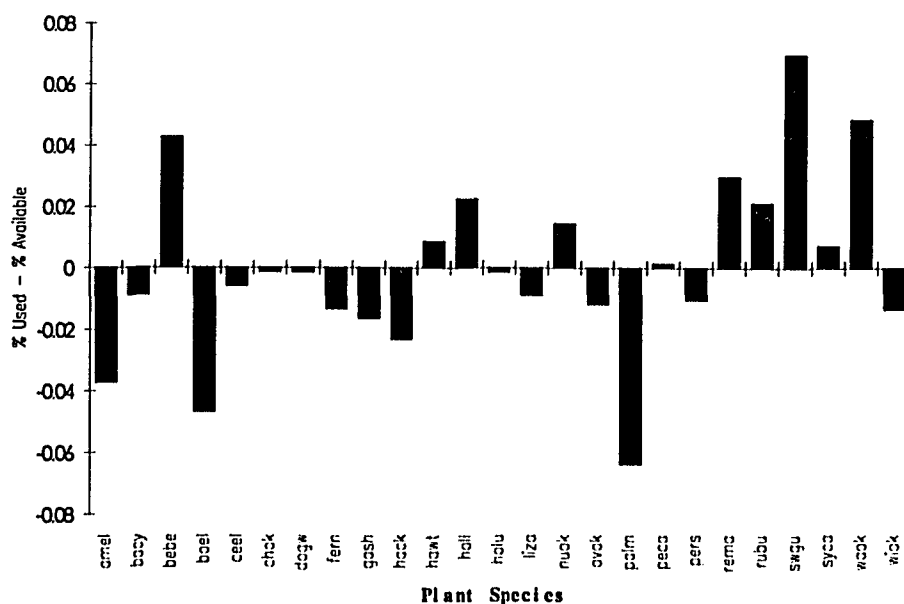


Figure 3.10. Differences in percent use and availability of nest plant species by White-eyed Vireos. Plant species codes are given in Appendix B.

Yellow-billed Cuckoo (*Coccyzus americanus*)

There was no difference in the percent ground cover, shrub density, mid-story density, or canopy closure for the 20 nest-sites measured and that expected by chance alone.

Sweet gum and deciduous holly were the most common nest plants used by Yellow-billed Cuckoos. Four of 17 nests (23.5 percent) were found in each of these plant species. Sweet gum was used 14.6 percent more often than expected and deciduous holly was used 15.8 percent more often than expected by chance (Figure 3.11). Two of 17 nests (11.7 percent) were found in both cedar elm and water oak. Cedar elm was used 7.0

percent more often than expected and water oak was used 8.2 percent more often than expected chance. No nests were found in American elm or hackberry.

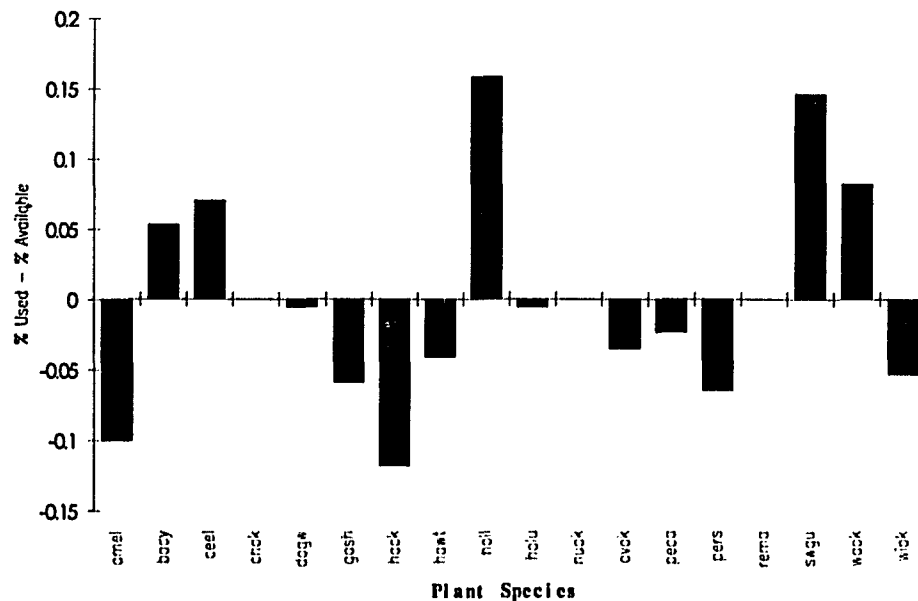


Figure 3.11. Differences in percent use and availability of nest plant species by Yellow-billed Cuckoos. Plant species codes are given in Appendix B.

To summarize these results, I grouped cover and density measures into three categories: low = 0 to 39 percent, medium = 40 to 59 percent, high = 60 to 100 percent. I considered a category as "chosen" if it was used significantly more often than expected and as "avoided" if it was used significantly less often than expected (Table 3.20).

Table 3.20. Nest-site habitat features chosen and avoided by 12 species.

Species	Features Chosen	Features Avoided
Acadian Flycatcher	low shrub density	high midstory density
American Redstart	low canopy closure	low midstory density

(table con'd.)

Carolina Wren	low shrub density	high shrub density
Hooded Warbler	none	none
Kentucky Warbler	high ground cover low shrub density low midstory density	low ground cover medium shrub density high midstory density
Northern Cardinal	high midstory density low canopy closure	high canopy closure
Northern Parula	none	none
Prothonotary Warbler	low ground cover low shrub density	high shrub density
Red-eyed Vireo	medium ground cover medium midstory density	none
Ruby-throated Hummingbird	low midstory density	high midstory density
White-eyed Vireo	high shrub density	low shrub density low midstory density
Yellow-billed Cuckoo	none	none

Note: low = 0 to 39 percent, medium = 40 to 59 percent, high = 60 to 100 percent.

