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Ecology of Small Insectivorous Birds in a Bottomland Hardwood Forest.

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ECOLOGY OF SMALL INSECTIVOROUS BIRDS
IN A BOTTOMLAND HARDWOOD FOREST

A Dissertation

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by
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Finally, I wish to dedicate this dissertation to my children, Lindsey Christine Barrow and W. Clark Barrow, III, in hope that they will learn to appreciate the natural world in which they exist, and perhaps one day contribute to its conservation for their children.

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ABSTRACT

Changes in species composition and abundance, habitat use patterns and foraging behavior of 19 bird species in a bottomland hardwood forest in Louisiana were studied during the 1984-1989 breeding seasons. Species that used only one macrohabitat included the Yellow-throated Warbler along oxbow lake margins and the American Redstart, Swainson's Warbler, and Hooded Warbler in non-flooded oak-gum-elm forest. The Northern Parula and Kentucky Warbler used 2 macrohabitats -non-flooded forest and oxbow lake margins. Thirteen species used 3 macrohabitats (non-flooded forest, seasonally flooded forest, and oxbow lake margins).

I distinguished 6 groups of species that used similar microhabitat and foraging behavior. Ecological partitioning occurred primarily by (1) foraging height and height-related characters, (2) foraging locations within the forest canopy, and (3) differential use of foraging substrates and foraging maneuvers. Vegetation structure and height may be important in determining the abundance and combination of insectivorous birds existing at Tensas.

Implications for management and conservation are discussed. To conserve migrant insectivorous birds, we must know the ranges, habitats, and patterns of habitat use. I selected a representative species, the Hooded Warbler, and compared habitat use and foraging ecology at a breeding and wintering site.

Hooded Warbler winter distribution is concentrated along the Gulf of Mexico coast and Caribbean Slope from southcentral Veracruz to Honduras. Winter habitat is typically undergrowth of humid forest; second-growth habitats are also important.

At Tensas, hoodeds preferred dense foliage in the shrub and subcanopy layers, and captured prey primarily from the lower surfaces

of leaves. At Los Tuxtlas, they were more generalized and captured prey from air and leaves, used a variety of other substrates, and foraged in open portions of the lower levels of the forest.

Macro- and microhabitat use by Hooded Warblers were different at my study sites in the breeding and non-breeding ranges. I believe, the use of habitats varies between locations such as the wintering and breeding grounds for many species; to evaluate the relative importance of any proposed habitat changes, we must know how the changes will affect macro- and microhabitat and how the species use macro- and microhabitat.

Chapter 1. INTRODUCTION

Many forest-inhabiting birds are extremely sensitive to habitat change. Because of this high sensitivity, habitat variables are present that can be measured and manipulated to influence the occurrence of these particular birds (Hooper and Crawford 1969). To understand what habitat variables are most important to particular species, one must first understand how each species uses its habitat and what habitat components influence abundance and survival.

The optimal design of nature preserves and the impact of forest management practices on migrant birds have attracted increasing interest in recent years (Wilcove et al. 1986). In forests managed for multiple use, managers would like to know what bird species will be beneficially or detrimentally affected when particular areas of forest are harvested or otherwise altered.

Bottomland hardwoods is a term generally used to describe the forest type occurring in river floodplains of the United States. The forest occurs on soils that are moisture-saturated or inundated during a portion of a year to an extent that the plant species which become established are adapted to moist soil conditions(Wharton et al. 1982). Because of their proximity to rivers and streams, bottomland hardwoods fit within the general definition of riparian vegetation (Turner et al. 1981).

Harvests of bottomland hardwood forest of the southeastern river valleys of the United States became one of the most controversial natural resource issues of the 1970's (U. S. Fish and Wildlife Service 1984). These forests were being extensively diked, cleared, and usually planted in soybeans, and were thereby largely removed from the

natural riverine ecosystem (MacDonald et al. 1979).

Extent of the declines have been documented for several regions. In southeast Missouri by the mid 1970s, 1 million hectares of bottomland hardwoods have been reduced to 39,000 hectares, of which only 11,000 hectares is in blocks of 400 hectares or more (Korte and Frederickson 1977). Forests covered 1.7 million hectares of the Arkansas delta region in 1940 and only about 0.7 million hectares in 1970 (Holder 1970). Losses in the Carolinas, Georgia, and northern Florida have been less severe, where a total of about 2.1 million hectares remain (Wharton et al. 1982). With about 1.2 million hectares of bottomland hardwoods in 1978 (MacDonald et al. 1979), Louisiana leads the nation in area remaining. Thus, it might be possible to still have large tracts of bottomland hardwoods in Louisiana and it is appropriate that research and conservation efforts should be centered in this state.

Throughout the world, riparian habitat is known to support a higher diversity and density of birds than adjacent habitats. Remsen (1984) reported that 14.3 percent of the total land bird avifauna of the Amazon Basin was restricted to river-created habitats. In western North America, floodplain forests are important to bird populations (Carothers et al. 1974, Hehnke and Stone 1978, Stamp 1978, Rosenberg et al. 1982). In California, conservation of riparian woodland has been listed as top priority in a report on the state's bird species of special concern (Remsen 1978).

Research directly related to bird use of bottomland hardwood forests is very limited (Sampson 1979). Most studies have been confined to breeding bird censuses in various bottomland habitats (Dickson 1973, Hightower et al. 1974, Ortego and Noble 1975). Seasonal and vertical distributions of birds have been examined for an area in

south central Louisiana (Dickson 1978a, Dickson 1978b, Dickson and Noble 1978, Dickson 1979). The avifauna of the Atchafalaya River Basin has also been analyzed (Kennedy 1977).

In a Massachusetts forested wetland, Swift et al. (1984) found that breeding bird density (especially of foliage gleaners) and species' richness were larger at sites with deeper organic soils and greater coverage by seasonal surface water. Smith (1977) documented the association of several bird species to habitat components affected by a forest moisture gradient.

Lowland hardwood forests are important for insectivorous birds during migration. Parnell (1969) evaluated the habitat relations of warblers in six different vegetation types during spring migration in North Carolina. He found that floodplain forest habitat contained the largest group of regularly occurring warbler species. Graber and Graber (1980) found that at the peak of spring migration in Illinois, the population of migrant warblers was more than three times greater in bottomland than in upland forest.

Most authorities generally agree that habitat preferences by passerine birds are strongly influenced by vegetation structure (Lack 1933, MacArthur and MacArthur 1961, MacArthur 1964, Karr and Roth 1971, Willson 1974). Recently, multivariate techniques have been used to identify significant habitat components for a single species (James et al. 1984), a few bird species (Noon 1981, Shy 1984), and communities (James 1971, Anderson and Shugant 1974, Whitmore 1975).

Robinson and Holmes (1982) suggested that the foraging strategies of forest birds are influenced by branching patterns, the spatial arrangement of leaves, and other parameters of foliage structure. Mauer and Whitmore (1981) found differences in the foraging behavior of five species of forest-inhabiting birds in two watersheds with

contrasting structures. Recently, several investigators have provided evidence that some bird species may forage preferentially in certain kinds of trees (Holmes and Robinson 1981, Bock and Bock 1984, Rice et al. 1984, Robinson and Holmes 1984). Thus, vegetation structure of a particular forest type apparently provides a set of opportunities and constraints that influence how and where birds forage and, as a consequence, may determine which bird species can successfully exploit and survive in a particular habitat.

Differences in habitat use among forest-inhabiting birds, also depend on the constraints of morphology on behavior. Difference in bill, wing, and leg morphology, and body weight may differentially affect the accessibility to certain vegetation structures and associated prey items (Moermond and Denslow 1985).

The first objective of this study was to first examine the distribution, relative abundance, habitat use, and foraging behavior by several small species of passerine birds foraging for insects among the foliage of a bottomland hardwood forest. A second objective was to investigate the seasonal variation in habitat use and foraging ecology of a representative species, the Hooded Warbler (*Wilsonia citrina*), a long-distance, neotropical migratory species.

LITERATURE CITED

Anderson, S. R., and H. H. Shugart. 1974. Habitat selection in an east Tennessee deciduous forest. Ecology, 55:828-837.

Bock, C. E., and J. H. Bock. 1984. Importance of sycamores to riparian birds in Southeastern Arizona. J. Field Ornithol. 55:97-103.

Carothers, S. W., R. R. Johnson and S. W. Aitchison. 1974. Population structure and social organization of Southwestern riparian birds. Am. Zool. 14:97-108.

Dickson, J. G., 1973. Mature bottomland hardwood forest. Page 973 *in* W. T. Van Velzin (ed.), Thirty-seventh breeding bird census. Am. Birds 27.

Dickson, J. G. 1978a. Forest bird communities of the bottomland hardwoods. Pages 66-73 *in* R. M. DeGraaf, tech. coord. Management of southern forests for nongame birds. USDA For. Serv., Gen. Tech. Rep.SE-14. Asheville, N. C.

Dickson, J. G. 1978b. Seasonal bird populations in a south central Louisiana bottomland hardwood forest. J. Wildl. Manage. 42(4):875-883.

Dickson, J. G. 1979. Seasonal populations of insectivorous birds in a mature bottomland hardwood forest in south Louisiana. Pages 261-268 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Krull, and J. A. Jackson, eds. Proceedings of a symposium, the role of insectivorous birds in forest ecosystems. Academic Press, New York.

Dickson, J. G., and R. E. Noble, 1978. Vertical distribution of birds in a Louisiana bottomland hardwood forest. Wilson Bull. 90(1):19-30.

Hehnke, M., and C. P. Stone. 1978. Value of riparian vegetation to avian populations along the Sacramento River System. Pages 228-235 *in* R. R. Johnson, J. F. Mccormick, tech. coords. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA For. Serv., Gen. Tech. Rep. WO-12. Callaway Gardens, Georgia.

Hightower, S. B., C. D. Fisher, and M. C. Butts. 1974. South floodplain forests. Page 1011 *in* W. T. Van Velzen (ed.) Thirty-eight breeding bird census. Am. Birds 28.

Holder, T. H. 1970. Disappearing wetlands in eastern Arkansas. Arkansas Planning Commission, Little Rock. 72 p.

Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia (Berlin) 48: 31-35.

Hooper, R. G., and H. S. Crawford. 1969. Woodland habitat research for nongame birds. Trans. North Amer. Wildl. and Nat. Res. Conf. 34:201-207.

James, F. C. 1971. Ordinations of habitat relationships among birds.

Wilson Bull. 83:215-236.

James, F. C., R. F. Johnson, N. O. Wamer, G. J. Niemi, and W. J. Boecklen. 1984. The grinnellian niche of the Wood Thrust. Am. Nat. 124:17-30.

Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423-435.

Kennedy, R. S. 1977. Ecological analysis and population estimates of the birds of the Atchafalaya River basin in Louisiana. Ph.D. dissertation. Louisiana State University, Baton Rouge. 201 pp.

Korte, P. A., and L. H. Frederickson. 1977. Loss of Missouri's lowland hardwood ecosystem. Trans. North Amer. Wildl. Nat. Res. Conf. 42:31-41.

Lack, D. 1933. Habitat selection in birds. J. Anim. Ecol. 2:239-262.

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

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacDonald, P. O., W. E. Frayer, and J. K. Clauser. 1979. Documentation, chronology, and future projections of bottomland hardwood habitat loss in the lower Mississippi alluvial plain. U. S. Fish and Wildl. Serv. Div. of Ecological Serv. 133 p.

Maurer, B. A., and R. C. Whitmore. 1981. Foraging of five bird species in two forests with different vegetation structure. Wilson Bull. 93:478-490.

Moermond, T. C., and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. In Neotropical Ornithology pp. 865-897, (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds.) Ornithol. Monogr. no. 36, Amer. Ornithol. Union, Washington, D. C.

Noon, B. 1981. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol. Monogr. 51:105-124.

Ortego, B., and R. E. Noble. 1975. Tupelo swamp. Pages 1097-1098 *in* W. T. Van Velzen (ed.), Thirty-ninth breeding bird census. Am. Birds 29.

Remsen, J. V., Jr. 1978. Bird species of special concern in California. Calif. Dept. of Fish and Game Tech. Rep. 54 pp.

Remsen, J. V., Jr., and T. A. Parker, III. In press. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica.

Rice, J., B. W. Anderson, and R. D. Omhart. 1984. Comparison of the importance of different habitat attributes to avian community organization. J. Wildl. Manage. 48:895-911.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918-1931.

Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672-684.

Rosenberg, K. V., R. D. Omhart, and B. W. Anderson. 1982. Community organization of riparian breeding birds: response to an annual resource peak. Auk 99:260-274.

Sampson, F. B. 1979. Lowland hardwood bird communities. Pages 49-66 *in* R. M. DeGraaf and K. E. Evans (eds.), Management of north central and northeastern forests for nongame birds. USDA For. Serv. Gen. Tech. Rep. NC-51.

Shy, E. 1984. Habitat shift and geographical variation in North American tanagers (Thraupinae: *Piranga*). Oecologia 63:281-285.

Smith, K. G. 1977. Distributions of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810-819.

Stamp, N. E. 1978. Breeding birds of riparian woodland in south-central Arizona. Condor 80:64-71.

Swift, B. L., J. S. Larson, and R. M. DeGraaf. 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. Wilson Bull. 96:48-59.

Tanner, J. T. 1942. The Ivory-billed Woodpecker. Nat. Aud. Soc. Res. Rep. No. 1. 99 pp.

Turner, R. E., S. W. Forsythe, and N. J. Craig. 1981. Bottomland hardwood forest land resources in the southeastern United States. Pages 13-28 *in* J. R. Clark and J. Benforado, eds. Wetlands of bottomland hardwood forests. Elsevier Scientific Publ. Co., New York.

U. S. Fish and Wildlife Service. 1984. Blue ribbon panel for bottomland hardwoods. U. S. Dept. of Interior, Fish and Wild. Serv., Vicksburg, Miss.

Wharton, C. H. 1980. Values and functions of bottomland hardwoods. Trans. North Amer. Wildl. Nat. Res. Conf. 45:341-353.

Wharton, C. H., W. M. Kitchens, E. C. Pendleton, and T. W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast: a community profile. U. S. Fish and Wildlife Service, Biological Services Program, Washington, D. C. FWS/OBS-81/37. 133 pp.

Whitemore, R. C. 1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

Wilcove,D. S.,C. H. Mclellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. In Conservation Biology, The Science of Scarcity and Diversity, pp.237-256 (M. E. Soule, ed.), Sinauer Associates, Inc., Sunderland, Mass.

Willson, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

Chapter 2. HABITAT USE AND FORAGING ECOLOGY OF SMALL INSECTIVOROUS FOREST BIRDS OF THE TENSAS RIVER BASIN

INTRODUCTION

> "The Singer Tract is important for the conservation of other forms of wildlife as well as the Ivory-bill. It is unique in that every form of animal native to the region, except those extinct, is still living there. Deer and Wild Turkey are abundant; wolves, including black individuals, bear, and panther are present; big alligators still swim in the lakes; and smaller animals and birds are everywhere abundant. The richness of the plant life is another reason for its preservation. Big trees of several species stand throughout the forest and make it a beautiful place. This forest affords an excellent example, and is the last remaining large stand, of the primeval forest that once covered all the bottomlands of the Mississippi Delta."
>
> James T. Tanner 1942 (p. 90)

The Mississippi River floodplain has changed dramatically since the arrival of Europeans on this continent. In 1937, the Mississippi alluvial floodplain south of Kentucky and Missouri contained 5.2 million ha forest land. Only 2.9 million ha remained in the mid 1970s (MacDonald et al. 1979). A recent study has estimated the total annual clearing rate in the Lower Mississippi River Valley to be about 44,600 ha per year (U.S. Fish and Wildlife Service 1984).

In Louisiana, flood control, bank stabilization, and agricultural drainage projects have removed much of the state's vast bottomland hardwood forest. At one time, 42 percent of the state was covered by bottomland hardwoods. By 1980, only 21 percent (1.2 million ha) of the state was covered and the removal rate was

determined to be 16,400 ha annually (Turner and Craig 1980). At this depletion rate only 931,000 ha of the present 1.03 million ha will remain in 1995 (MacDonald et al. 1979). Even with these dramatic reductions, Louisiana still has the most bottomland hardwoods of any state in the nation with 57 percent of the total acreage in the lower Mississippi River Valley (Turner et al. 1981).

The loss of this productive forest habitat is a major threat to forest wildlife, especially to forest-inhabiting birds. George (1971) indicated that 8 of 16 bird species that no longer breed in Illinois were residents of the Mississippi River floodplain. In the South at least one species, the Ivory-billed Woodpecker (*Campephilus principalis*), most probably extinct, declined as a result of the disappearance of mature lowland forest and swamps (Tanner 1942). Unfortunately, specific environmental requirements of resident and migratory birds in bottomland hardwood forests are little known (Sampson 1979). Thus, the goal of this chapter is to provide quantitative descriptions of habitat use and foraging behavior of the syntopic neotropical migrant bird species and their resident counterparts that inhabit the forests of the Tensas River Basin. More specifically, the objectives of the study are to:

1. Determine the relative abundance of the small (<22 g) insectivorous birds breeding in the three major habitat types of bottomland hardwood forests (seasonally flooded forest, non-flooded forest, and oxbow lake edges) during 1984 through 1989.
2. Describe the habitat use of small insectivorous birds in terms of foraging microhabitat and broad habitat types, and,

3. Determine the similarities and differences among the small insectivorous birds in terms of how they exploit food resources.

STUDY AREAS AND METHODS

STUDY SITES

Habitat measurements, foraging observations, and bird counts were made during the spring and summer in the Tensas River Basin on the Tensas River National Wildlife Refuge, Madison Parish, Louisiana (91°22'W,32°21'N). Relative abundance was determined from late March to early August 1984-1989. Habitat and foraging data were collected from late March to late July 1984-1987.

The vegetation of the Tensas River Basin is dominated by the bottomland hardwood forest type. The refuge preserves part of a forest tract comprising approximately 40,470 ha and is essentially an island amid an expanse of intensive agricultural development.

The mosaic distribution of floodplain microtopography, soil types, and plant communities make recognition of extensive, distinct habitat types somewhat difficult. However, three contiguous broad habitat types were selected and representative study sites were selected after preliminary field observations during the summer of 1983. The three habitat types were forest, flat, and oxbow; study sites will be identified by the habitat type they represent. They are described below.

Forest. - This study site is a second-terrace forest of the Lower Mississippi River Floodplain and does not seasonally flood, except for small depressions of parallel scour channels approximately 25 m wide. The area encompasses approximately 240 ha. The forest is relatively mature (approximately 75 yrs. old); the canopy is dominated by sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), willow oak (*Q.phellos*), and various species of elm (*Ulmus spp.*) (U.S. Fish and Wildlife Service 1988, compartment no. 7). The

understory consists primarily of saplings, swamp palmetto (*Sabal minor*), deciduous holly (*Ilex decidua*), and numerous vines such as *Rhus radicans*, *Berchemia scandens*, and *Ampelopsis arborea*.

Flat.- This study site is a first terrace flat or backswamp, comprising approximately 120 ha. This habitat is representative of the most poorly drained flats of the floodplain, where water usually stands well into the growing season (Wharton 1980). The canopy is dominated by overcup oak (*Quercus lyrata*) and bitter pecan (*Carya aquatica*). Associate species include hackberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanica*), America elm (*Ulmus americana*), honeylocust (*Gleditsia triacanthos*), Nuttall oak (*Quercus nuttallii*), and swamp privet (*Forestiera acuminata*). (U.S. Fish and Wildlife Service 1988, compartment no. 6). The extended hydroperiod in these sites inhibits herb growth, and thus the understory is restricted to small trees and shrubs (Eyre 1980).