NEST COVER

Vegetation density within 1 m of the nest was measured using the MacArthur board. Mean nest cover values ranged from a low of 4.1 percent for the Downy Woodpecker to a high of 87.5 percent for the Swainson's Warbler (*Limnothlypis swainsonii*) (Table 3.21). Four of the five lowest mean values were in cavity-nesting species.

Table 3.21. Nest cover measures with mean, minimum, and maximum values.

Species	Mean \pm Std. Dev., (N)	Minimum	Maximum
Acadian Flycatcher	39.2 \pm 13.0, (221)	10.0	80.0
American Redstart	60.3 \pm 14.5, (16)	30.0	80.0

(table con'd.)

Blue-gray Gnatcatcher	36.0 ± 9.3, (10)	20.0	50.0
Carolina Wren	35.6 ± 30.6, (45)	10.0	75.0
Downy Woodpecker	7.0 ± 10.3, (5)	2.5	14.4
Eastern Wood-Pewee	25.0 ± 7.0, (2)	20.0	30.0
Tufted Titmouse	4.1 ± 3.7, (6)	0.0	10.0
Great Crested Flycatcher	28.3 ± 40.7, (3)	0.0	75.0
Hooded Warbler	56.2 ± 20.7, (35)	20.0	90.0
Indigo Bunting	66.4 ± 20.1, (7)	35.0	80.0
Kentucky Warbler	73.3 ± 14.6, (21)	40.0	95.0
Northern Cardinal	66.5 ± 14.8, (100)	30.0	95.0
Northern Parula	30.4 ± 10.7, (25)	10.0	50.0
Prothonotary Warbler	16.6 ± 17.1, (82)	0.0	80.0
Red-bellied Woodpecker	10.7 ± 14.2, (7)	0.0	30.0
Red-eyed Vireo	52.5 ± 14.8, (44)	30.0	85.0
Ruby-throated Hummingbird	26.5 ± 10.6, (29)	10.0	50.0
Summer Tanager	40.0 ± 10.9, (11)	25.0	60.0
Swainson's Warbler	87.5 ± 10.6, (2)	80.0	95.0
White-eyed Vireo	55.0 ± 17.4, (143)	10.0	90.0
Wood Thrush	75.0 ± 21.2, (2)	60.0	90.0
Yellow-billed Cuckoo	59.0 ± 17.8, (20)	25.0	85.0

DISTINGUISHING NEST-SITES AND RANDOM SITES

I used quadratic discriminant function analysis to distinguish nest-sites from random sites based on all microhabitat measures. The number of successful classifications ranged from a low of 71.3 percent for Northern Cardinals to a high of 97.8 percent for Kentucky Warblers (Table 3.22).

Table 3.22. Percent of successful classifications between nest-sites and random sites based on discriminant function analysis.

Species	Percent of observations successfully classified
Acadian Flycatcher	84.9
Carolina Wren	92.8

(table con'd.)

Hooded Warbler	92.3
Kentucky Warbler	97.8
Northern Cardinal	71.3
Prothonotary Warbler	92.9
Red-eyed Vireo	91.3
White-eyed Vireo	74.5

NEST HEIGHT AND NEST PLANT HEIGHT

Analysis of nest height and nest plant height were performed for those species with the largest sample sizes. The mean nest heights of 4 species Kentucky Warbler (a ground nester), Carolina Wren, Hooded Warbler, and White-eyed Vireo, were less than 2 m. Two species Northern Cardinal and Prothonotary Warbler, had mean nest heights between 2 and 4 m. Three species, Acadian Flycatcher, Red-eyed Vireo, and Yellow-billed Cuckoo, had mean nest heights between 6 and 10 m. Three species had mean nest heights greater than 10 m - American Redstart, Northern Parula, and Ruby-throated Hummingbird. The species with the greatest mean nest height (11.3 m) was the American Redstart (Table 3.23).

The species with the smallest average nest plant height was the Hooded Warbler (1.6 m). Three species, Northern Cardinal, Prothonotary Warbler, and White-eyed Vireo, had mean nest plant heights between 5 and 7 m. The remainder of the species had mean nest plant heights greater than 10 m. Ruby-throated Hummingbirds had the largest mean nest plant height (18.7 m) (Table 3.23).

I calculated the ratio of nest height to nest-plant height for 11 species (Table 3.23). The mean ratios of nest height to plant height for two species, Carolina Wren and White-eyed Vireo, were less than 0.50. The mean ratio of nest height to plant height for 6 species, Acadian Flycatcher, Ruby-throated Hummingbird, Red-eyed Vireo, Prothonotary Warbler, Hooded Warbler, and Northern Parula, was between 0.50 and 0.70. The Northern Cardinal, Yellow-billed Cuckoo and American Redstart had mean ratios greater than 0.70. The largest mean ratio (0.86) occurred with the Yellow-billed Cuckoo and the smallest ratio (0.35) occurred with the Carolina Wren.

Table 3.23. Nest and plant heights with mean ratios for 11 species.

Species Sample Size	Mean Nest Ht. \pm SD Range (m)	Mean Plant Ht. \pm SD Range (m)	Mean Ratio of Nest Ht. to Plant Ht. with Standard Error and Median
Acadian Flycatcher N = 221	8.8 \pm 3.2 2.3 - 22.0	14.9 \pm 6.1 3.0 - 32.0	0.63 \pm 0.01 0.63
American Redstart N = 16	11.3 \pm 2.9 7.8 - 18.0	14.2 \pm 4.4 8.0 - 22.5	0.82 \pm 0.03 0.85
Carolina Wren N = 45	1.4 \pm 1.5 0.0 - 7.5	10.2 \pm 9.3 0.4 - 33.0	0.35 \pm 0.05 0.30
Hooded Warbler N = 35	0.8 \pm 0.4 0.3 - 1.8	1.6 \pm 0.4 1.0 - 2.4	0.52 \pm 0.03 0.47
Northern Cardinal N = 100	3.9 \pm 2.9 0.4 - 14.0	5.6 \pm 4.3 0.7 - 26.0	0.72 \pm 0.02 0.78
Northern Parula N = 25	10.1 \pm 3.8 4.0 - 17.5	16.3 \pm 6.4 5.4 - 26.8	0.67 \pm 0.03 0.65
Prothonotary Warbler N = 82	3.3 \pm 1.9 0.4 - 11.5	6.2 \pm 4.3 0.8 - 21.3	0.64 \pm 0.3 0.65

(table con'd.)

Red-eyed Vireo N = 44	9.1 ± 4.2 4.1 - 22.6	15.1 ± 8.1 5.8 - 33.1	0.65 ± 0.02 0.67
Ruby-throated Hummingbird N = 29	11.2 ± 3.3 6.0 - 20.5	18.7 ± 5.4 8.3 - 34.0	0.63 ± 0.02 0.65
White-eyed Vireo N = 143	1.9 ± 1.9 0.3 - 10.3	5.1 ± 6.1 0.6 - 33.5	0.47 ± 0.01 0.45
Yellow-billed Cuckoo N = 20	8.3 ± 4.1 3.0 - 17.5	11.3 ± 6.2 4.2 - 23.0	0.86 ± 0.2 0.87

NEST-SITE HABITAT AND NEST SUCCESS

I tested for differences in the percent canopy closure, midstory density, shrub density, ground cover, nest cover, and nest height between successful and unsuccessful nests. For species with larger sample sizes, Acadian Flycatcher, Carolina Wren, Hooded Warbler, Northern Cardinal, Prothonotary Warbler, and White-eyed Vireo, I used MANOVA. No differences occurred between successful and unsuccessful nests for any of these species (Table 3.24, also see Figures 3.14 - 3.19). For species with smaller sample sizes, American Redstart, Kentucky Warbler, Red-eyed Vireo, Ruby-throated Hummingbird, and Yellow-billed Cuckoo, I tested each variable separately with t-tests. Only one difference among the 30 comparisons was noted for these species, which is within the range of that expected by chance alone. The percent midstory density of successful American Redstart nests (0.94 ± 0.11) was more than that at unsuccessful nests (0.71 ± 0.16) ($t = -2.53$, $P = 0.03$, $df = 8$) (see Figures 3.13 - 3.18).

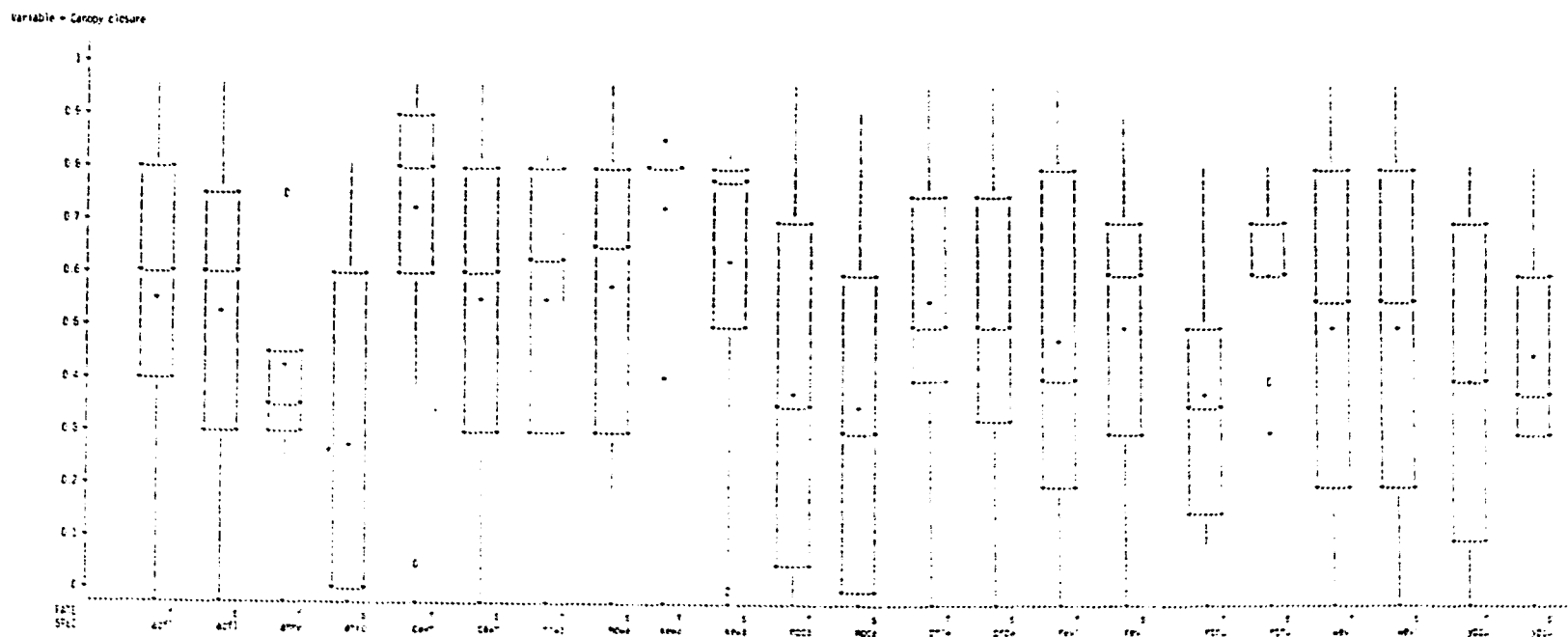


Figure 3.12. Variation in percent canopy closure of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.