Oxbow. - This site consists of the vegetation along the edges of oxbow lakes. Two oxbow lakes connected by an approximately 200 m long, narrow slough were selected as study areas. There are approximately 4 km of water-forest edge. Baldcypress (*Taxodium distichum*) is the dominate canopy species. Associate species include bitter pecan, overcup oak, and cedar elm (*Ulmus crassifolia*). (U.S. Fish and Wildlife Service 1988, compartment no. 6). Common buttonbush (*Cephalanthus occidentalis*) is the most prominent shrub present. Various species of vines range from the shrub layer through the canopy.

The study area is in a subtropical, transitional climatic region. Mean monthly minimum and maximum temperatures have ranged between -7.8°C and 36°C (Soil Conservation Service 1982). The average annual precipitation was 1306 mm over a 10-year period. During the breeding season (April-July), the average annual

precipitation for 10 years was 447 mm (Soil Conservation Service 1982). More specific climatic data for the study areas during the course of the study can be found in Figures 2, 3, and 4, and APPENDIX A and APPENDIX B.

FIELD METHODS

Nineteen species of birds were selected for study based on preliminary field observations. In general, they are the small (< 22 g) neotropical migratory species and their resident counterparts, and include the Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher (*Empidonax virescens*), Carolina Chickadee (*Parus carolinensis*), Tufted Titmouse (*Parus bicolor*), Carolina Wren (*Thryothorus ludovicianus*), Ruby-crowned Kinglet (*Regulus calendula*), Blue-gray Gnatcatcher (*Polioptila caerulea*), White-eyed Vireo (*Vireo griseus*), Yellow-throated Vireo (*Vireo flavifrons*), Red-eyed Vireo (*Vireo olivaceus*), Tennessee Warbler (*Vermivora peregina*), Northern Parula (*Parula americana*), Yellow-rumped Warbler (*Dendroica coronata*), Yellow-throated Warbler (*Dendroica dominica*), American Redstart (*Setophaga ruticilla*), Prothonotary Warbler (*Protonotaria citrea*), Swainson's Warbler (*Limnothlypis swainsonii*), Kentucky Warbler (*Oporornis formosus*), and Hooded Warbler (*Wilsonia citrina*). Habitat use was investigated at two spatial scales: (1) macrohabitat (among types) and (2) microhabitat (within vegetative types). Macrohabitat use was compared among the three habitats over a 6-year period. I sampled relative abundance by conducting a series of five minute counts along two transects in each of the three study sites. Each pair of transects was contiguous, but were oriented in different directions. Each bird observed, by sight or sound, during a 5 minute period was noted. I walked at a fairly uniform pace, and a new count began every 5 minutes. I attempted to never count an

Table 1. Description of the census transects in each of the three study sites.

Characteristic	Forest		Flat		Oxbow	
	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Length (m)	650	1560	710	1000	850	1000
Elevation (m)	23	23	18	18	18-23	18-23
Orientation (m)	E-W	W-S	E-N	NE-SW	E-W	E-W

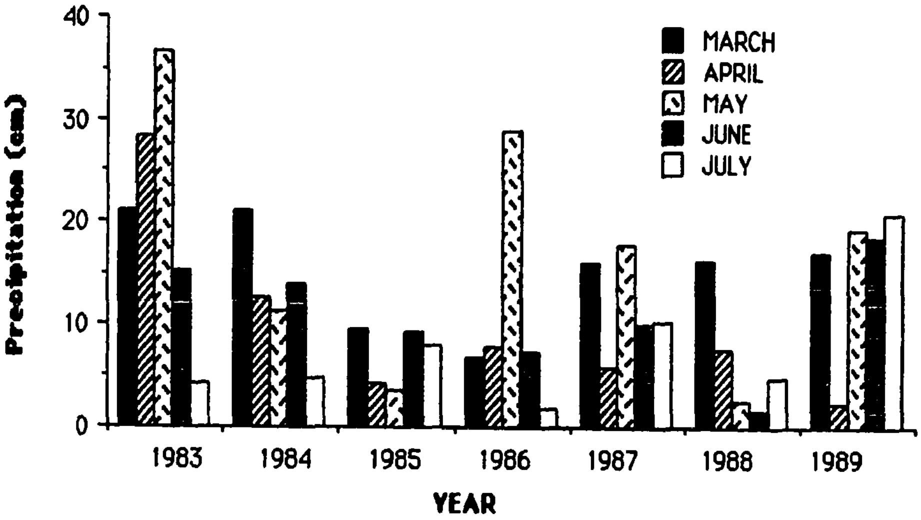


Figure 1. Monthly precipitation values for March, April, May, June, and July 1983 to 1989 in Madison Parish, Louisiana.

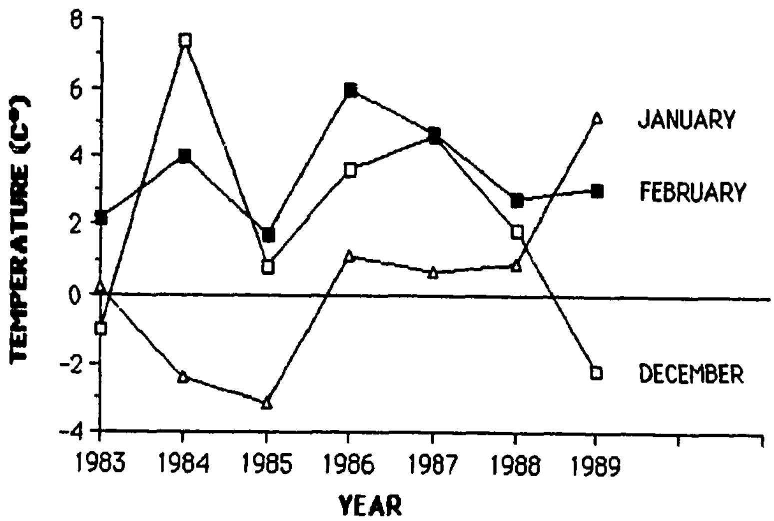


Figure 2. Mean monthly temperature values for December, January, and February 1983 to 1989 in Madison Parish, Louisiana.

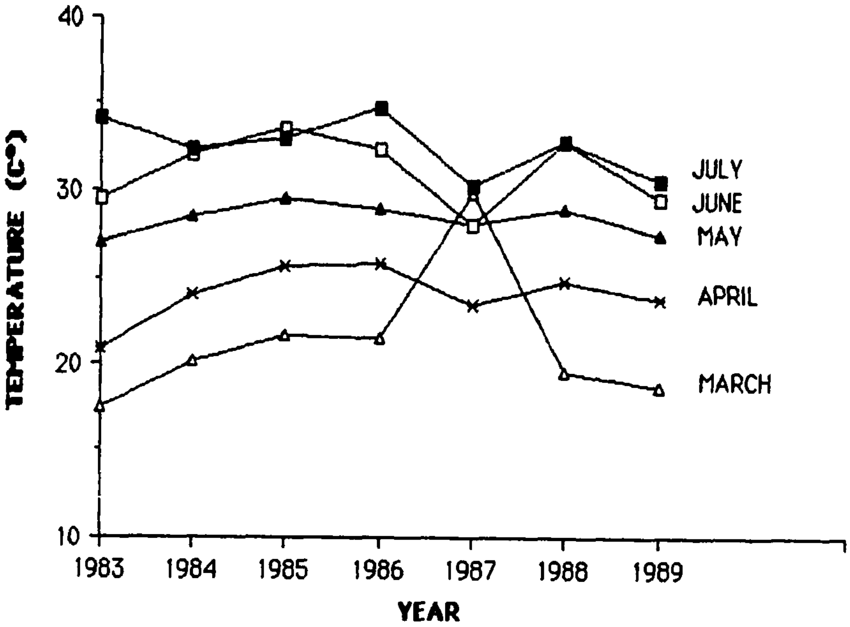
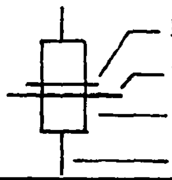


Figure 3. Mean monthly temperature values for March, April, May, June, and July 1983 to 1989 in Madison Parish, Louisiana.

individual bird twice within any one period, but it could have been counted in each of several periods. All sampling was conducted between 0630 and 1130. The length of time for each sampling period ranged between one-half hour and 2 hours, with most consisting of 12 consecutive 5-minute counts. I calculated relative frequency of each species by summing the number of individuals recorded per period. Relative abundance of each species was estimated by dividing the species relative frequency by the sum of all species frequencies. All graphical plots of relative abundance are combined data for each transect pair, unless noted otherwise (see APPENDIX C, APPENDIX D, and APPENDIX E for separate transect data). Terminology used throughout the text for expression of abundance for breeding (May-July) and nonbreeding (15 March-April) birds are as follows: abundant, >2.0 individuals/5 min.; common, >0.5-2.0 ind./5 min.; uncommon, >0.1-0.5 ind./5 min.; and rare, ≤0.1 ind./5 min. My intent is to eventually compare replicate censuses of the 3 macrohabitat types conducted throughout the Tensas Watershed to determine if patterns of macrohabitat use occur at the watershed level.

I compared microhabitat use and availability at all three study areas. Notations used in graphs throughout the chapter are described in Table 2.. Microhabitat was sampled at the site where an individual's first foraging maneuver was observed. An imaginary cylinder (referred to as "feeding cylinder" throughout the text) with a diameter of 2 m and centered on the bird was divided into four height categories: ground (<0.5m), shrub (0.5-2m), subcanopy (2.1-10m), and canopy (>10m) (the diameter of the cylinder in the canopy layer was expanded to 10m). The percent volume volume of vegetation was estimated in each strata; the canopy height was measured with a range finder. The percent cover of habitat features

Table 2. Notations used in box plot figures in Chapter 2.

Notations			
Bird code	Site code	Box plot	Description
AF			Acadian Flycatcher
AR			American Redstart
BG			Blue-gray Gnatcatcher
CC			Carolina Chickadee
CW			Carolina Wren
EP			Eastern Wood-Pewee
HD			Hooded Warbler
KT			Kentucky Warbler
NP			Northern Parula
PW			Prothonotary Warbler
RK			Ruby-crowned Kinglet
RV			Red-eyed Vireo
SW			Swainson's Warbler
TN			Tennessee Warbler
TT			Tufted Titmouse
WV			White-eyed Vireo
YR			Yellow-rumped Warbler
YV			Yellow-throated Vireo
YW			Yellow-throated Warbler
	FO		Forest site availability
	FL		Flat site availability
	OX		Oxbow site availability
			Mean
			Transformed mean
			95% Confidence limit
			Observed range

[palmetto (*Sabal minor*), switchcane (*Arundinaria gigantea*), Spanish moss (*Tillandsia usneoides*), and vines] characteristic of bottomland hardwood forests was estimated on a subjective scale from 0 to 5 within a 5-m radius circular plot centered on the initial foraging observation point of each foraging bout: "0" = no vegetative cover, "1" = 10 - 25% cover, "2" = >25 - 50% cover, "3" = >50 - 75% cover, "4" 75 - 90% cover, and "5" = >90 - 100% cover. I used the same methods at randomly located points within 100 m of census transects to determine "availability of microhabitat".

I sampled foraging behavior of birds by regularly and repeatedly traversing the study areas and recording foraging data as I encountered birds. All foraging observations occured within 100m of census transects. I recorded species, sex, time of day, types of foraging maneuver, foraging height, height of the substrate, spherical vegetation density (estimated vegetation volume [in %] within an imaginary 1-meter diameter sphere centered in the foraging bird), foraging rate, perch diameter category (<1 cm or > 1 cm), plant species, and if in a tree, whether the prey attack occurred in the region proximal to the main axis of the trunk or distal, and dbh of the plant. Because some bird species were monochromatic, I combined foraging data for sexes.

I used the scheme of Remsen and Robinson (1989) to classify foraging maneuveres: "flake" -- brush aside loose substrate, usually dead leaf litter, with sideways, sweeping motions of the bill, "leap" -- a launch into the air to reach prey too far for a "reach" but too close for a "sally"; "glean" --prey taken by a perched or moving bird from a substrate, including the ground, by picking or reaching; "hammer" -- a series of pecks without pausing between pecks; "probe" -- inserting the bill into cracks or holes in firm substrate

(e.g., bark or crevice between tree trunk and vine) or directly into softer substrates such as moss or dead leaf litter to capture hidden prey; "gape" --inserting the bill into the substrate as in a probe, but the bill is opened to widen the opening; "hang" -- using the legs and toes to suspend the body below the feet to reach food that cannot be reached from any other perched position; "sally" -- to fly from a perch in pursuit of flying prey (and then return to a perch); "sally-glean" -- flying bird took prey from a substrate (here, I have lumped Remsen and Robinson's (1989) "sally-strike" and "sally-hover" maneuvers); "flutter-chase" -- to flush or dislodge prey from a substrate and to then chase the prey; "flush-pursue" -- similar to "flutter-chase" except that species that use this maneuver deliberately (vs. accidentally) flush prey from hiding places and then pursue the flying, running, or falling prey. Because categories are not mutually exclusive, on occasion I used compound names to define maneuvers (Remsen and Robinson 1989). The above descriptions are directly from Remsen and Robinson's paper (except for "sally-glean"; "glean", where I included their "reach" category; I lumped their "lunge" category with "glean" or if appropriate with "flutter-chase" or "flush-pursue" or ground foraging birds). I recommend consulting their paper for a more detailed account. The substrates were leaf litter, herbs, fallen debris (fallen trees, logs, or branches), tree truck, branch (>1 cm),twig (<1 cm), leaf (dead or live), flower, fruit, moss, air and other (water, spider web, cypress knee). If discernable, the leaf surface (upper or lower) at which a maneuver was directed was recorded. Each bird was followed until it performed 10 foraging maneuvers or until it was lost from sight.

DATA ANALYSIS

Foraging heights were grouped into the four categories described

above. Relative height was calculated as foraging height / substrate height. For each foraging sequence longer than 20 seconds (*sensu*) Robinson and Holmes 1982), we calculated foraging rate (number of prey-attacking maneuvers/min.). Based on prey attack rate, species were classified as slow ($\leq$ 2.2 attacks / min.), moderate speed (2.3-3.1 attacks/min.), or fast ($\geq$ 3.2 attacks/min.) foragers. I used student's test to compare means (use vs. availability). Due to deviations from normal distributions because variables were recorded as percents, I used logit transformation on microhabitat variables. Untransformed means, transformed means, confidence limits, and range are shown in all relevant figures; probability values are based on transformed variables. G-tests were performed on the special habitat features to test for homogeneity of distribution of bird centered plots vs. random plots.

Niche breadth of foraging height, foraging maneuver, foraging substrate, and substrate species were calculated as $\frac{1}{B} = \sum p_i^2$,

where *pi* is the proportion in category *i* among the categories in each dimension. I compensated for the varying number of categories for each foraging variable by standardizing niche breadth by $B_{standard}$ = (B-1)/(n-1), where n is the maximum number of categories (Reynolds and Meslow 1984).

To provide an objective classification of the similarities and differences among these syntopic insectivores in terms of how they exploit food resources, and to help describe guild organization of the Tensas forest birds, I performed a hierarchical cluster analysis (maximum method, Holmes et al. 1979). This analysis was performed on the data matrix consisting of 16 breeding bird species by 33 foraging

characters. The foraging characters consisted of x foraging height, foraging height standard deviation, x substrate height, x vegetation density around the bird, x body weight, frequency of observations proximal or distal to main axis of the plant, frequencies of foraging maneuvers, and frequencies of foraging substrates. Characters representing utilization frequencies of foraging categories were log-transformed to reduce skewness. All characters were standardized to bring the means to 0 and the variances to 1.

RESULTS

HABITAT STRUCTURE

In the non-flooded forest, the canopy was the densest layer, more than twice as dense as the other layers (Figure 4.). In the seasonally flooded flat, the ground and shrub layer were sparse; the canopy was approximately twice as dense as the subcanopy (Figure 4.). Along the margins of the oxbow lakes, the canopy was the densest layer, but relatively open (Figure 4.).

SPECIES ACCOUNTS

I will present the results section in a "species accounts" format. Each account will include results on macrohabitat distribution and abundance, microhabitat use compared to available microhabitat characteristics, and foraging behavior patterns. For each species that has a statistically significant difference in foraging behavior between macrohabitats, I will present these data; otherwise I have combined foraging data for all three sites. Although some species breed in more than one macrohabitat (Table 3.), I did not always have a large enough sample size to test for significant differences in microhabitat use and foraging behavior among sites. This was usually because a species was uncommon to rare within a particular macrohabitat.

TYRANNIDAE

Eastern Wood-Pewee. - The Eastern Wood-Pewee was uncommon to common in the seasonally-flooded flat and oxbow lake edge, although it was absent at the oxbow site in 1984 (Figure 5.). In the non-flooded forest the pewee ranged in abundance from absent in 1985 to uncommon in 1989 (Figure 5.). The flat appears to be the pewee's preferred habitat in the Tensas River Basin, where it was

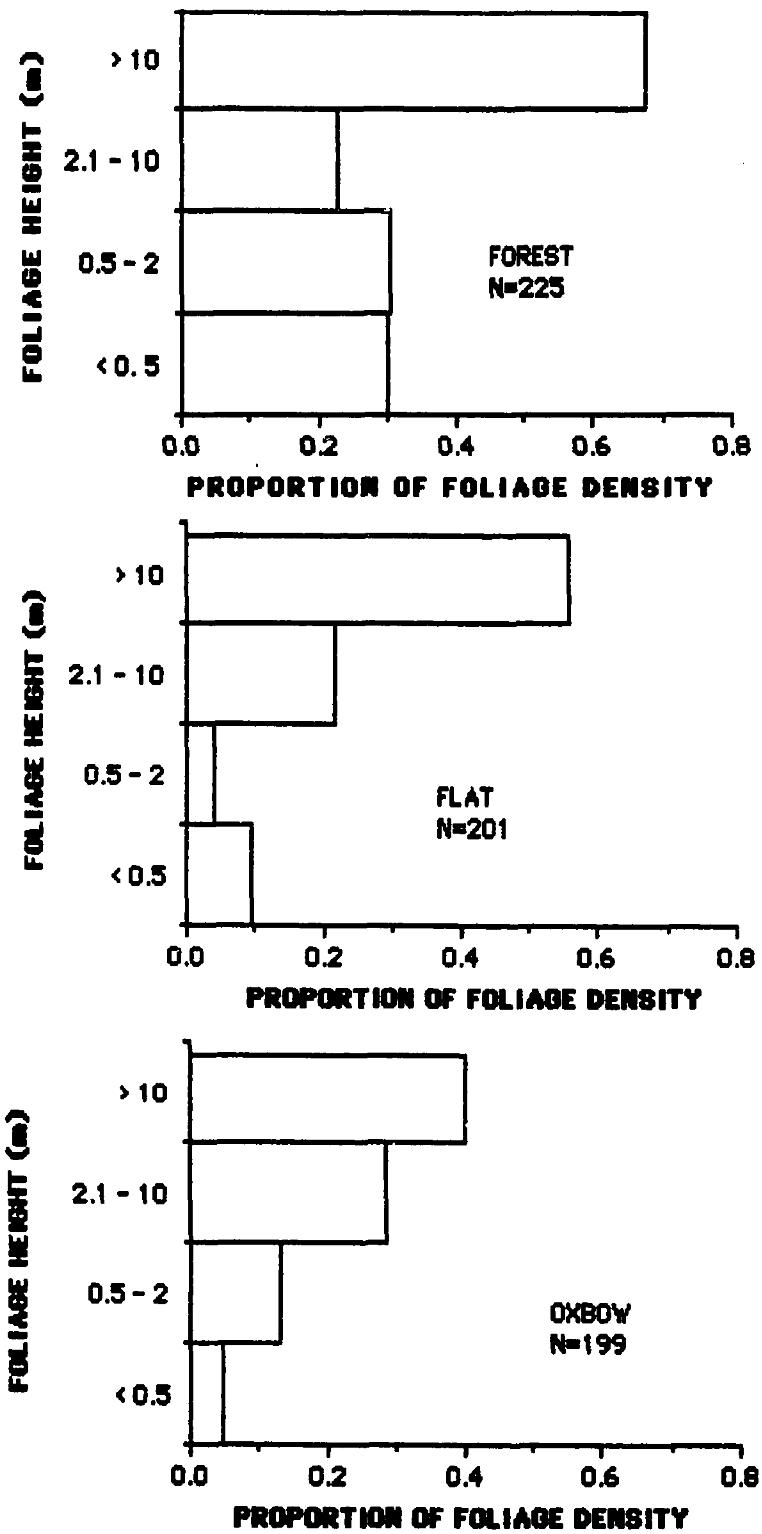


Figure 4. Mean foliage-height profiles of the three study sites in the bottomland hardwood forest.