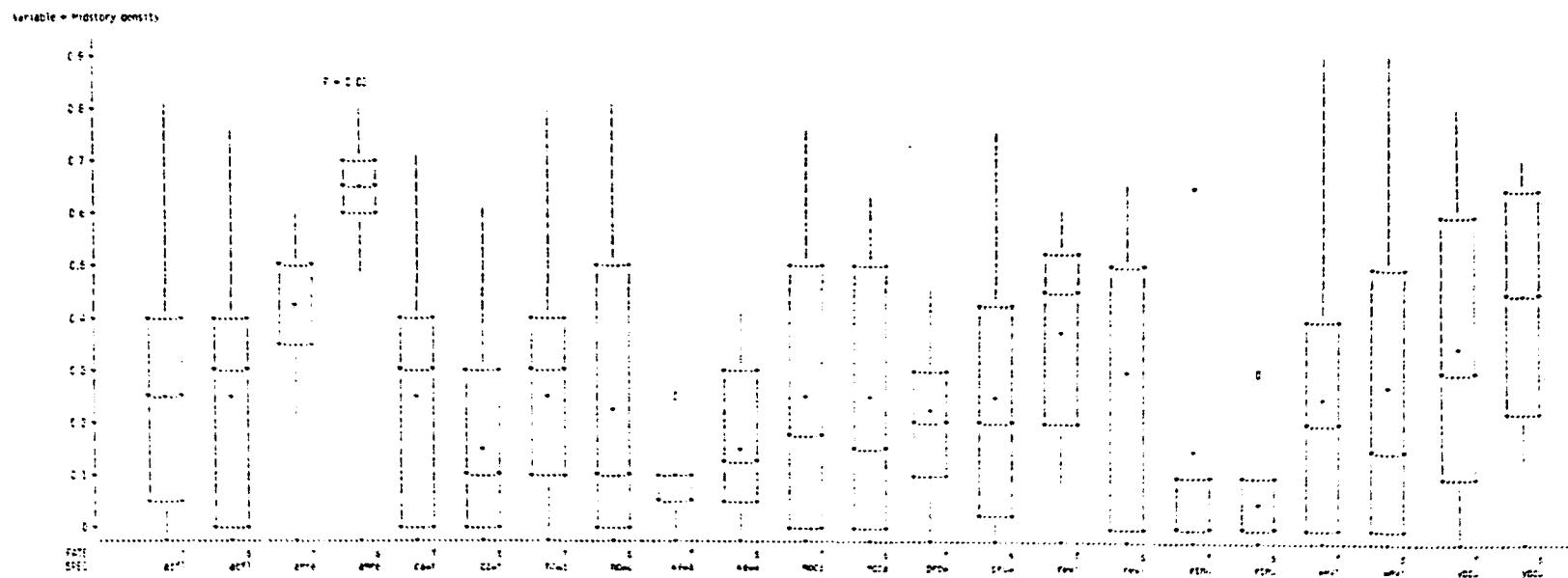


Figure 3.13. Variation in percent midstory density of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.