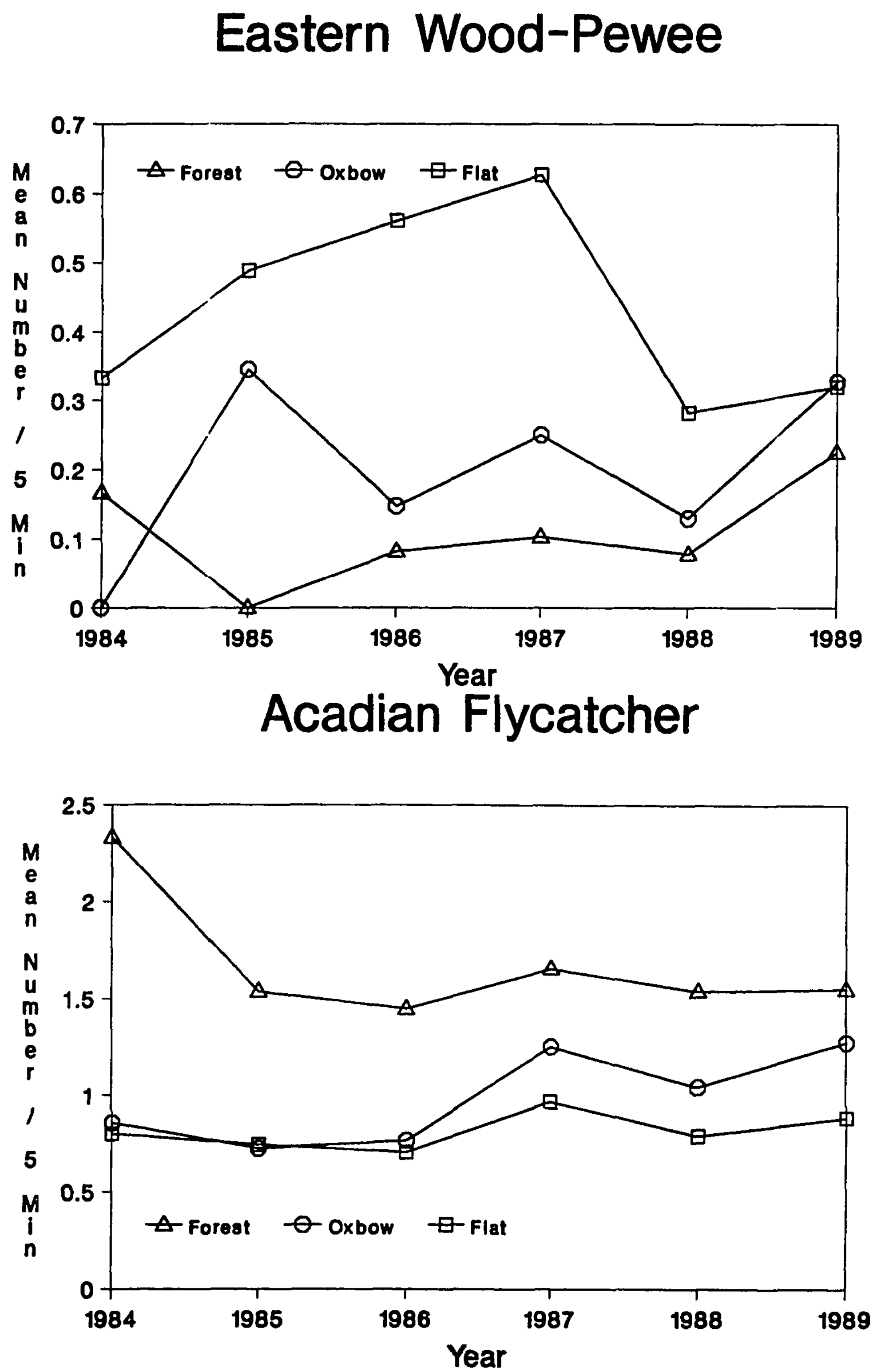


Figure 5. Population trends of two flycatchers at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

Table 3. Study species with ecological, morphological, and distributional characteristics of each species.

Species	Code	Mean body weight(g)[2]	Relative abundance[1] Forest	Oxbow	Flat	Residency[3]	Winter Location[4]
Eastern Wood-Pewee	EP	14.1	.010	.013	.051	SR	SA
Acadian Flycatcher	AF	12.9	.114	.077	.070	SR	SCA
Carolina Chickadee	CC	10.2	.059	.071	.110	PR	ST,NT
Tufted Titmouse	TT	21.6	.123	.095	.152	PR	ST,NT
Carolina Wren	CW	21.0	.157	.118	.100	PR	ST
Ruby-crowned Kinglet	RK	6.7	.003	.001	.005	WR	ST,NT,NCA
Blue-gray Gnatcatcher	BG	6.0	.015	.021	.038	SR	ST,NCA
White-eyed Vireo	WV	11.4	.120	.126	.136	SR	ST,NCA
Yellow-throated Vireo	YV	18.0	.017	.010	.038	SR	CA,CB
Red-eyed Vireo	RV	16.7	.089	.031	.068	SR	SA
Tennessee Warbler	TN	10.0	.013	.003	.008	TM	SCA
Northern Parula	NP	8.6	.113	.235	.042	SR	CB,NCA
Yellow-rumped Warbler	YR	12.6	.005	.005	.002	WR	ST,NT,NCA
Yellow-throated Warbler	YW	9.4	.000	.064	.006	SR	CB,NCA,ST
American Redstart	AR	8.3	.028	.002	.001	SR	CB,CA,SA
Prothonotary Warbler	PW	16.2	.035	.088	.163	SR	SCA,CB
Swainson's Warbler	SW	18.9	.017	.006	.001	SR	CB,NCA
Kentucky Warbler	KT	14.0	.026	.022	.006	SR	CA
Hooded Warbler	HD	10.5	.057	.012	.004	SR	NCA,CB

[1] Relative abundance is based on all years combined (May-July).
[2] Body weights taken from Dunning (1984) and Clench and Leberman (1978).
[3] Residency: SR=summer resident, PR=permanent resident, WR=winter resident, TM=transient migrant.
[4] Winter locations: NT=North temperate, mostly nonmigratory; ST=south temperate/subtropical, southeastern USA through northern Mexico; CA=Central America, Mexico through northern South America; NCA= northern Central America, central Mexico through Guatemala; SCA=southern Central America, Panama through northern South America; SA=South America, mostly Columbia, Ecuador, Peru, and Brazil; CB= Caribbean and surrounding continental areas, occurring mostly throughout the Greater Antilles and in some cases along the Caribbean slope of Central America and northern South America. Based on distributional ranges in A.O.U. (1983), Pashley (1989), and Pashley and Martin (1988).

increasingly abundant from 1984 through 1987 (Figure 5.).

The Eastern Wood-Pewee perched relatively high on branches of tall trees (Table 4. and Table 5.), where it used sites with significantly less canopy foliage density than available in both the flat and oxbow habitats (Figure 6.). Foraging sites in the oxbow habitat had significantly less Spanish moss and vine foliage than available randomly (Table 6.). Presumably, more freedom of flight among the canopy branches was desirable because the pewee captured its food almost exclusively by "sallying" (Table 7.) at a relatively slow rate (Table 8.). Baldcypress, bitter pecan, and dead snags comprised 44% of the tree used for perch sites (Table 10.). Of the 19 species in this study, the Eastern Wood-Pewee was the most highly specialized in terms of foraging maneuver and substrate type used (Table 13.).

Pewees in the flat habitat foraged more frequently in the subcanopy and shrub strata than in the oxbow habitat (22.6 vs. 3.7%); however, the significance could not be tested ($p = .03$) because 67% of the cells had expected counts less than five. The more open lower strata of the flat (Figure 4.) may have allowed pewees to maneuver more freely.

Acadian Flycatcher.- The Acadian Flycatcher bred commonly in all three habitat types, although it was approximately twice as abundant in the non-flooded forest than in the seasonally flooded forest (Figure 5.).

Acadian Flycatchers foraged at sites with more water cover than randomly available in the forest site (Figure 7.). In the forest, old, parallel scour channels (often referred to as 'swales') were a common feature and water persisted in these low sites throughout all years of the study, except 1988. Acadians often frequented these

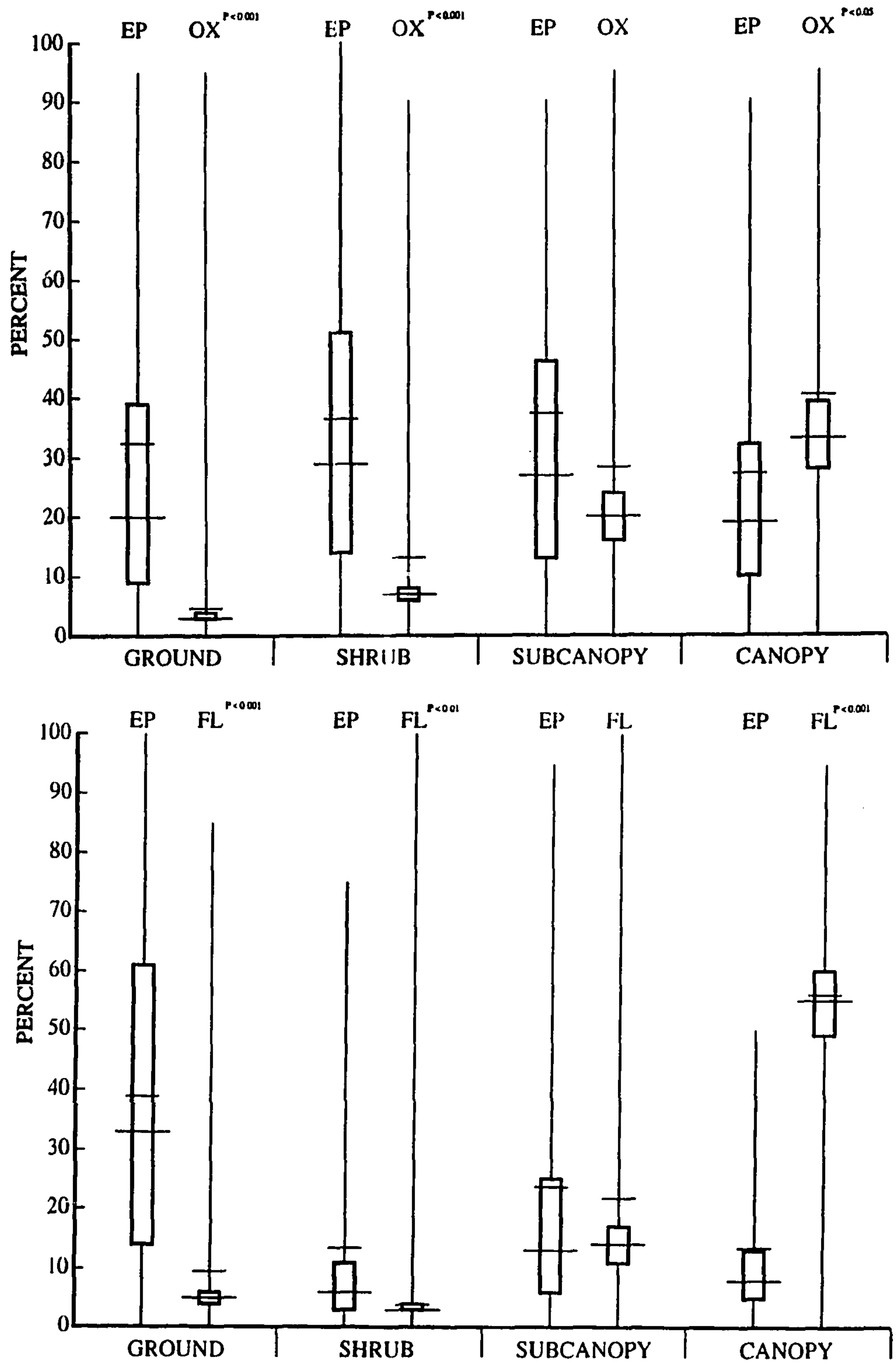


Figure 6. Foliage density use and availability by Eastern Wood-Pewees of four height strata in a bottomland hardwood forest.

Table 4. Foraging height categories used by 19 birds species in the bottomland hardwood forest of the Tensas River Basin.

Species	N	Frequency of forest strata use			
		Ground (<0.5m)	Shrub (0.5-2.0m)	Subcanopy (>2.0-10.0m)	Canopy (>10.0m)
Eastern Wood-Pewee	66	.00	.11	.32	.57
Acadian Flycatcher	131	.00	.05	.77	.18
Carolina Chickadee	112	.01	.05	.64	.30
Tufted Titmouse	79	.09	.06	.58	.27
Carolina Wren	54	.15	.50	.35	.00
Ruby-crowned Kinglet	18	.06	.06	.44	.44
Blue-gray Gnatcatcher	74	.00	.04	.28	.68
White-eyed Vireo	98	.02	.16	.74	.08
Yellow-throated Vireo	47	.00	.00	.08	.92
Red-eyed Vireo	85	.00	.00	.51	.49
Tennessee Warbler	40	.00	.02	.25	.73
Northern Parula	218	.05	.05	.43	.47
Yellow-rumped Warbler	37	.00	.05	.27	.68
Yellow-throated Warbler	146	.00	.00	.09	.91
American Redstart	52	.00	.00	.40	.60
Prothonotary Warbler	146	.16	.29	.50	.05
Swainson's Warbler	17	.71	.29	.00	.00
Kentucky Warbler	50	.30	.54	.14	.02
Hooded Warbler	90	.07	.21	.55	.17
Mean Frequency for all species	1,560	.09	.13	.38	.40

Table 5. Plant height categories used by 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

Species	N	Frequency of plant height use			
		Ground (<0.5m)	Shrub (0.5-2.0m)	Subcanopy (>2.0-10.0m)	Canopy (>10.0m)
Eastern Wood-Pewee	66	.00	.06	.12	.82
Acadian Flycatcher	131	.00	.00	.33	.07
Carolina Chickadee	112	.00	.01	.29	.70
Tufted Titmouse	79	.06	.04	.27	.63
Carolina Wren	54	.11	.15	.30	.44
Ruby-crowned Kinglet	18	.06	.00	.11	.83
Blue-gray Gnatcatcher	74	.00	.00	.11	.89
White-eyed Vireo	98	.01	.04	.35	.60
Yellow-throated Vireo	47	.00	.00	.04	.96
Red-eyed Vireo	85	.00	.00	.18	.82
Tennessee Warbler	40	.00	.00	.10	.90
Northern Parula	218	.02	.01	.19	.78
Yellow-rumped Warbler	37	.00	.03	.05	.92
Yellow-throated Warbler	146	.00	.00	.03	.97
American Redstart	52	.00	.00	.10	.90
Prothonotary Warbler	146	.05	.22	.42	.31
Swainson's Warbler	17	.35	.30	.35	.00
Kentucky Warbler	50	.20	.14	.48	.18
Hooded Warbler	90	.03	.02	.38	.57
Mean frequency for all species	1,560	.05	.05	.22	.68

Table 6. Means and Standard deviations of special habitat features available and at bird foraging locations in the "oxbow" study site of the Tensas River Basin.

Species	N	Palmetto[1]		Vine		Moss		Cane	
		x	sd	x	sd	x	sd	x	sd
Eastern Wood-Pewee	27	0.4	1.2	1.7	1.8^{*}[2]	2.1	2.0^{**}	0.8	1.6
Acadian Flycatcher	20	0.5	1.0^{***}	3.3	1.5^{*}	1.9	1.7	1.4	1.6
Carolina Chickadee	22	0.2	0.5	2.5	2.1	1.3	1.7^{***}	0.8	1.6
Tufted Titmouse	12	0.2	0.4	2.2	2.0	1.7	1.5	0.7	1.7
Carolina Wren	10	0.5	0.8	4.1	1.8	2.0	2.2	0.0	0.0
White-eyed Vireo	17	0.6	1.0	1.7	2.0	2.0	2.0	1.0	1.8
Northern Parula	105	0.6	1.1	2.4	1.8	1.9	1.6^{***}	1.5	1.9
Yellow-throated Warbler	141	0.9	1.0	1.6	1.4^{***}	3.9	1.7	0.4	1.2^{***}
Prothonotary Warbler	58	1.6	0.7	0.8	1.6^{***}	1.3	1.6^{***}	0.3	1.0
Availability	199	0.6	1.0	2.7	2.0	3.3	1.8	1.0	1.7

1. Vegetative density of the special habitat features were estimated for each plot on a subjective scale from 0 to 5. A value of 0 indicates no vegetative density of the habitat feature within a 5 m radius circular plot and a value of 5 indicates a density of 90-100%.
2. The percent density of bird-centered plots vs. random plots (availability) are followed by significance levels for a G-test (for homogeneity of distribution, classes 0 to 5): * = P <= .05; ** = P <=.01; *** = P<= .001.

sites, presumably because of its scarcity of dense vegetation structure, that would limit acadians ability to maneuver (sally-glean). In habitats with sparse shrub foliage (flat and oxbow, see Figure 4.), acadians selected sites with relatively denser foliage in the shrub strata (Figure 7.). In the flat, acadians foraged at sites with relatively dense palmetto and vine cover, although not at statistically significant levels (Table 12.). In all three habitats, acadians used sites with denser foliage in the canopy stratum than randomly available (Figure 7.). In the forest site, acadians used sites with vine foliage denser than, and palmetto foliage less than randomly available (Table 19.). Eighteen percent of the acadians' prey attacks were directed toward a vine leaf (Table 10. and Table 11.).

The Acadian Flycatcher foraged in foliage density ranging from 25-38% in the subcanopy of relatively tall trees (Figure 7. and Table 5.). Prey were captured most often by "sally-gleaning" the lower surfaces of live leaves (Table 7. and Table 14.). Acadians had the second smallest foraging maneuver niche breadth (Table 13.).

Although Acadian Flycatchers in the flat foraged higher within the subcanopy ($x = 8.0 \pm 3.2$ vs. 6.4 ± 2.8) than those inhabiting the forest ($G = 12.46$; $n = 19, 92$; $df = 2$; $p = .002$), they are relatively stereotyped in their foraging behavior; they searched for and attacked prey in the same manner regardless of habitat type. Their rate of prey encounter was slow, but constant among the habitat types (forest = 2.1 ± 1.7, flat = 2.2 ± 1.3).