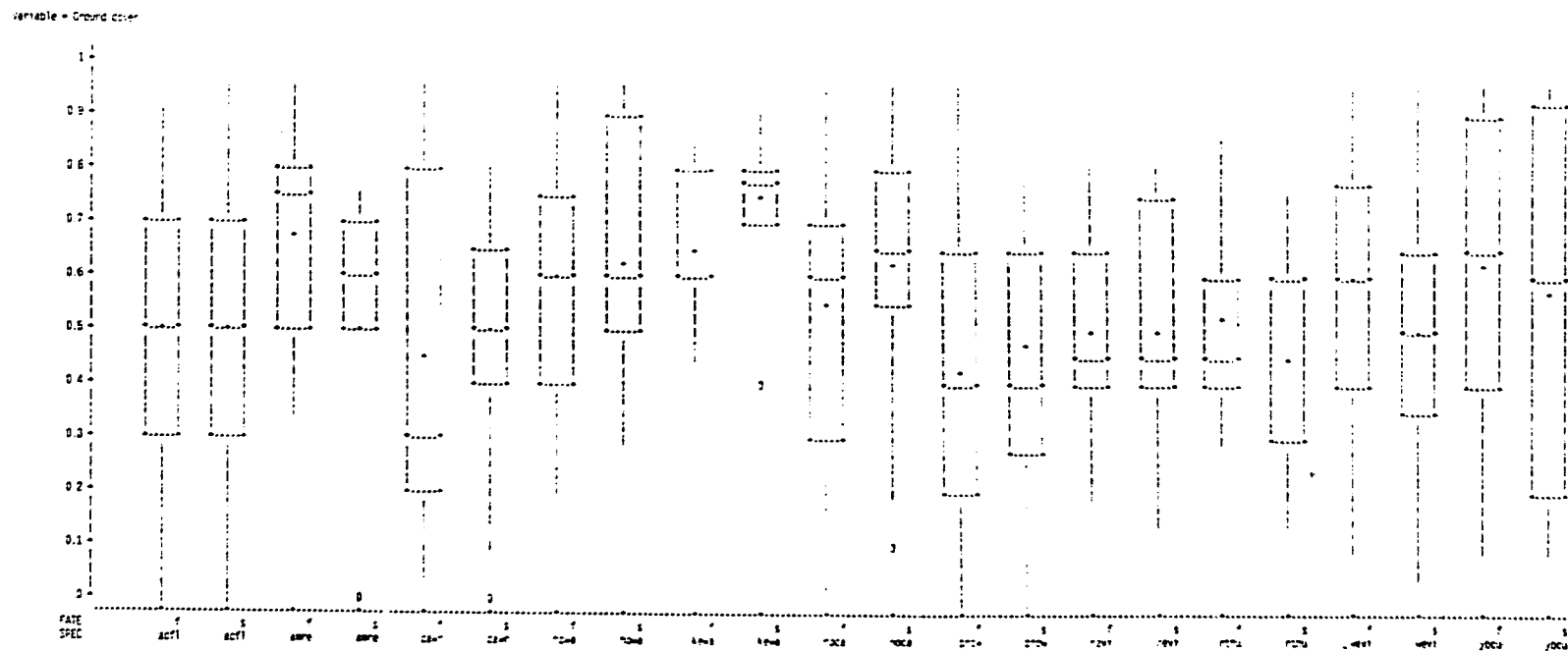


Figure 3.15. Variation in percent ground cover of successful and unsuccessful nest-sites for 11 species breeding in bottomland hardwood study sites. Note: f = fail; s = success. SPEC = species.

Table 3.24. Results of MANOVA tests for differences in nest-site microhabitat variables of successful and unsuccessful nests.

Species	Wilks' Lambda	<i>F</i> df	<i>P</i> -value
Acadian Flycatcher	0.99	0.25 6,152	0.95
Carolina Wren	0.80	1.24 6,31	0.31
Hooded Warbler	0.95	0.22 6,26	0.96
Northern Cardinal	0.92	0.93 6,68	0.48
Prothonotary Warbler	0.95	0.39 6,46	0.88
White-eyed Vireo	0.92	1.27 6,97	0.28

MAJOR SOURCES OF VARIABILITY

The principal components analysis was performed on the nest-site microhabitat variables for all sites and species combined. The first four principal components accounted for 78 percent of the total variation in the data set. The first principal component (eigenvalue = 2.74) accounted for 34 percent of the variation and was most strongly represented by measures of plant height and diameter, and nest height (Table 3.25). The interpretation of this component relates to the variety of plant heights and diameters used by the different bird species and the variation in height of nest placement. The second principal component (eigenvalue = 1.40) accounted for 17.5 percent of the total variation and was representative of mid-story density, shrub density, ground cover, and nest cover. I interpret this component as a measure of the diversity of vertical vegetation density and cover used by nesting species. The third principal component

(eigenvalue = 1.19) accounted for 15 percent of the total variation and was most strongly represented by an inverse relationship of canopy cover and ground cover. This component is indicative of the variation between tree fall gaps, which are characterized by low canopy cover and high ground cover, and non-gap areas of the forest where the opposite of this situation occurs. The fourth principal component (eigenvalue = 0.90) accounted for 11 percent of the total variation and was representative of an inverse relationship of canopy cover and shrub cover and a positive measure of ground cover. I interpret this component to be an extension of the variation of gap and non-gap areas displayed more clearly by the third principal component.

Table 3.25. Eigenvectors of first four principal components of nest-site microhabitat variables.

Variable	Principal Component 1	Principal Component 2	Principal Component 3	Principal Component 4
Plant height	0.543	0.201	0.081	0.045
Plant diameter	0.519	0.175	0.048	0.002
Nest height	0.497	0.198	0.229	-0.0277
Nest cover	-0.331	0.424	0.233	0.188
Canopy closure	0.051	0.111	-0.667	0.627
Ground cover	-0.176	0.218	0.595	0.528
Shrub density	-0.206	0.487	-0.109	-0.536
Mid-story density	-0.039	0.641	-0.268	-0.013

CLUSTER ANALYSIS

I used agglomerative hierarchical cluster analysis to determine groups of species with similar measures of nest-site microhabitat characteristics. As in other studies (e.g.

Holmes et al. 1979, Barrow 1990), groupings are defined as those species or groups of species separated from one another by distances greater than the mean distance among species. The dendrogram graphically depicts groupings of species that are similar in nest-site characteristics (Figure 3.20).

The mean normalized distance in this analysis was 0.85. From the 33 species entered into the analysis, 8 clusters were recognized. The first cluster contained open-cup species that nest at mid-height levels and also a separate subset of cavity nesters. The second cluster contained low shrub, open-cup nesters and one cavity nester, the Carolina Chickadee (*Parus carolinensis*). The third cluster contained two open-cup species with high average nest heights and a separate subset of two cavity nesters. The fourth cluster contained Downy and Hairy woodpeckers (*Picoides pubescens* and *P. villosus*) along with two mid-to-high height open-cup species and the Northern Parula. The fifth group was comprised of only the Eastern Wood-Pewee (*Contopus virens*). Nests of this species were only found at the extreme upper branches of the largest trees. The sixth group contained only the Pileated Woodpecker (*Dryocopus pileatus*) and Great Crested Flycatcher (*Myiarchus crinitus*), two of the larger cavity-nesters. Both species nest in large snags or dead branches in large, live trees. The seventh group contained only the Mississippi Kite (*Ictinia mississippiensis*), whose nests were found primarily in mid-to-large size trees. The eighth group contained the Red-shouldered Hawk (*Buteo lineatus*) and the Yellow-crowned Night-Heron (*Nycticorax violaceus*). Nests of both of these species were typically found in the largest trees.

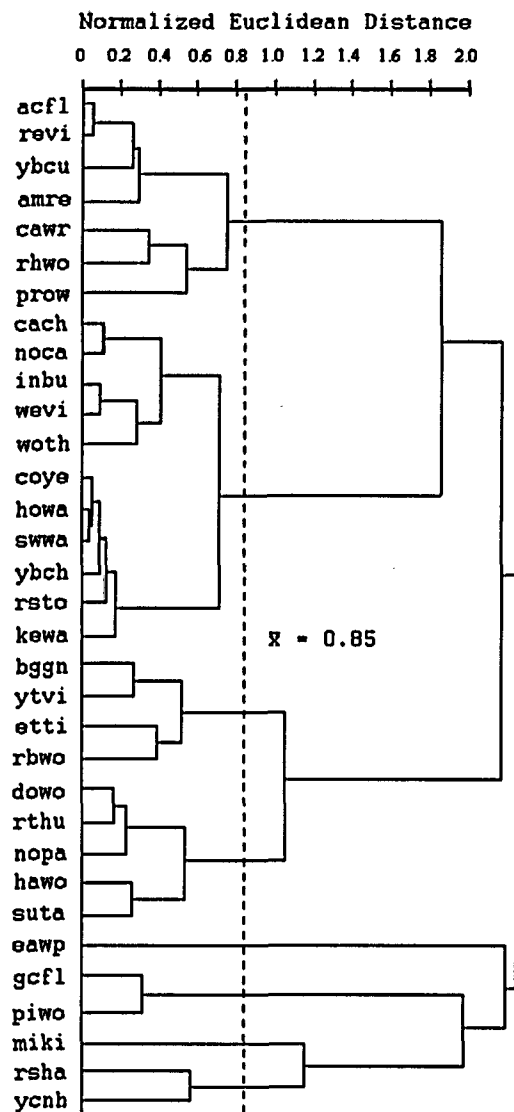


Figure 3.18. Cluster analysis dendrogram depicting species relationships based on nest-site characteristics. Bird species abbreviations are presented in Appendix A.

DISCUSSION

Description of the habitat use by bird communities in bottomland hardwood forests has received comparatively little attention. Two studies conducted in Louisiana (Barrow 1990, Dickson and Noble 1978) have both provided evidence of ecological partitioning of habitat by breeding songbirds.

Dickson and Noble (1978) examined the vertical distribution of birds in a bottomland hardwood forest during different seasons of the year. They found that Red-headed Woodpecker (*Melanerpes erythrocephalus*), Pileated Woodpecker and Blue Jay (*Cyanocitta cristata*) were most restricted to the canopy zone (7.6 m to canopy top), whereas White-eyed Vireo, Kentucky Warbler, and Carolina Wren were most restricted to the midstory zone (0.6 m to 7.6 m). Other species were not as highly restricted to a vertical profile or zone within the forest. They observed a winter to summer height distribution change, whereby the species distribution was nearly equal at all levels in the winter but was dominated by species in the midstory and canopy during the summer. They concluded that the distributional shift was a response of the birds to the seasonal change in foliage profile and food supply, but did not measure these variables. Their samples were only taken on birds encountered while walking a 1.6 km transect and did not include data from actual nest-sites.

Barrow (1990) examined the habitat use by foraging songbirds during the breeding season on the Tensas River National Wildlife Refuge in Louisiana. Using correspondence analysis, he found the foraging activity of the 16 species studied was

ordinated according to a foraging height gradient and a foliage density gradient. Swainson's Warbler was found to be a ground forager (<0.5 m), and Kentucky Warbler and Carolina Wren were shrub height foragers (0.5-2.0 m). Prothonotary Warbler foraged primarily at the junction of the shrub and subcanopy layers. Hooded Warbler, Tufted Titmouse, Carolina Chickadee, Acadian Flycatcher, and White-eyed Vireo foraged most in the subcanopy (2.1-10 m). Yellow-throated Vireo (*Vireo flavifrons*), Yellow-throated Warbler (*Dendroica dominica*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Eastern Wood-Pewee, and American Redstart used the canopy layer (>10 m). Northern Parula and Red-eyed Vireo foraged primarily at the junction of the canopy and subcanopy layers. Species foraging in sparse foliage (<30 percent) included the Acadian Flycatcher, Eastern Wood-Pewee, Tufted Titmouse, and Swainson's Warbler. Carolina Wren, American Redstart, Kentucky Warbler, and Hooded Warbler all foraged in dense foliage (>50 percent). The remainder of the species foraged in moderate foliage density (30-50 percent).

A comparison of the foraging height and foliage density in Barrow's (1990) study with nest height and foliage density from this study can be useful in determining patterns of habitat use by these species (Table 3.26). The study areas were different (although both were in bottomland forests of Louisiana), and minor differences exist in methods used in the two studies, but a general comparison is still possible.

Table 3.26. Comparison of foraging height and foliage density with nest height and foliage density.