PARIDAE

Carolina Chickadee.- The Carolina Chickadee's abundance patterns oscillated from one year to the next in the oxbow habitat, and ranged from uncommon in 1984 to abundant in 1987 (Figure 8.). The same

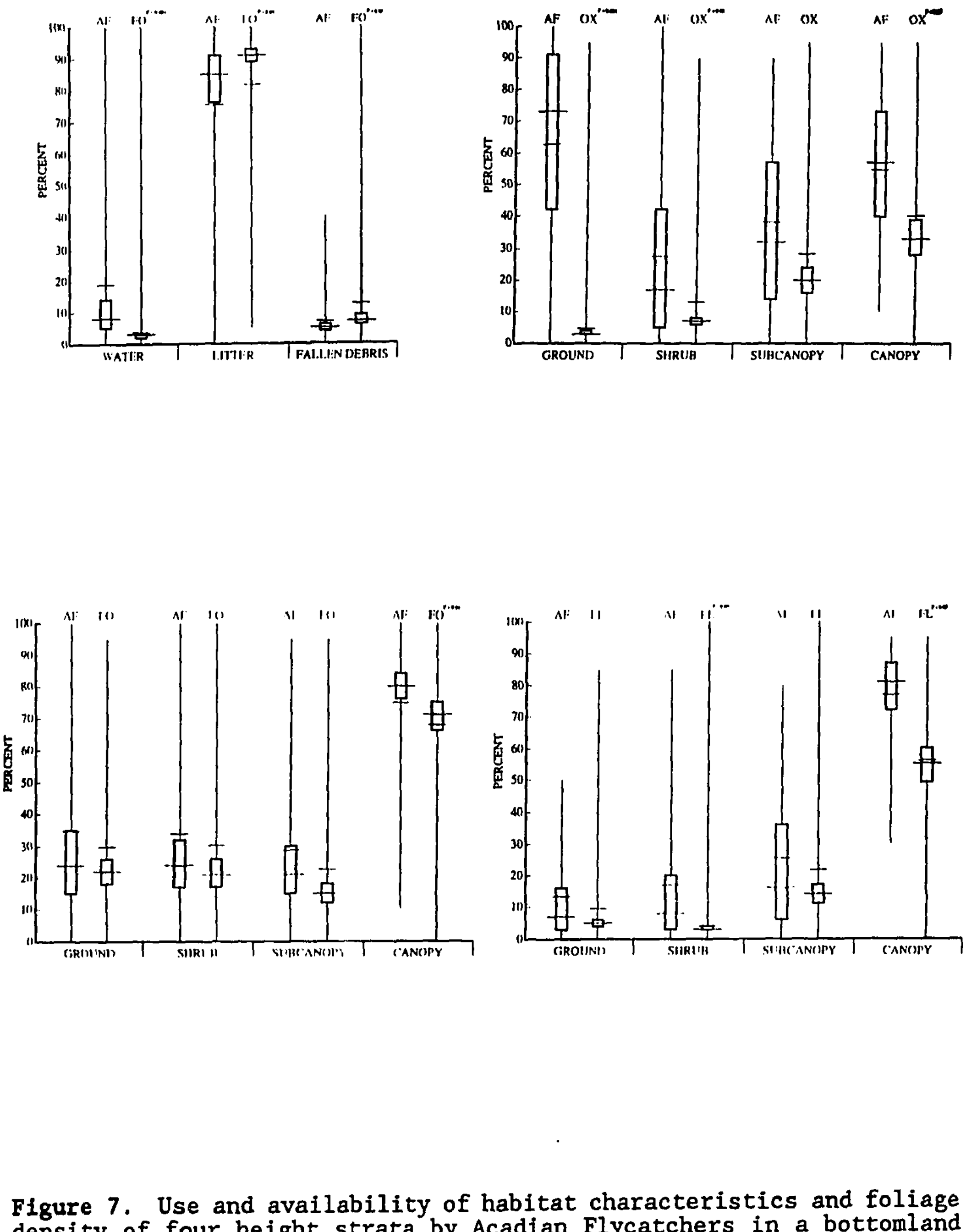


Figure 7. Use and availability of habitat characteristics and foliage density of four height strata by Acadian Flycatchers in a bottomland hardwood forest

Table 7. Foraging maneuvers used by 19 bird species in the bottomland and hardwood forest of the Tensas River Basin.

		Proportion total foraging maneuvers												
Species	N	Flake	Leap	Glean	Hammer	Probe	Gape	Hang	Hang-probe	Sally	Sally-glean	Sally-probe	Flutter-chase	Flush-pursue
Eastern Wood-Pewee	66 (242)'			.01						.85	.14			
Acadian Flycatcher	131 (314)			.04						.13	.82		.01	
Carolina Chickadee	112 (411)			.42		.01		.43	.10		.04			
Tufted Titmouse	79 (194)			.60	.01	.12		.14	.05		.07		.01	
Carolina Wren	54 (74)	.03		.65		.27					.04		.01	
Ruby-Crowned Kinglet	18 (71)			.41					.01	.09	.48		.01	
Blue-gray Gnatcatcher	74 (226)			.42				.01		.11	.35			.12
White-eyed Vireo	98 (152)			.49				.04		.01	.44	.02	.01	
Yellow-throated Vireo	47 (90)			.80				.01			.19			
Red-eyed Vireo	85 (158)			.57		.01		.08	.01	.01	.31		.02	
Tennessee Warbler	40 (166)			.82		.02		.05			.10		.01	
Northern Parula	218 (559)			.58		.04		.08	.01	.02	.24	.01	.02	
Yellow-rumped Warbler	37 (144)			.53						.06	.38	.02	.01	
Yellow-throated Warbler	146 (323)			.54		.07		.05	.10	.01	.15	.04	.04	
American Redstart	52 (147)			.16						.19	.51			.14
Prothonotary Warbler	146 (375)			.76		.09	.02	.01		.02	.12	.02	.02	
Swainson's Warbler	17 (41)	.63		.32							.05			
Kentucky Warbler	50 (80)	.05	.13	.62							.20		.01	
Hooded Warbler	90 (224)			.36						.05	.47	.01	.01	.10
Mean Frequency for all species	1,560 (3,991)	.01	<.01	.46	<.01	.03	<.01	.07	.01	.09	.27	.01	.01	.02

'individuals observed (total #maneuvers)

Table 8. Mean Number, standard deviation, and range of prey attacks per minute for foraging bouts > 20 seconds of 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

	Prey attacks per minute			
Species	x	sd	Range	N
Eastern Wood-Pewee	2.2	2.0	0.1-10.9	59
Acadian Flycatcher	2.1	1.6	0.4-9.3	100
Carolina Chickadee	4.2	2.9	0.8-16.2	92
Tufted Titmouse	2.9	2.0	0.6-9.0	62
Carolina Wren	3.1	1.5	0.9-6.0	26
Ruby-crowned Kinglet	3.1	1.6	1.0-6.0	16
Blue-gray Gnatcatcher	3.3	2.8	0.6-13.3	58
White-eyed Vireo	2.0	1.3	0.2-5.6	69
Yellow-throated Vireo	1.9	1.4	0.2-7.1	34
Red-eyed Vireo	2.7	2.2	0.3-14.3	62
Tennessee Warbler	3.2	2.2	0.7-9.7	28
Northern Parula	3.1	2.2	0.4-12.6	155
Yellow-rumped Warbler	3.1	2.1	0.6-9.5	35
Yellow-throated Warbler	2.2	1.2	0.4-6.5	124
American Redstart	2.6	1.6	0.4-6.2	39
Prothonotary Warbler	2.3	1.8	0.4-15.0	120
Swainson's Warbler	5.6	2.4	3.5-9.6	6
Kentucky Warbler	2.8	1.9	0.2-7.5	29
Hooded Warbler	2.9	1.7	0.6-8.4	58

Table 9. Foraging substrate use by 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

		Frequency of substrate use												
Species	N	Live leaf	Dead leaf	Trunk	Branch	Twig	Moss	Ground litter	Fallen debris	Herb	Flo-wer	Fruit	Air	Other
Eastern Wood-Pewee	242	.07		<.01	.02	.02	.03		<.01	<.01			.85	<.01
Acadian Flycatcher	314	.75	.01	.02	.03	.04	.01						.14	<.01
Carolina Chickadee	411	.41	.12	.02	.22	.11	.03			<.01	.06	.03	<.01	
Tufted Titmouse	194	.30	.08	.11	.26	.07	.07	.04	.02		.04	.01	<.01	
Carolina Wren	74	.12	.07	.32	.16	.11	.04	.10	.07				.01	
Ruby-crowned Kinglet	71	.54	.06	.01	.10	.15		.01			.03		.10	
Blue-gray Gnatcatcher	226	.43	.02	.01	.12	.12					.05		.22	.02
White-eyed Vireo	152	.66	.01	.02	.11	.16	.02			.01			.01	
Yellow-throated Vireo	90	.20		.04	.44	.22				.01	.09			
Red-eyed Vireo	158	.77	.03	.01	.11	.03	.01						.03	.01
Tennessee Warbler	166	.67	.02	<.01	.04	.06					.20		.01	
Northern Parula	559	.70	.03	.01	.04	.07	.05			.02	.05		.03	
Yellow-rumped Warbler	144	.66	.01	.03	.07	.10	.03				.04		.07	
Yellow-throated Warbler	323	.26		.02	.38	.05	.21				.03		.05	
American Redstart	147	.60		.01	.02	.04							.33	
Prothonotary Warbler	375	.45	.06	.07	.15	.12	.04	.01	.02	.03	<.01		.03	.02
Swainson's Warbler	41	.15	.07					.63	.12	.03				
Kentucky Warbler	80	.51	.03	.04	.05	.09		.12	.04	.11			.01	
Hooded Warbler	224	.55	.02	.03	.09	.10	.01	.04	.01					.15
Mean frequency for all species	4059	.46	.03	.03	.13	.08	.04	.02	.01	.01	.04	<.01	.12	<.01

Table 10. Plant species used by 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

Species	N	Frequency of prey attacks directed at each plant species													
		American Elm	Buttonbush	Baldcypress	Bitter Pecan	Switchcane	Cedar Elm	*Crataegus* spp.	Deciduous Holly	Green Ash	Hackberry	Herb spp.	Honey Locust	Willow Oak	Nuttall Oak
Eastern Wood-Pewee	66			.15	.17		.03			.08			.06		.03
Acadian Flycatcher	128	.06			.02		.03	.02	.01	.10	.09		.02	.04	.04
Carolina Chickadee	112	.04		.04	.11		.06	.03	.03	.03	.07		.03	.05	.02
Tufted Titmouse	79	.06	.03	.04	.05		.03	.04	.01	.03	.05	.01	.03	.06	.01
Carolina Wren	54				.04	.02			.02	.02	.04		.02	.02	
Ruby-crowned Kinglet	18			.06			.22		.06					.06	
Blue-gray Gnatcatcher	74	.01	.01	.04	.12		.01	.01		.04	.10		.08	.08	.03
White-eyed Vireo	98	.04	.01	.01	.02	.02	.09	.01	.02	.02	.06	.01	.01	.05	.02
Yellow-throated Vireo	47				.06					.09	.04		.06	.11	.13
Red-eyed Vireo	85	.05		.01	.05		.02			.06	.17		.02	.05	.08
Tennessee Warbler	40			.03	.05		.03		.03	.03	.03		.08	.05	
Northern Parula	218	.04	.01	.06	.06	.01	.08		.05	.03	.06	.01	.05	.09	.03
Yellow-rumped Warbler	37			.11			.24		.03		.05		.05	.11	.08
Yellow-throated Warbler	146			.41	.03		.01				.01			.33	
American Redstart	52	.04					.02			.02	.06		.06	.02	.02
Prothonotary Warbler	146	.03	.14	.04	.05	.01	.01	.01	.01	.01	.05	.03	.01	.03	
Swainson's Warbler	17										.24				.06
Kentucky Warbler	50	.04				.02	.04		.06		.06	.06			
Hooded Warbler	90	.05					.07	.01		.01	.08		.01	.03	.02
Mean frequency for all species	1,557	.03	.02	.07	.05	<.01	.05	.01	.01	.03	.06	.01	.03	.08	.03

Table 11. (CONTINUED)

Species	N	Frequency of prey attacks directed at each plant species													
		Overcup Oak	Palmetto	Red Maple	Red Oak	*Rubus* spp.	Sweetgum	Sweet Pecan	Spanish Moss	Swamp Privet	Vine spp.	Water Elm	Water Oak	Dead Snag	Other
Eastern Wood-Pewee	66	.14					.05		.03	.02	.03		.03	.12	.08
Acadian Flycatcher	128	.07		.05			.10		.01	.06	.18		.09	.02	.02
Carolina Chickadee	112	.13		.01	.01		.07		.04	.04	.12	.05	.03	.01	
Tufted Titmouse	79	.17	.01				.05		.04	.05	.08	.03	.08	.01	.06
Carolina Wren	54	.02	.05				.06		.06		.32	.02	.07	.04	.20
Ruby-crowned Kinglet	18				.06		.06				.28		.17		.06
Blue-gray Gnatcatcher	74	.08		.03			.15				.10		.07	.01	.03
White-eyed Vireo	98			.01		.03	.06		.01	.01	.37		.08	.01	.02
Yellow-throated Vireo	47	.20					.02	.02		.04			.23		
Red-eyed Vireo	85	.13					.06			.09	.09		.11		.01
Tennessee Warbler	40	.40					.03			.03					.03
Northern Parula	218	.05		.05	.05		.07		.05		.17	.01	.11	.01	.03
Yellow-rumped Warbler	37	.03					.03				.11		.16		
Yellow-throated Warbler	146	.01					.01	.01	.15		.01	.01	.01		
American Redstart	52	.04					.33	.02			.23		.15		
Prothonotary Warbler	146	.08	.01	.01			.02		.02	.15	.10	.03	.03	.04	.08
Swainson's Warbler	17		.29								.06				.35
Kentucky Warbler	50					.04	.06			.02	.32		.06		.22
Hooded Warbler	90	.05	.02			.01	.09				.39	.01	.10		.05
Mean frequency for all species	1,557	.08	.01	.01	<.01	<.01	.07	<.01	.03	.03	.16	.01	.08	.02	.05

Table 12. Means and standard deviations of special habitat features available and at bird foraging locations in the "flat" study site of the Tensas River Basin.

		Palmetto		Vine		Moss		Cane	
Species	N	x	sd	x	sd	x	sd	x	sd
Eastern Wood-Pewee	31	0.0	0.0	1.3	1.9	0.0	0.0	0.0	0.0
Acadian Flycatcher	19	1.0	2.1	1.8	2.3	0.0	0.0	0.0	0.0
Carolina Chickadee	43	0.0	0.0	1.0	1.8	0.0	0.0	0.0	0.0
Tufted Titmouse	29	0.0	0.0	0.4	1.1	0.1	0.6	0.0	0.0
Blue-gray Gnatcatcher	34	0.0	0.0	1.7	2.1	0.6	1.4	0.4	1.3
Yellow-throated Vireo	20	0.1	0.2	1.0	1.4	0.0	0.0	0.0	0.0
Red-eyed Vireo	38	0.0	0.0	0.3	1.1	0.0	0.0	0.0	0.0
Tennessee Warbler	24	0.0	0.0	0.2	0.7	0.0	0.0	0.0	0.0
Northern Parula	20	0.3	0.7	2.2	2.3	0.0	0.0	0.0	0.0
Prothonotary Warbler	53	0.0	0.0	0.5	1.4	0.0	0.0	0.0	0.0
Availability	201	0.01	0.1	0.5	1.4	0.0	0.0	0.0	0.0

1. Vegetative density of the special habitat features were estimated for each plot on a subjective scale from o to 5. A value of 0 indicates no vegetative density of the gabitat feature within a 5 m radius circular plot and a value of 5 indicates a density of 90-100%.

pattern holds for the chickadee in the flat from 1985 through 1989, where it ranged from common to nearly rare (Figure 8.). Abundance of chickadees inhabiting the forest site was less variable during the six years of this study (Figure 8.).

The chickadee foraged relatively fast in the subcanopy (64%) and canopy (30%) of tall trees (Table 8., Table 4., and Table 5.). In the flat, it foraged at locations where the subcanopy foliage was in concordance to its availability, but in the other two habitats the subcanopy was denser than the average (Figure 9.). The canopy in chickadee's feeding cylinder was less dense than available at all three sites, but the difference was significant only in the forest and flat (Figure 9.). The foliage density in the chickadee feeding cylinder in this strata was less, although similar to that in the subcanopy ranged from 35.2% in the oxbow to 57.9% in the forest. In the heavily moss-covered oxbow habitat, chickadees tended to forage in sites with less moss than randomly available (Table 6.).

The Carolina Chickadee used the "glean" and "hang" foraging maneuvers with equal frequency (Table 7.). Chickadees foraged at a relatively rapid rate among foliage of branches and twigs (Table 8. and Table 14.). Prey were most frequently captured from the lower surface of live leaves, and to a lesser extent the bark of branches (Table 9. and Table 14.). "Hanging" dead leaves were used as a foraging substrate more often (12%) by this species than any other at Tensas River NWR. The "hang-probe" maneuver is usually used when attacking prey in curled leaves (dead or live).

The foraging patterns of this species differed between macrohabitats more than any other species in this study. Comparison of chickadees inhabiting the forest site vs. the flat site revealed that the "sally-glean" (8.5 vs. 2.3%) and "hang-probe" (14.9 vs. 0%)

maneuvers occurred more frequently and the "hang" maneuver less frequently (27.7 vs. 48.8%) in the forest site. Twigs were used more frequently than branches in the forest than the flat where they were used with nearly equal frequency (Two-tailed Fisher's exact test, P = .002). The outer-halves of tree crowns were used more frequently in the forest and the inner-halves more so in the flat site (Two-tailed Fisher's exact test, p = .01). In addition, the chickadee was the only species to forage at a statistically different foraging rate between macrohabitats (flat, 3.80 attacks/min; forest 4.61; t = -1.99, n = 43, 47, df = 88, p = .04). They foraged in the shrub stratum more frequently in the oxbow site (13.6 vs. 0.0%) than the flat (G-test not valid).

Thus, the Carolina Chickadee is relatively flexible in its range of foraging heights, vegetation strata used, foraging technique employed and plant species used (Table 13.). The chickadee had the third largest mean overall niche breadth value (.297).

Tufted Titmouse.- The Tufted Titmouse was recorded as abundant (1984 and 1989) to uncommon (1988) in the flat, and common (1984-1988) to abundant (1989) in the forest and oxbow sites (Figure 8.). The abundance patterns for the titmouse from 1984 through 1989 were very similar to those of the chickadee; 1986 and 1988 were years of low abundance, and 1985, 1987, and 1989 were years of high abundance (Figure 8.).

The Tufted Titmouse foraged at all heights, from on or near the ground to the top of the canopy (Table 4. and Table 5.). It searched among a variety of plant species and had the largest niche breadth value for that category (Table 13.). The titmouse is generalized in its microhabitat use; foliage density was used in concordance to availability in all strata of the forest, and all but the canopy

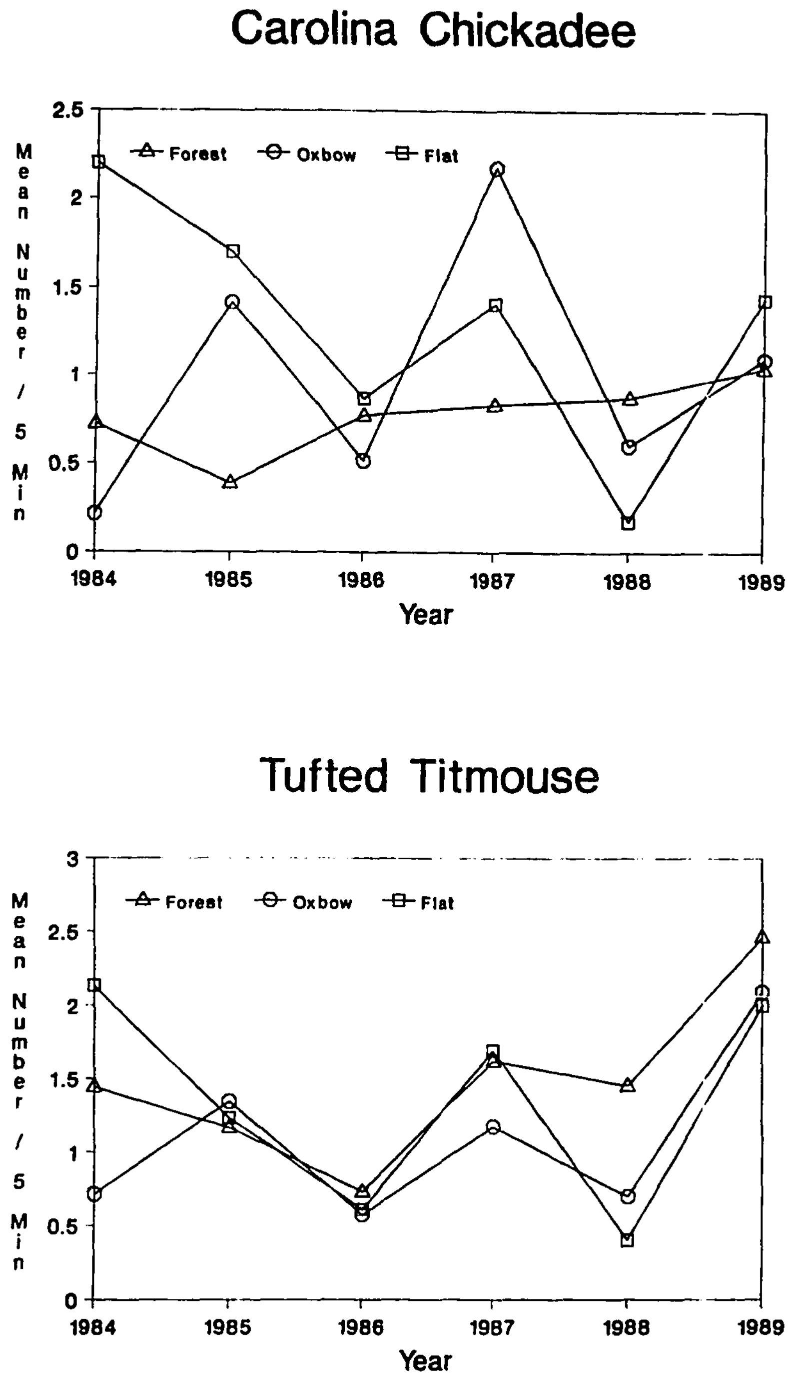


Figure 8. Population trends for two parids at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

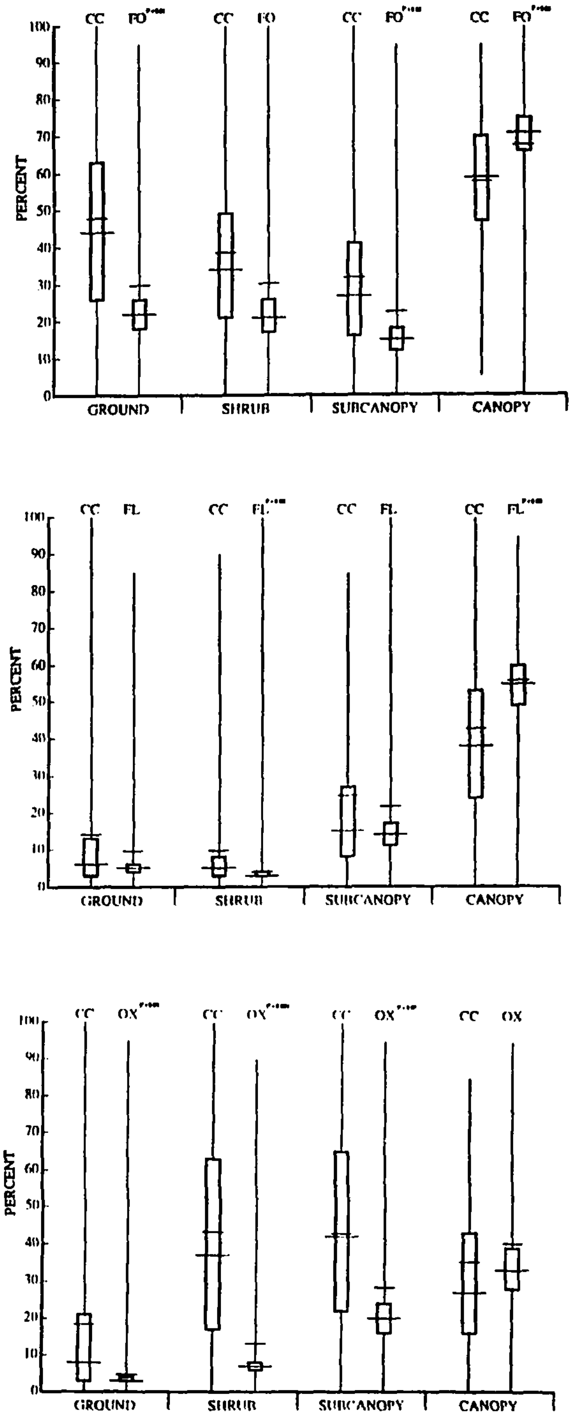


Figure 9. Foliage density use and availability by Carolina Chickadees of four height strata in a bottomland hardwood forest.

Table 13. Standardized niche breadth values for 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

Species	Foraging maneuver	Foraging height	Foraging substrate	Plant species
Eastern Wood-Pewee	.029	.407	.031	.302
Acadian Flycatcher	.038	.197	.059	.377
Carolina Chickadee	.140	.330	.252	.467
Tufted Titmouse	.124	.460	.356	.476
Carolina Wren	.084	.510	.390	.188
Ruby-crowned Kinglet	.122	.513	.163	.172
Blue-gray Gnatcatcher	.173	.280	.231	.386
White-eyed Vireo	.108	.240	.093	.185
Yellow-throated Vireo	.040	.057	.203	.225
Red-eyed Vireo	.112	.333	.054	.348
Tennessee Warbler	.038	.227	.085	.170
Northern Parula	.123	.477	.083	.370
Yellow-rumped Warbler	.123	.287	.098	.086
Yellow-throated Warbler	.166	.067	.234	.086
American Redstart	.161	.307	.093	.151
Prothonotary Warbler	.055	.573	.248	.431
Swainson's Warbler	.083	.233	.106	.099
Kentucky Warbler	.104	.497	.193	.175
Hooded Warbler	.146	.517	.158	.157
Mean niche breadth values for all species	.104	.343	.165	.255

Table 14. Characteristics of foraging substrates and perches used by 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

		Leaf surface and frequency of use				
		Leaf surface			Perch Diameter(cm)	
Species	N	Lower	Upper	N	<1	>1
Eastern Wood-Pewee	8	.63	.37	54	.39	.61
Acadian Flycatcher	219	.87	.13	81	.58	.42
Carolina Chickadee	53	.64	.36	83	.70	.30
Tufted Titmouse	31	.61	.39	61	.39	.61
Carolina Wren	8	.63	.37	44	.30	.70
Ruby-crowned Kinglet	31	.87	.14	11	.82	.18
Blue-gray Gnatcatcher	78	.85	.25	55	.62	.38
White-eyed Vireo	82	.76	.24	63	.73	.27
Yellow-throated Vireo	12	.67	.33	45	.24	.76
Red-eyed Vireo	94	.82	.18	59	.59	.41
Tennessee Warbler	77	.83	.17	17	.82	.18
Northern Parula	320	.77	.23	127	.87	.13
Yellow-rumped Warbler	86	.69	.31	21	.81	.19
American Redstart	82	.87	.13	33	.85	.15
Prothonotary Warbler	147	.67	.33	94	.54	.46
Swainson's Warbler	3	.00	.00	6	.67	.33
Kentucky Warbler	34	.74	.26	26	.58	.42
Hooded Warbler	103	.88	.12	64	.75	.25
Mean Frequency for all species	1,508	.75	.25	1,071	.61	.39

Table 15. Characteristics of foraging sites used by 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

Species	Foliage Density		Frequency of crown position use		N
	x	sd	inner ½	outer ½	
Eastern Wood-Pewee	5.8	11.9	.25	.75	53
Acadian Flycatcher	26.2	18.2	.40	.60	89
Carolina Chickadee	21.5	20.2	.41	.59	55
Tufted Titmouse	21.4	25.4	.48	.52	62
Carolina Wren	29.8	26.0	.95	.05	49
Ruby-crowned Kinglet	22.8	18.4	.27	.73	11
Blue-gray Gnatcatcher	28.3	26.0	.33	.67	55
White-eyed Vireo	38.7	23.9	.30	.70	64
Tennessee Warbler	32.9	24.4	.05	.95	19
Northern Parula	37.7	23.8	.41	.59	152
Yellow-rumped Warbler	23.5	22.1	.33	.67	21
Yellow-throated Warbler	30.5	22.4	.15	.85	130
American Redstart	39.9	20.7	.22	.78	36
Prothonotary Warbler	22.4	23.6	.55	.45	91
Swainson's Warbler	38.8	28.0	.50	.50	6
Kentucky Warbler	42.7	27.2	.82	.18	22
Hooded Warbler	31.2	23.3	.68	.32	68

stratum of the flat, where the mean foliage density in the feeding cylinder was 44.8% and 56.0% was available (Figure 10.).

The titmouse foraged most frequently by "gleaning" prey from live leaves and bark of branches (Table 7. and Table 9.). "Hanging" on live and dead leaves, and "probing" bark and dead leaves were used less frequently (Table 7. and Table 9.). Both the proximal and distal portions of the tree crowns were used with nearly equal frequency (Table 15.). The titmouse was one of four species that used branch perches more frequently than twig perches (Table 14.). The titmouse had the largest mean overall niche breadth (.354) of the 19 species in this study.

Like its congener, the titmouse is relatively plastic in its foraging behavior among macrohabitats. Titmice foraging in the flat used larger diameter perches (76.2% >1cm, 23.8% <1cm) than in the forest (46.7% >1cm, 53.3% <1cm) (Fisher's exact test, p = .04). There was also an indication that the titmouse foraged on bark substrates (fallen logs, trunks, branches, and twigs) more frequently in the flat than the forest (G-test, p = .06).

TROGLODYTIDAE

Carolina Wren.- The Carolina Wren was common to abundant (forest, 1987) at all three study sites, 1984-1989. However, Carolina Wrens in the non-flooded forest were approximately twice as abundant as those inhabiting the seasonally flooded flat and oxbow lake edge (Figure 11.).

The Carolina Wren foraged from the ground stratum through the subcanopy stratum; half of all observations occurred in the shrub stratum (Table 4.). However, the height of the plants actually used most frequently were in the canopy (44%) and subcanopy (30%) strata.

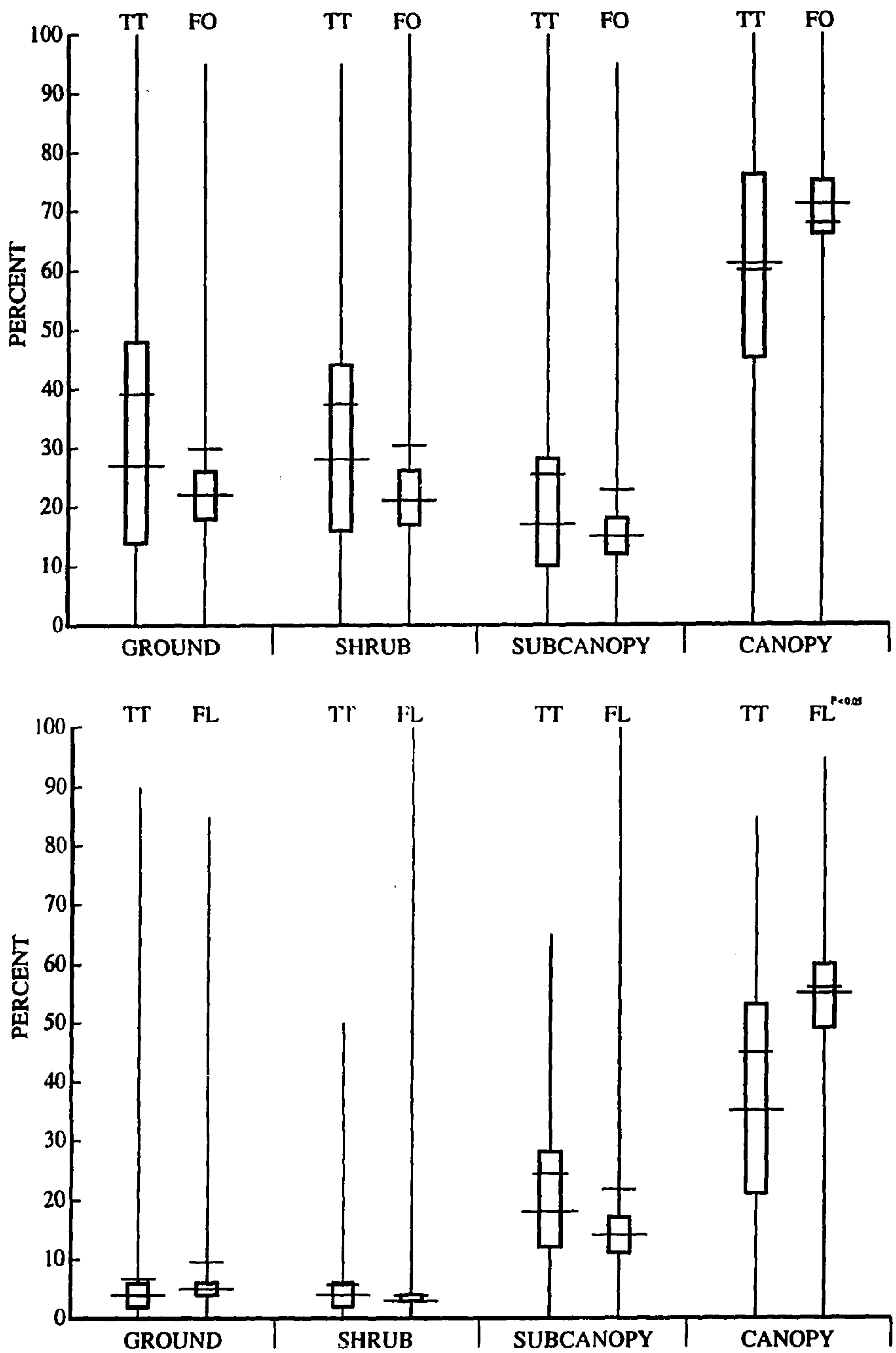


Figure 10. Foliage density use and availability by Tufted Titmice of four height strata in a bottomland hardwood forest.

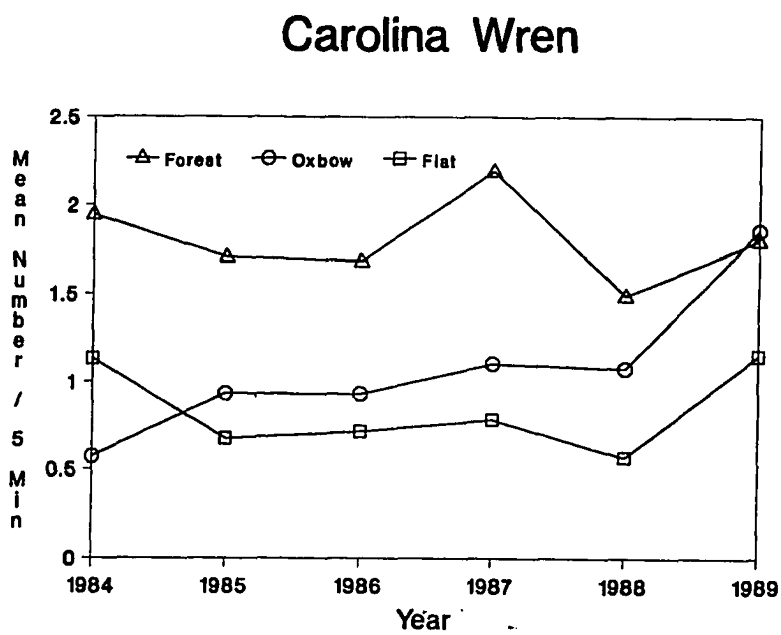
Because Carolina Wrens foraged on the bark of tree trunks (Table 9.) and in the crevices between tree trunks and clinging vine stems (95% of observations were in the inner half of the tree crown, n = 44), thus relative foraging height was the second lowest of the 19 species (0.36). Although the Carolina Wren most frequently "gleaned" while foraging, it used the "probe" maneuver more than any other species (Table 7.).

The Carolina Wren feeding cylinder had a foliage density of 50.5% in the shrub stratum and 46.9% in the subcanopy. Significantly denser foliage was used in these two strata than randomly available (Table 10.). In the forest, foraging sites with vines denser than randomly available were used by Carolina Wrens (Table 10.). Vines were an important foraging substrate for wrens (Table 13. and Table 11.). The Carolina Wren had the largest foraging substrate niche breadth of
the 19 study species (Table 13.)

MUSCICAPIDAE

Ruby-crowned Kinglet.- The Ruby-crowned Kinglet is a winter visitor to the Tensas River Basin; it arrives in late October to November and departs in late April to early May (Moore 1987). Kinglets ranged from absent to uncommon in all three habitat types (Figure 13.). Kinglets oscillated, in abundance between years, and like the parids, were relatively abundant in 1985, 1987, and 1989 (Figure 13.).

In the Spring, Ruby-crowned Kinglets foraged at all heights from the ground to the canopy, but 88% of observations were divided evenly between the subcanopy and canopy (Table 4.). Kinglets "sally-gleaned" and "gleaned" insects mostly from the lower surfaces of live leaves (Table 7., Table 9., and Table 14.); prey were also attacked



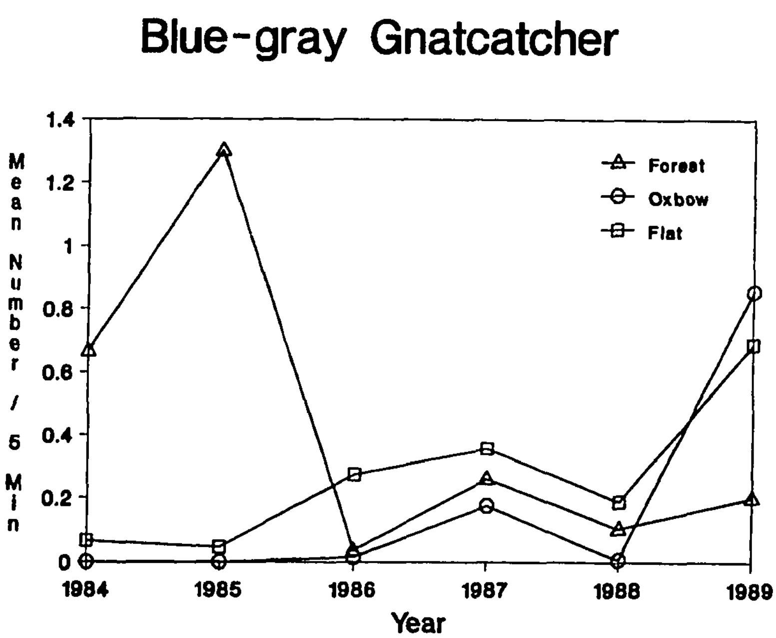


Figure 11. Population trends of the Carolina Wren and Blue-gray Gnatcatcher at Tensas River NWR, 1984-1989.