Species	Foraging Height Class	Nest Height Class	Foraging Foliage Density Class	Nest Foliage Density Class
Swainson's Warbler	ground	shrub	sparse	dense
Kentucky Warbler	shrub	ground	dense	dense
Carolina Wren	shrub	shrub	dense	moderate
Prothonotary Warbler	shrub-subcanopy	subcanopy	moderate	sparse
Hooded Warbler	subcanopy	shrub	dense	dense
Acadian Flycatcher	subcanopy	subcanopy	moderate	moderate
White-eyed Vireo	subcanopy	shrub	moderate	dense
Blue-gray Gnatcatcher	canopy	canopy	moderate	moderate
American Redstart	canopy	canopy	dense	dense
Northern Parula	subcanopy - canopy	canopy	moderate	moderate
Red-eyed Vireo	subcanopy - canopy	subcanopy	moderate	dense

Note: Height and foliage density data and classification scheme from Barrow 1990. For the height classes, ground = < 0.5 m, shrub = 0.5-2.0 m, subcanopy = 2.1-10.0 m, canopy = > 10.0 m. For the foliage density classes, sparse = < 30 percent, moderate = 30-50 percent, dense = > 50 percent.

One species, Swainson's Warbler, forages predominately at lower levels than it nests. Two species, Hooded Warbler and White-eyed Vireo, forage at predominately

higher levels than they nest. The remaining species forage and nest at approximately the same level in the forest.

Swainson's Warbler, White-eyed Vireo, and Red-eyed Vireo forage primarily in vegetation that is less dense than that used for nesting whereas Carolina Wren and Prothonotary Warbler forage in vegetation that is more dense than that used for nesting. The vegetation density of nest-sites and foraging sites is approximately the same for the remaining species.

Differences in habitat characteristics at nest-sites and randomly selected points were noted for most species in this study. Similar results have been documented for a variety of species in other habitats (e.g., MacKenzie and Sealy 1981, Petersen and Best 1985, Bekoff et al. 1987, Petit et al. 1988) but this study is the first to do so for nest-sites of birds breeding in the bottomland forests of Louisiana. Also, classification of nest-sites and random sites with the discriminant function analysis was rather accurate. The use-availability analyses are beneficial in determining nest-site habitat parameters that are selected for by species in the avian community (see Table 3.20). Groups of species with similar nest-site characteristics were determined with the use of cluster analysis, and this information could be incorporated into a habitat management scheme.

I did not detect significant differences in the microhabitat characteristics between successful and unsuccessful nests for most species. The lone exception occurred with significantly higher midstory density of successful American Redstart nest-sites. One variable thought to be important in nest success is the amount of nest cover (Martin

1993), yet I found no significant difference in this variable between nests that failed or succeeded. Reports in the literature vary on the importance of cover to nest success in songbirds. Best and Stauffer (1980) examined 302 nests of 13 species in Iowa and found that nest concealment was not significantly related to nesting outcome. Anderson and Storer (1976) showed that there was no difference in the nest cover of successful and unsuccessful Kirtland's Warbler nests. Caccamise (1977) found that nest cover did not differ between successful and unsuccessful Red-winged Blackbird (*Agelaius phoeniceus*) nests, and the same results were reported by Best (1978) for Field Sparrows (*Spizella pusilla*). Conner et al. (1986) found "no significant correlation" in nest concealment and nest success for Northern Cardinals. However, Patonde and White (1992) found that for 256 nests of 4 species in Georgia, nests with higher cover had significantly higher daily survival rates. Nolan (1978) found that the success of Prairie Warbler (*Dendroica discolor*) nests was directly related to the amount of nest cover, and Martin (1988) reported the same results for Hermit Thrush (*Catharus guttatus*) in Arizona.

As indicated, this bird community includes a wide array of species with a variety of different nest-site habitat requirements. The main sources of variability are indicated in the principal components analysis, and the information from this analysis can also be included in a management program. My interpretation of the principal components analysis is that selection of nest-site habitat by species in this community has evolved around the vegetation characteristics common to old-growth or climax bottomland hardwood forest. The first principal component was indicative of a large variety of tree

heights and diameters, the second principal component was indicative of variation in the vertical vegetation density profile, and the third and fourth principal components related to contrasting vegetation characteristics of tree fall gaps and non-gap areas. All of these characteristics describe the vegetation of old growth bottomland forest (K. Ouchley, manuscript in preparation). The *variability* of these characteristics is either lacking or is usually diminished in present day "managed forests" that are comparably younger than virgin timber.

MANAGEMENT CONSIDERATIONS

Allowing the forest to return to a climax condition is a management form that in most cases would provide the wide range of habitat conditions needed by nesting songbirds. However, this solution is not feasible on the majority of commercial timberland in the region. I concur with other researchers (Barrow 1990, Martin 1992, Pashley and Barrow 1993) that on private, commercial lands, forestry management techniques and harvest practices that increase the structural and floristic diversity should be stressed. Management practices that closely resemble natural processes such as tree fall gaps should be used to accomplish this goal. An example of this type of management is single-tree selection (Pashley and Barrow 1993). Where possible, longer rotation periods and snag management should be implemented for the benefit of species using larger trees such as Eastern Wood-Pewee, Mississippi Kite, and Red-shouldered Hawk, and species using cavities such as Great Crested Flycatcher, Prothonotary Warbler, Carolina Wren, Carolina Chickadee, and woodpeckers.

Concentrating on the floristic aspect of this study, a rather unique pattern is noticed. For six of eight migrant species, sweet gum was the most commonly used nest plant: Acadian Flycatcher, American Redstart, Red-eyed Vireo, Ruby-throated Hummingbird, White-eyed Vireo, and Yellow-billed Cuckoo. Sweet gum also was used more often than its availability for four of these species: Acadian Flycatcher, American Redstart, Ruby-throated Hummingbird, and White-eyed Vireo. It ranked number two in this category with the Yellow-billed Cuckoo and number three with the Red-eyed Vireo.