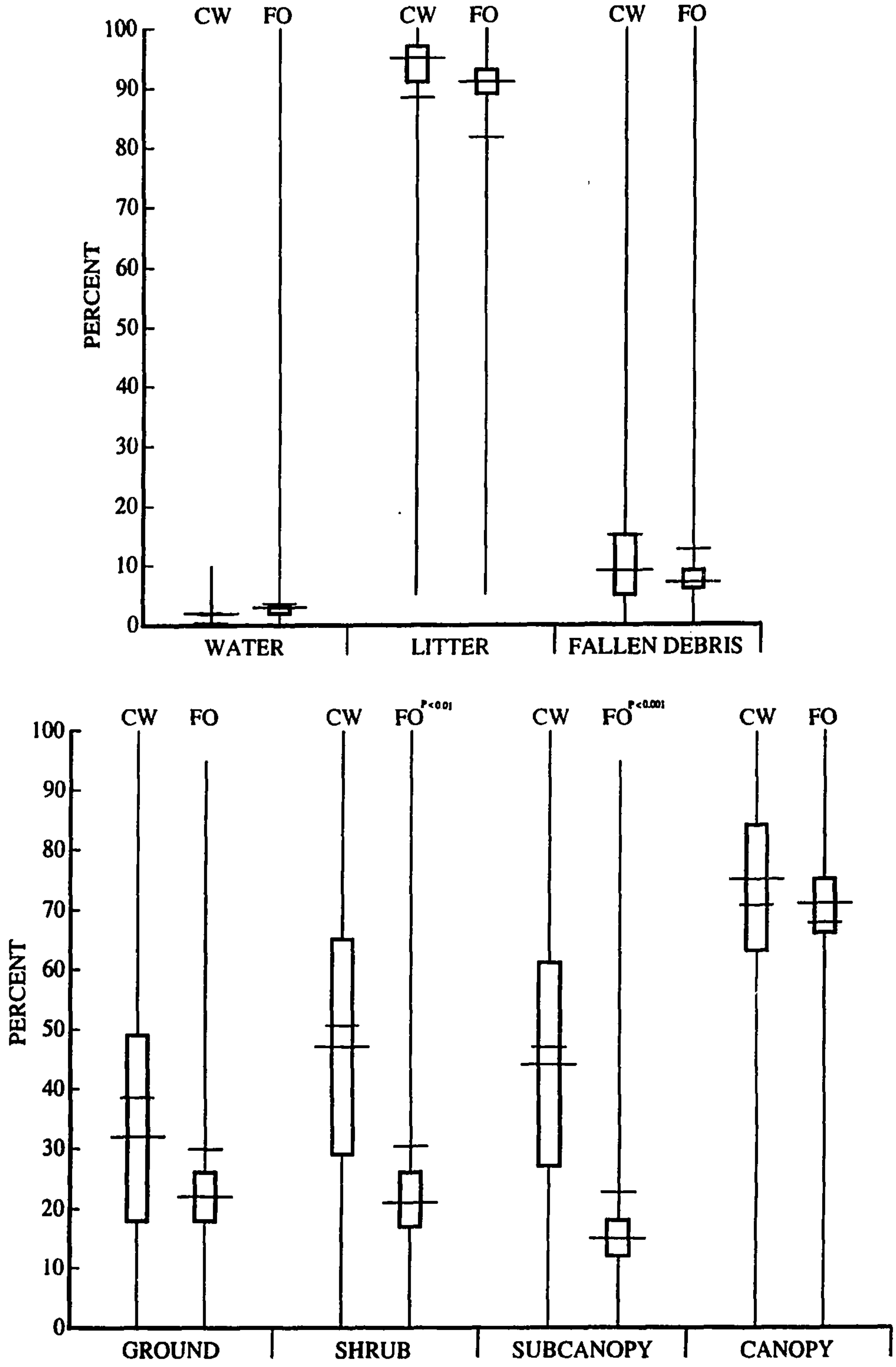


Figure 12. Use and availability of habitat characteristics and foliage density of four height strata by Carolina Wrens in a bottomland hardwood forest.

on bark substrates, (Table 9.). Kinglets had the third largest niche breadth value for foraging height (Table 6.).

Blue-gray Gnatcatcher.- The Blue-gray Gnatcatcher was found to be rare (1984-85) to common (1989) in the flat, absent (1984-1985) to common (1989) in the oxbow, and rare (1986) to common (1984-85 in the forest (Figure 11.). In general, the gnatcatcher is a relatively uncommon breeding bird in the bottomland hardwoods of the Tensas River Basin.

The Blue-gray Gnatcatcher foraged predominantly in the canopy of the forest (Table 4., Table 5., and Table 16.) and tended to select sites with a smaller proportion of canopy foliage than with random sites (Figure 14.). Twenty-two percent of foraging observations were directed at the air, and 24% at branches: They foraged at sites with a mean canopy foliage density of 34.7% in the flat to 37.4% in the forest.

The "glean" and "sally-glean" were the most frequently employed maneuvers (Table 7.). Gnatcatchers appeared to frequently flush prey from hiding places among the foliage and branches by flashing their white outer retrices. This behavior accounted for 12% of all foraging observations (Table 7.). In addition, gnatcatchers used the "sally" maneuver in 11% of all attacks directed at prey. The Blue-gray Gnatcatcher was one of three species in this study to be classified as attacking prey at a fast rate ($x = 3.2$ attacks/min.). The gnatcatcher had the largest niche breadth value for foraging maneuver among the 19 species in the study (Table 13.).

Gnatcatchers typically searched for prey among the foliage and bark along small branches and twigs (Table 14.); however, there was an indication that gnatcatchers inhabiting the flat used branch perches more frequently than gnatcatchers in the forest site (52 vs. 25%; $p = .052$).

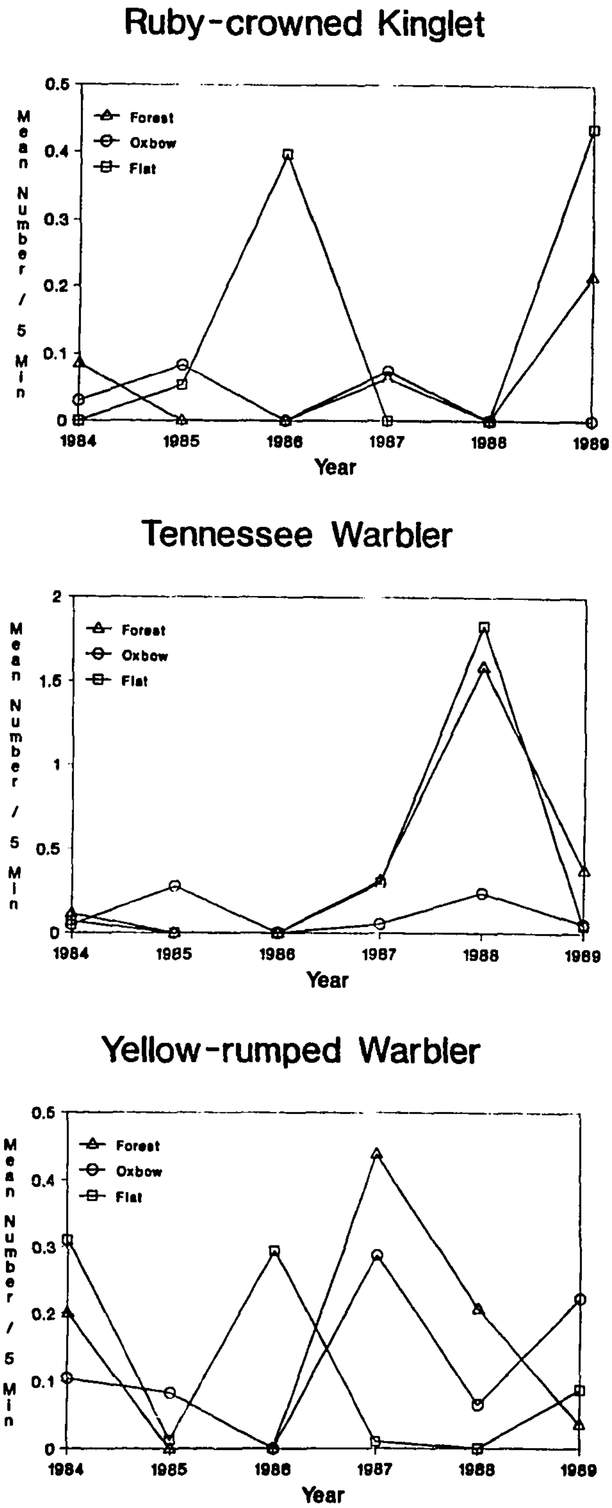


Figure 13. Population trends for two winter residents and a transient migrant at Tensas River NWR, 1984-1989.

VIREONIDAE

White-eyed Vireo.- The White-eyed Vireo is a common breeding bird in all three habitat types (Figure 15.). Unlike most species in this study, White-eyed Vireos were most abundant in 1986 and 1988.

The White-eyed Vireo, like the Acadian Flycatcher, is a subcanopy specialist; 74% of all foraging observations were recorded in this stratum. Sixteen percent of the observations occurred in the shrub stratum and eight percent in the canopy layer. It selects foraging locations with a mean foliage density of approximately 50%, which is significantly denser than at random sites (Figure 16.). In the forest, White-eyed Vireos also selected foraging sites with more palmetto cover and vine density than available randomly (Table 19.). Apparently, vines are an important component of White-eyed Vireo habitat; 37% of all prey-attacks were directed at vine leaves.

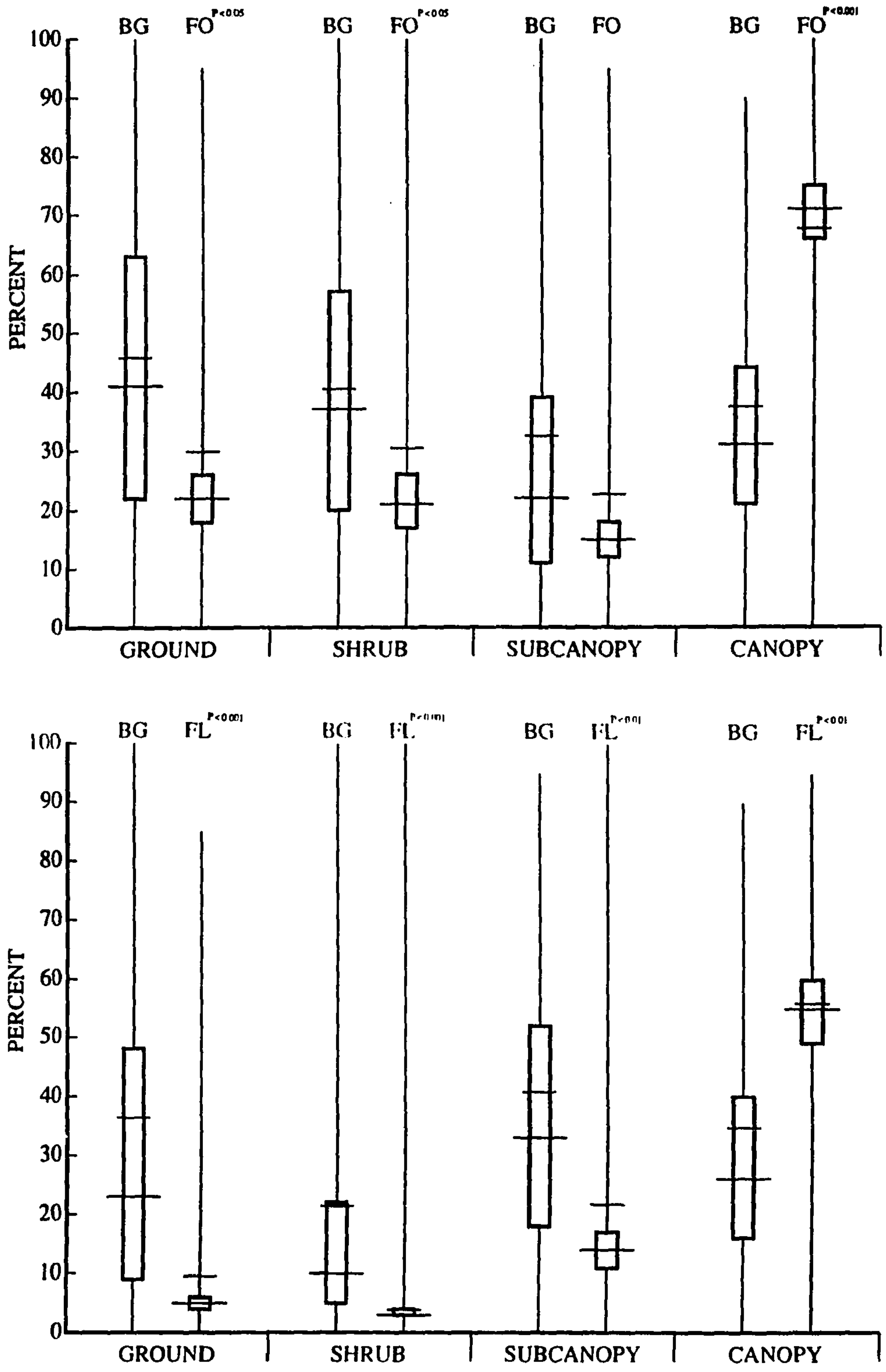


Figure 14. Foliage density use and availability by Blue-gray Gnatcatchers of four height strata in a bottomland hardwood forest.

Table 16. Characteristics of foraging sites used by 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

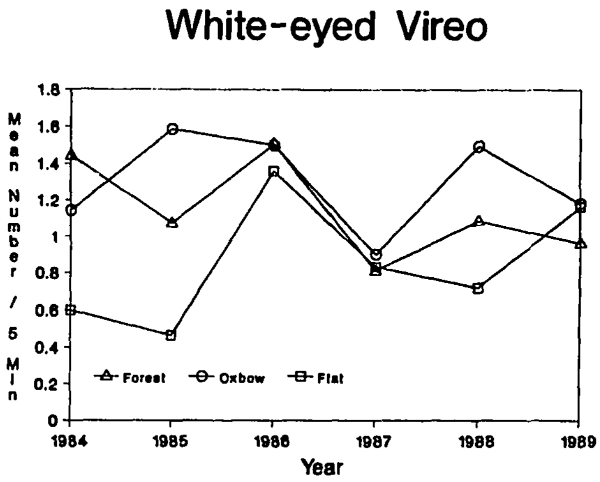
Species	N	Mean height (m) above ground		Mean plant height(m)		Relative Position
		x	sd	x	sd	
Eastern Wood-Pewee	66	10.8	6.3	16.1	7.0	.67
Acadian Flycatcher	131	6.6	3.1	12.5	5.5	.53
Carolina Chickadee	112	7.9	4.0	12.7	6.0	.62
Tufted Titmouse	79	8.1	4.9	12.6	7.4	.56
Carolina Wren	54	2.3	2.3	9.2	7.8	.25
Ruby-crowned Kinglet	18	9.7	6.3	15.9	8.5	.61
Blue-gray Gnatcatcher	74	12.1	5.2	16.7	5.8	.72
White-eyed Vireo	98	5.1	3.0	11.4	6.1	.45
Yellow-throated Vireo	47	16.3	5.0	20.9	5.1	.78
Red-eyed Vireo	85	10.4	4.2	15.6	5.9	.67
Tennessee Warbler	40	13.5	5.8	17.1	5.7	.79
Northern Parula	218	9.7	5.2	15.5	6.5	.63
Yellow-rumped Warbler	37	11.6	5.0	17.4	5.7	.67
Yellow-throated Warbler	146	13.8	4.6	17.3	5.5	.80
American Redstart	52	11.3	3.7	18.4	6.0	.61
Prothonotary Warbler	146	3.6	3.5	7.1	6.1	.50
Swainson's Warbler	17	0.4	0.5	2.0	2.5	.20
Kentucky Warbler	50	1.4	1.8	4.9	5.4	.29
Hooded Warbler	90	5.4	3.9	12.2	7.6	.44

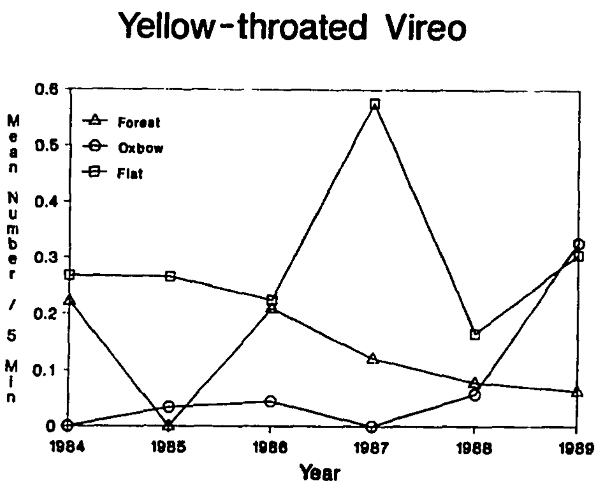
White-eyed Vireos used the "glean" and "sally-glean" maneuvers to capture prey at a relatively slow rate, prey were primarily captured from the lower surfaces of live leaves (Table 8., Table 7., Table 14., and Table 9.). They used small diameter perches within the proximal portion of tree crowns (Table 14. and Table 15.). The White-eyed Vireo had a relatively small mean overall niche breadth value (.157).

Yellow-throated Vireo.- The Yellow-throated Vireo was uncommon to common (1987) in the flat, and absent to uncommon in the forest and oxbow sites (Figure 15.). Because it occurred in greater numbers and its relative abundance was more stable during the 6 years of this study, the flat appears to be the Yellow-throated Vireo's preferred macrohabitat. In the forest, their abundance declined steadily since 1986 (Figure 15.).

The Yellow-throated Vireo foraged at a slow rate (Table 8.) almost exclusively in large trees and in the canopy layer (Table 4., Table 5., and Table 17.). The Yellow-throated Vireo had the second highest relative foraging height (Table 16.). The mean density of Yellow-throated Vireo feeding cylinders in the canopy was restricted to a narrow range in both the forest and flat (Figure 17.). These means are significantly less than randomly available at both study sites (Figure 17.).

Its primary prey-attacking maneuver was the "glean"; the "sally-glean" technique was employed less frequently (Table 7.). The Yellow-throated Vireo searched among and secured prey from the bark of large (>1 cm) branches in the canopy layer (Table 14.). Four species of oaks accounted for 67% of the trees used by foraging Yellow-throated Vireos (Table 10., Table 11.). Smaller branches, twigs, and live leaves are used as foraging substrates less frequently (Table 9.).





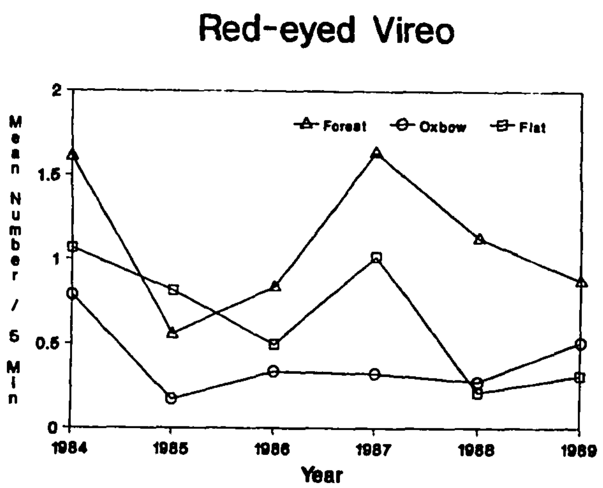


Figure 15. Population trends of three vireos at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

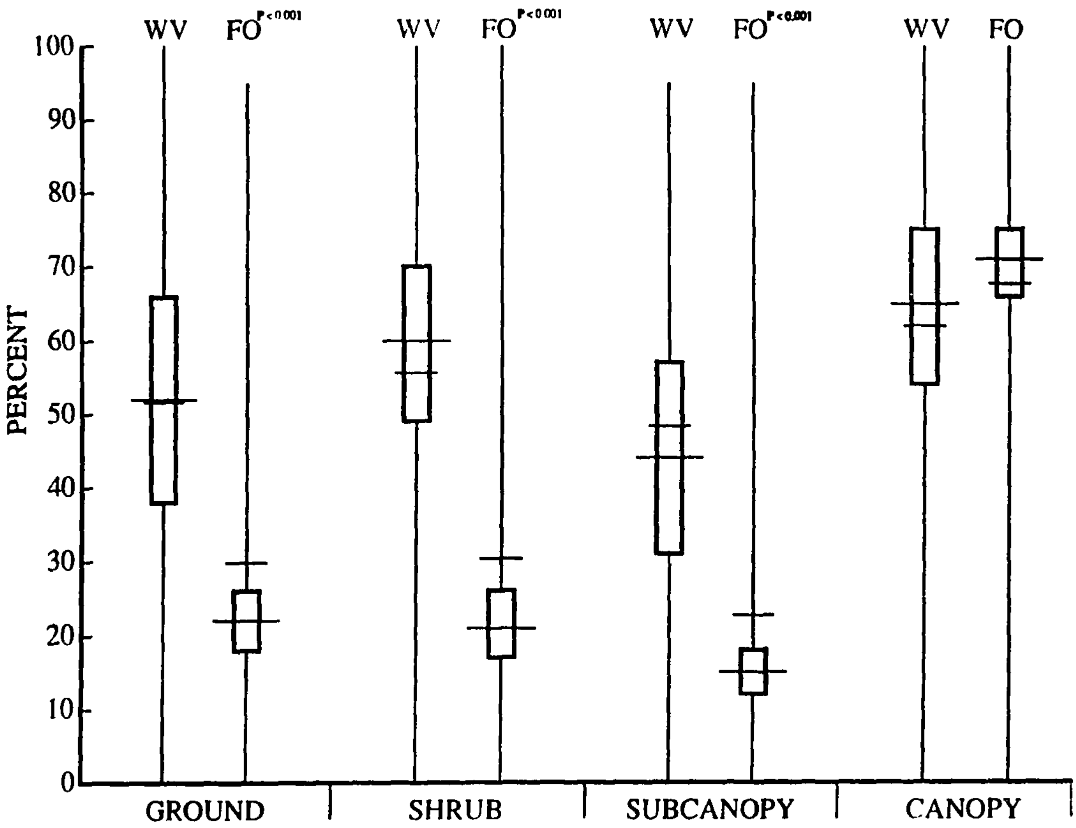


Figure 16. Foliage density use and availability by White-eyed Vireos of four height strata in a bottomland hardwood forest.

Thus, the Yellow-throated Vireo is relatively stereotyped in its foraging patterns; it uses the same foliage density, it uses the same vegetative stratum, and it attacks prey in the same manner regardless of macrohabitat. The Yellow-throated Vireo had the smallest foraging height niche breadth and the third smallest foraging maneuver niche breadth of the 19 species in this investigation (Table 13.). It had the second smallest mean overall niche breadth (.131).

Red-eyed Vireo.- During the six years of this study, the Red-eyed Vireo was a common breeding bird in the forest (Figure 15.). In the flat, it was also common from 1984-1987; however, in the last 2 years of the study it became uncommon (Figure 15.). The Red-eyed Vireo was uncommon along the margins of the oxbow lakes, except in 1984, when it was common (Figure 15.). This species was consistently two to three times as abundant in transect 1 vs. transect 2 of the flat site (APPENDIX D). Because of beaver activity and a man-made structure (elevated, bisecting dirt road), about one-third of transect 2 held water on a permanent basis. The alteration of the hydrology in this site has resulted in a reduction of tree density. Currently along transect 2 only large, scattered trees (mostly baldcypress and dead snags) exist above an understory of buttonbush and swamp privet; transect 1 had denser subcanopy and canopy foliage layers (Figure 18.). Had transect 1 been the only census route for the flat site, Red-eyed Vireo abundance would have been similar for both the forest and flat.

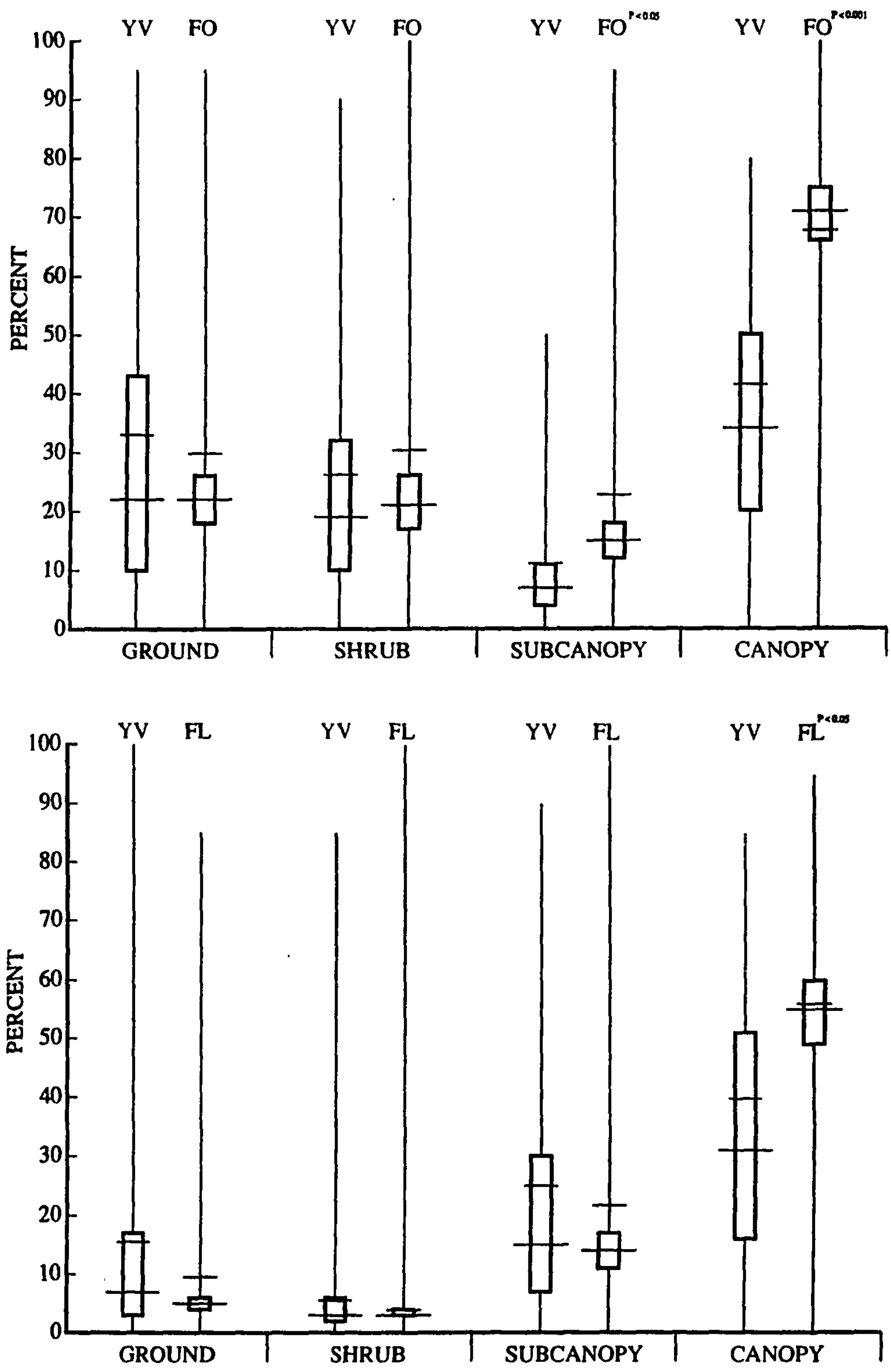


Figure 17. Foliage density use and availability by Yellow-throated Vireos of four height strata in a bottomland hardwood forest.

Table 17. Frequency of dbh class use by 19 bird species in the bottomland hardwood forest of the Tensas River Basin.

		DBH(cm)							
Species	N	<7.5	7.6-15.0	15.1-23.0	23.1-30.5	30.6-38.0	38.1-46.0	46.1-53.0	>53.0
Eastern Wood-Pewee	66	.12	.05	.11	.08	.15	.11	.15	.24
Acadian Flycatcher	131	.22	.18	.18	.15	.07	.10	.08	.02
Carolina Chickadee	112	.23	.17	.14	.18	.13	.05	.11	.05
Tufted Titmouse	79	.20	.13	.17	.10	.14	.08	.08	.11
Carolina Wren	54	.41	.13	.09	.09	.15	.02	.07	.04
Ruby-crowned Kinglet	18	.17	.11	.22	.11	.00	.06	.11	.22
Blue-gray Gnatcatcher	74	.10	.05	.14	.11	.19	.16	.10	.16
White-eyed Vireo	98	.27	.17	.19	.13	.08	.09	.02	.04
Yellow-throated Vireo	47	.00	.02	.06	.11	.21	.19	.15	.26
Red-eyed Vireo	85	.13	.11	.18	.12	.17	.07	.09	.14
Tennessee Warbler	40	.08	.08	.13	.23	.13	.15	.10	.13
Northern Parula	218	.14	.11	.13	.12	.12	,10	.15	.12
Yellow-rumped Warbler	37	.14	.03	.19	.19	.22	.05	.08	.11
Yellow-throated Warbler	146	.01	.03	.03	.37	.02	.01	.07	.47
American Redstart	52	.04	.04	.14	.21	.17	.12	.17	.12
Prothonotary Warbler	146	.36	.32	.12	.08	.06	.02	.01	.04
Swainson's Warbler	17	.71	.29	.00	.00	.00	.00	.00	.00
Kentucky Warbler	50	.74	.08	.04	.08	.04	.00	.00	.02
Hooded Warbler	90	.29	.13	.11	.12	.12	.11	.04	.06
Mean frequency for all species	1,560	.23	.11	.12	.14	.12	.08	.08	.12

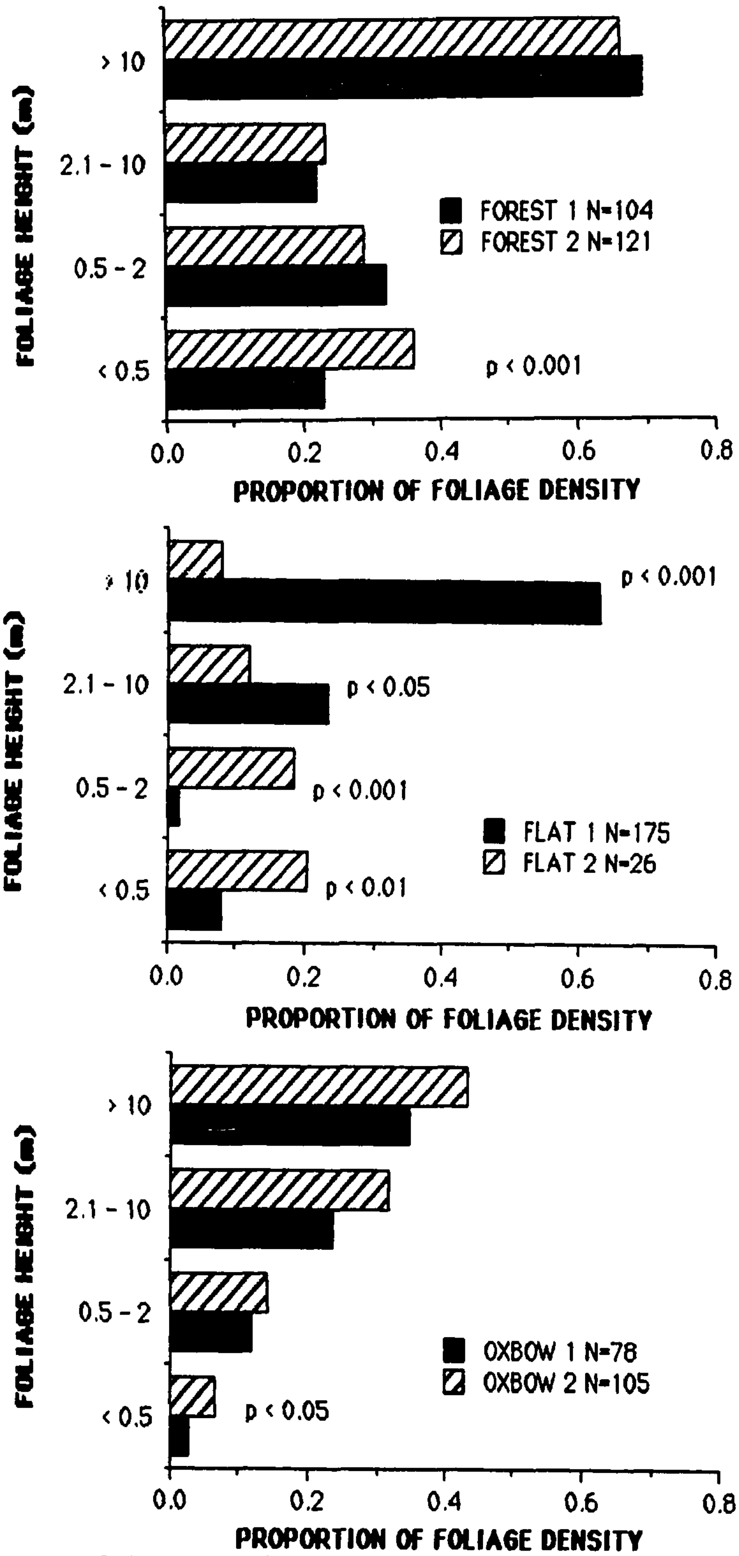


Figure 18. Mean foliage profiles of transect pairs in each study site at Tensas River NWR.

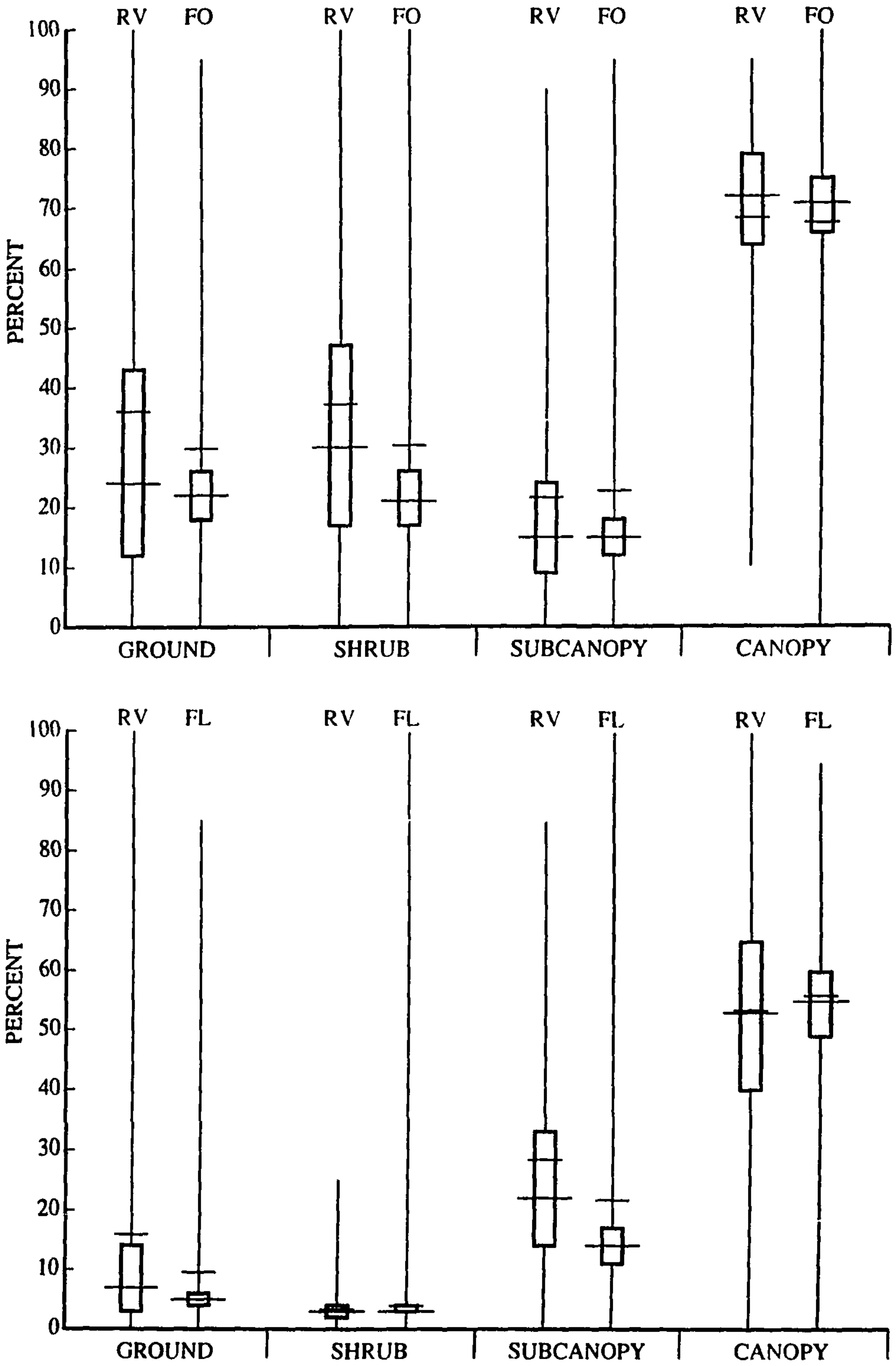


Figure 19. Foliage density use and availability by Red-eyed Vireos of four height strata in a bottomland hardwood forest.

The Red-eyed Vireo foraged with equal frequency in the subcanopy and canopy layers of mostly tall trees (Table 4. and Table 5.). Foliage density in these layers were used in concordance to random availability (Figure 19.), and, unlike its congeners, this species is a generalist with respect to foraging microhabitat selection.

Food was obtained primarily by "gleaning" and "sally-gleaning" insects from the lower surfaces of live leaves in the distal portion of tree crowns (Table 7., Table 14., Table 9., and Table 15.). "Hanging" from foliage arranged near the end of branches was also employed by this species (Table 7.). Because of its predilection for foraging at live leaves, the Red-eyed Vireo had the second smallest foraging substrate niche breadth of 19 species (Table 13.).

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Tennessee Warbler.- The Tennessee Warbler was an uncommon to nearly abundant (1988) species in the Tensas River Basin during April and early May (Figure 13.). These numbers are significant in that Tennessees do not breed in the Basin. These bottomland hardwoods are used only as a migratory stopover area during their northward migration. During the month of April, Tennessee Warblers in the forest study site had the seventh largest mean abundance value (0.48/5 min., 6 years combined) of the 19 species in this study (Barrow, unpublished data).

The Tennessee Warbler foraged primarily in the canopy of tall trees (Tables 3 and 4, Relative height = .77). Ninety percent of all foraging observations occurred in trees >10 m in height. In the flat, foliage density of the feeding cylinder was ($x = 40.8 \pm 29.2$) significantly less than randomly available in the canopy layer (Figure 20.). Because I sampled availability after trees had

completely leafed out and Tennessees were common in April, when most tree species in the flat were beginning to leaf out, the difference in foliage used and available may merely be a sampling artifact.

The Tennessee Warbler at Tensas River NWR primarily "gleaned" foliage for insects, "sally-glean" never accounting for more than 10% of the leaf-directed attacks (Table 6). Prey were captured mostly on the lower surfaces of leaves within the distal portion of tree crowns (Table 14. and Table 15.). Tennessees, more than any other species, used flowers (mostly catkins) as a foraging substrate for 20% of the total observations. Forty percent of all observed foraging maneuvers occurred in overcup oaks. Attack rates of Tennessees were fast in all three macrohabitats (forest, 3.2/min.; flat, 3.2/min.; oxbow, 4.0/min.). The Tennessee Warbler had the second smallest foraging maneuver niche breadth value (.038), and the smallest mean overall niche breadth value (.130) of the 19 species in this study.