The prominent selection of sweet gum as a nest plant is unique because the tree is used by a wide range species at all stages of the tree's life cycle. White-eyed Vireos use small saplings and shrubs, Yellow-billed Cuckoos use the trees as they begin to emerge above the shrub layer and into the midstory, and Acadian Flycatchers, Ruby-throated Hummingbirds, and American Redstarts use larger, more mature trees.

The selection of sweet gum does not in itself automatically warrant the endorsement of this species. If the birds were selecting sweet gum, and the nest success in this plant was worse than in other plant species, then little advantage could be gained by simply planting more sweet gum trees. However, for most species that select sweet gum, the number of young fledged per nest is better or equal to that in other nest plants (Table 3.27).

Table 3.27. Comparison of the mean number of young fledged per nest between nests in sweet gum trees and all other nest plants.

Species	Sweet gum	All others
	Mean \pm SD, (N)	Mean \pm SD, (N)
Acadian Flycatcher	1.09 \pm 1.14 (42)	0.94 \pm 1.17 (117)
American Redstart	1.40 \pm 1.51 (5)	2.00 \pm 2.00 (5)
Red-eyed Vireo	1.00 \pm 1.57 (7)	1.00 \pm 1.20 (23)
Ruby-throated Hummingbird	1.00 \pm 1.41 (2)	1.10 \pm 0.98 (10)
White-eyed Vireo	1.20 \pm 1.56 (15)	1.15 \pm 1.42 (88)
Yellow-billed Cuckoo	1.00 \pm 1.73 (3)	0.50 \pm 1.00 (12)

Why should sweet gum play a major in the nesting of these species? In millions of acres of virgin forest that once covered the Lower Mississippi Valley in Louisiana, sweet gum was one of, if not the dominant tree species (K. Ouchley, manuscript in preparation). The bird species that breed in these forests have evolved with sweet gum as a major component of the ecosystem. Sweet gum may provide certain structural characteristics that the species are keying on. Further exploration of this relationship is suggested.

Forestry practices in the early 1900's favored the removal of sweet gum (Tanner 1942). For the benefit of a certain contingent of species that breed in these forest, the encouragement of sweet gum regeneration and the practice of allowing sweet gums to reach maturity should be promoted. The growth and reproduction of mast-producing trees is commonly promoted as a management technique for game species (Reinecke 1994). Perhaps sweet gum should be included in a comprehensive wildlife management program.

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APPENDIX A.

LIST OF ABBREVIATIONS FOR BIRD SPECIES USED IN THIS TEXT.

Species	Abbreviation
Acadian Flycatcher	ACFL
American Redstart	AMRE
Blue-gray Gnatcatcher	BGGN
Carolina Chickadee	CACH
Carolina Wren	CAWR
Common Yellowthroat	COYE
Downy Woodpecker	DOWO
Tufted Titmouse	ETTI
Eastern Wood-Pewee	EAWP
Great Crested Flycatcher	GCFL
Hairy Woodpecker	HAWO
Hooded Warbler	HOWA
Indigo Bunting	INBU
Kentucky Warbler	KEWA
Mississippi Kite	MIKI
Northern Cardinal	NOCA
Northern Parula	NOPA
Pileated Woodpecker	PIWO
Prothonotary Warbler	PROW
Red-bellied Woodpecker	RBWO
Red-eyed Vireo	REVI
Red-headed Woodpecker	RHWO
Red-shouldered Hawk	RSHA
Ruby-throated Hummingbird	RTHU
Rufous-sided Towhee	RSTO
Summer Tanager	SUTA
Swainson's Warbler	SWWA
White-eyed Vireo	WEVI
Wood Thrush	WOTH
Yellow-billed Cuckoo	YBCU
Yellow-breasted Chat	YBCH
Yellow-crowned Night-Heron	YCNH
Yellow-throated Vireo	YTVI

APPENDIX B.

LIST OF ABBREVIATIONS FOR PLANT SPECIES USED IN THIS TEXT.

Species	Abbreviation
American beautyberry	BEBE
American elm	AMEL
Bald cypress	BACY
Box elder	BOEL
Cedar elm	CEEL
Cherrybark oak	CHOK
Swamp dogwood	DOGW
Fern (<i>Thelypteris</i> sp.)	FERN
Green ash	GASH
Hackberry	HACK
Hawthorn (<i>Crataegus</i> sp.)	HAWT
Deciduous Holly	HOLL
Honey Locust	HOLU
Lizard's tail	LIZA
Nuttall oak	NUOK
Overcup oak	OVOK
Palmetto	PALM
Pecan (<i>Carya</i> sp.)	PECA
Persimmon	PERS
Red maple	REMA
<i>Rubus</i> sp.	RUBU
Sweet gum	SWGU
Sycamore	SYCA
Water oak	WAOK
Willow oak	WIOK

VITA

Keith Ouchley was born on December 15, 1959 in New Iberia, Louisiana. He graduated from high school at Ridgedale Academy in West Monroe, Louisiana in 1977. In 1981, he obtained a B. S. with minors in Biology and Chemistry at Northeast Louisiana University in Monroe. He married Lila Susan Carter of Crossett, Arkansas in June 1984. In 1992, he recieved a M. S. in Biology from Northeast Louisiana University. He began his Ph.D. work in the School of Forestry, Wildlife, and Fisheries at Louisiana State University, Baton Rouge, in August 1992 and is currently a candidate for that degree.

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Hardwood Forests of Louisiana

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