Northern Parula.- The Northern Parula was common or abundant in the oxbow site, and uncommon to common in the non-flooded forest, 1984 to 1989 (Figure 21.). The parula ranged from rare to common in the flat site (APPENDIX D). Because Spanish moss (a nesting substrate requirement for parulas) was essentially absent from the flat site, I believe most of these birds were either individuals temporarily foraging there from adjacent oxbow and forest sites, or transient migrants. The leaves of most canopy trees in the flat, especially overcup oak and bitter pecan, did not leaf out until the end of April. If insects track newly emerging foliage, then perhaps the abundant parula does as well. Alternatively, because parulas were abundant and concentrated in patches of Spanish moss, these individuals may be nonbreeding "nomads". In other words, there may be more parulas than available nest sites. In the forest site,

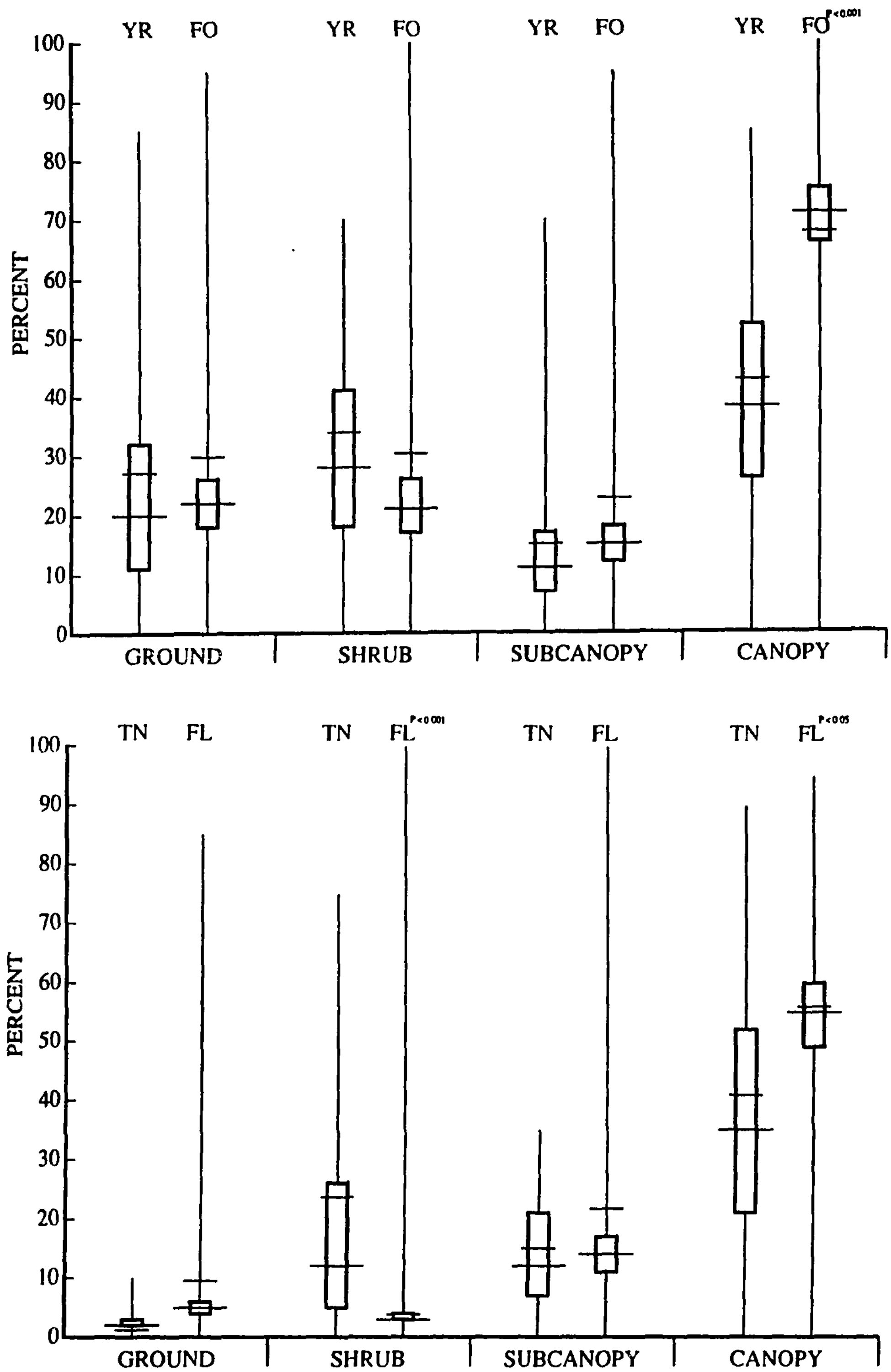


Figure 20. Foliage density use and availability by Tennessee Warblers and Yellow-rumped Warblers of four height strata in a bottomland hardwood forest.

Table 18. Special habitat features (within 100 m on either side) of the forest census transects.

		Palmetto density[1]		Cane density		Moss density		Vine density	
Transect	N	x	sd	x	sd	x	sd	x	sd
1	104	3.8	1.7	0.0	0.0	0.0	0.0	2.4	2.3
2	121	4.2	1.3	0.0	0.3	0.8	1.5***[2]	2.5	2.2

1. Vegetative density of the special habitat features were estimated for each plot on a subjective scale from 0 to 5. A value of 0 indicates no vegetative density of the habitat feature within a 5 m radius circular plot and a value of 5 indicates a density of 90-100%.
2. The percent density of the plots (transect 1 vs. 2) are followed by significance levels for a G-test (for homogeneity of distribution, classes 0 to 5): * = P <= .05; ** = P <=.01; *** = P <= .001.

parulas were more abundant along transect 2 vs. transect 1 by a factor of two to six during the 6 years of the study (Figure 22.). The foliage density in the shrub through canopy strata, where parulas nest and forage, did not significantly differ between the two transects (Figure 18.). However, the mean density of Spanish moss did differ significantly between the transects (Table 18. transect 1, x = 0.0; transect 2 x = 0.77; on a scale of 0 to 5). Trees draped with Spanish moss were found only in a concentrated area along the southern one-third of transect 2. Apparently, this patch of trees was sufficientto account for the difference in abundance; Northern Parulas use moss as a substrate in which to place its nest. Obviously, had only one transect been censused in this habitat type the result would have been a completely different picture of parula distribution and abundance.

The parula foraged primarily in the subcanopy and canopy with nearly equal frequency (Table 4.). Most foraging activity occurred in tall trees (Table 5.). In the forest, parulas selected sites with subcanopy and canopy density the same as in random sites (Figure 23.). However, parulas foraged at sites with more palmetto cover, and probably more importantly, denser moss than at random sites (Table 19.). In the oxbow, parulas foraged where the subcanopy density was in concordance with available foliage density, but they selected sites with denser foliage in the canopy layer (Figure 23.). Because of the spacing of large trees along the margins of the two oxbow lakes, available canopy foliage was sparse (x = 40.2 ± 28.3%). Although parulas used Spanish moss for nesting, they rarely foraged on or within moss (Table 9.); subsequently, they tended to avoid foraging sites with dense clumps of moss (Table 6.).

Northern Parulas used small diameter perches while searching for

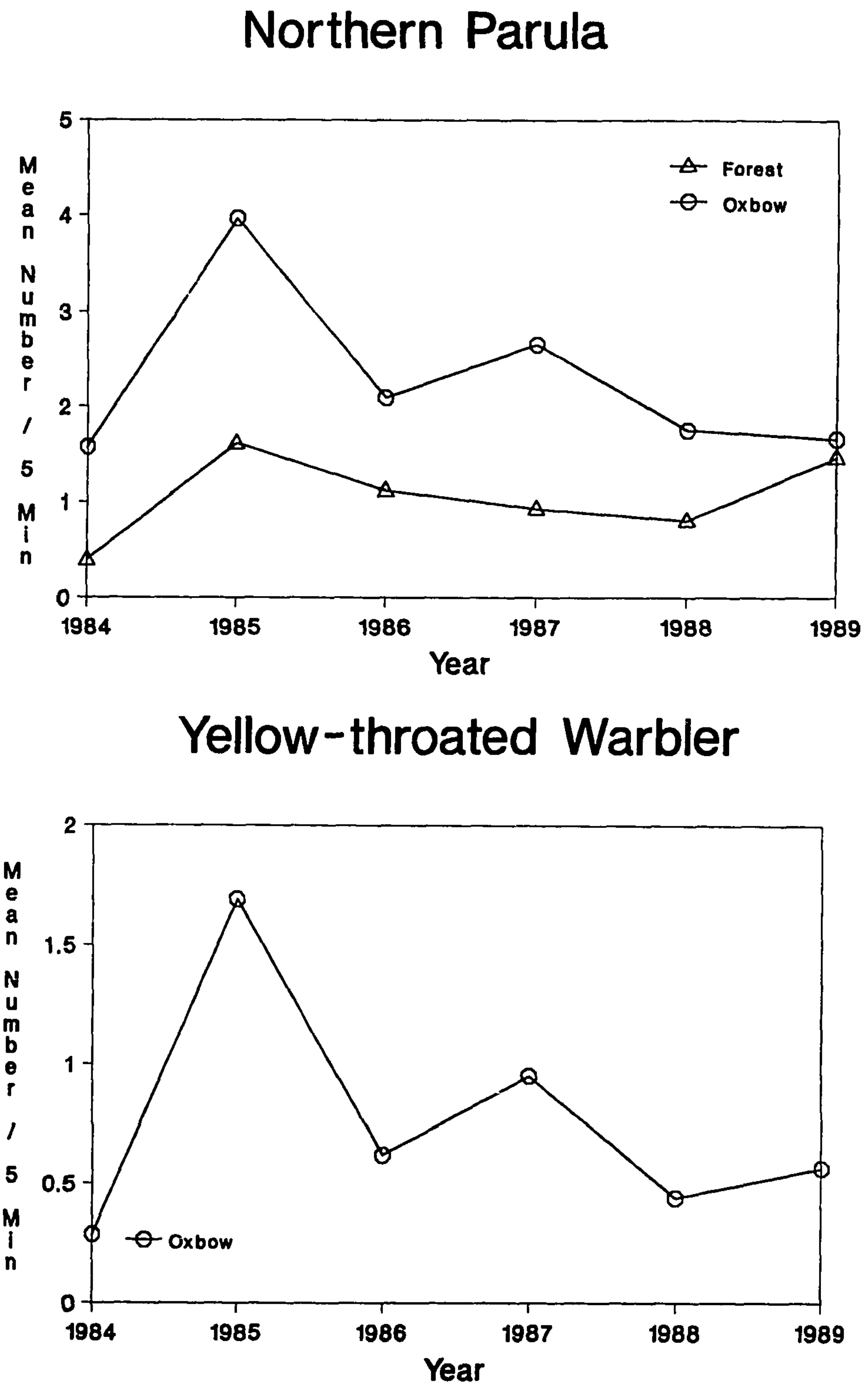


Figure 21. Population trends of two warblers at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

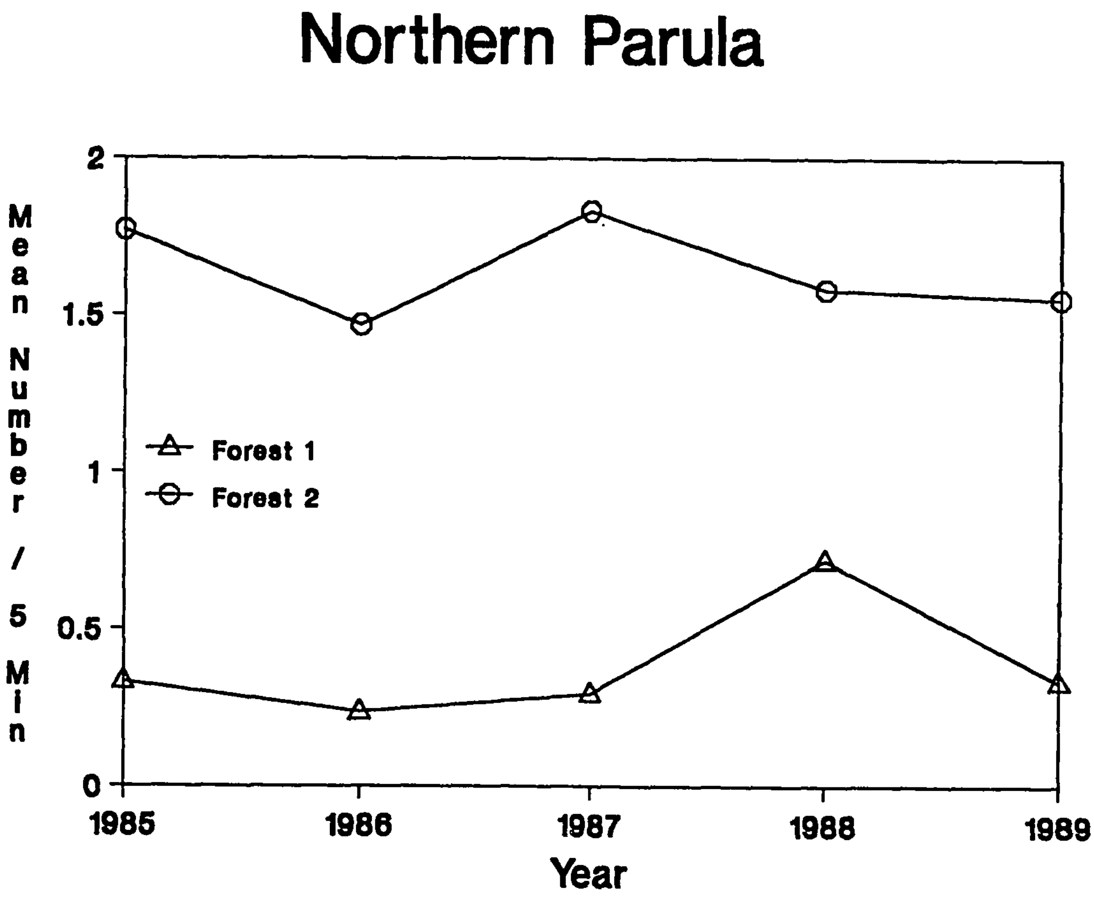


Figure 22. Population trends of Northern Parulas along the two transects in the "forest" site at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

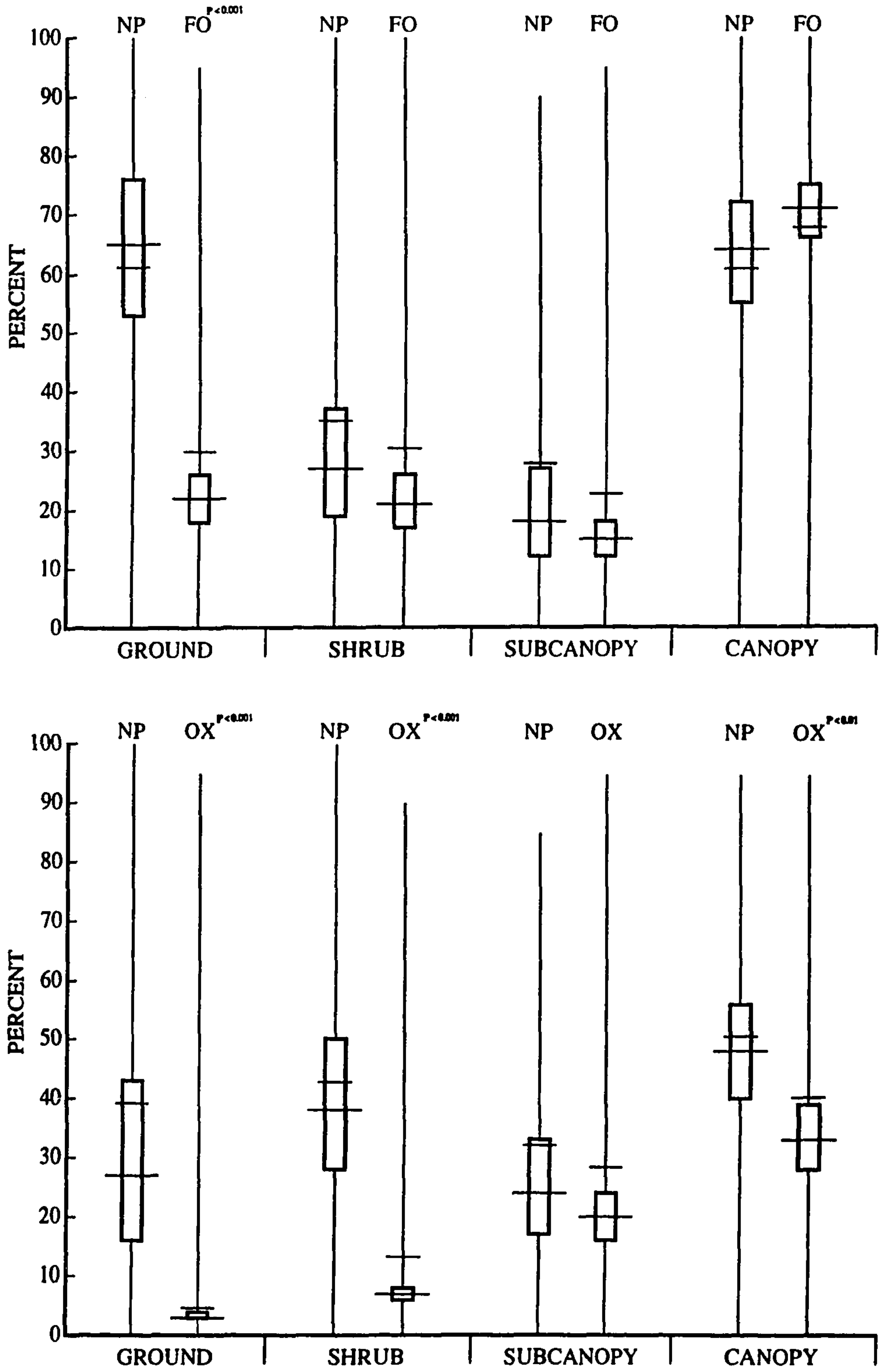


Figure 23. Foliage density use and availability by Northern Parulas of four height strata in a bottomland hardwood forest.

insects throughout tree crowns (Table 14. and Table 15.). Parulas captured prey primarily by "gleaning" the lower surfaces of live leaves (Table 7., Table 9., and Table 14.). "Sally-gleaning" was the second most frequently used maneuver (24%); "hanging" from leaves was occasionally used (8%).

Yellow-rumped Warbler.- At Tensas River NWR, the Yellow-rumped Warbler is a winter resident. During the spring, Yellow-rumped Warblers ranged from absent to uncommon in all three habitats; abundance patterns tended to fluctuate between 0.0 and about 0.3/5 min. annually (Figure 13.).

Yellow-rumped Warblers foraged primarily in the canopy and subcanopy strata; they used trees almost exclusively in heights exceeding 10.0 m (Table 4. and Table 5.). In the forest, foliage density used in the subcanopy stratum was in proportion to availability (Figure 20.). In the canopy, available foliage was denser than that used by yellow-rumps. Because most foraging observations of this species were in late March and early April during initial stages of leaf-out, and random sampling was conducted after full leaf-out; microhabitat analysis for this species is probably biased.

Yellow-rumped Warblers captured prey by "gleaning" and "sally-gleaning" live leaves (66%) and bark of tree trunks, branches, and twigs (20%) (Table 7. and Table 9.). Occasionally, yellow-rumps would capture flying insects in mid-air (6%). Like its winter-resident counterpart, the Ruby-crowned Kinglet, yellow-rumps frequently foraged in cedar elm trees (Table 10. and Table 11.). Perhaps there is an early spring insect that attacks cedar elms and provided a late winter/early spring food source for avian insectivores. Thirty-eight percent of all tree-directed foraging

attempts were in oaks (Table 10. and Table 11.). During the Spring, Yellow-rumped Warblers had the smallest niche breadth for plant species used (.086).

Yellow-throated Warbler.- The Yellow-throated Warbler was common to nearly common in the oxbow study area during all years of the study (Figure 21.). The Yellow-throated Warbler was recorded as rare in the flat in 1988 and 1989. In the flat, all observations occurred in one of two large (>24.0 cm dbh) baldcypress trees along transect 2 (APPENDIX D). The Yellow-throated Warbler did not breed in the forest study site. In the Tensas River Basin, Yellow-throated Warblers were observed, presumably breeding, in two other habitat types: cypress brakes (small patches [10-20 ha] of baldcypress stands in low-lying areas), and along the margins of the Tensas River (a habitat almost identical to the margins of oxbow lakes). All of these sites had two elements in common -- baldcypress trees and Spanish moss.

The Yellow-throated Warbler specialized in foraging in the canopy of tall trees (x dbh = 49.4 ± 24.3 cm) (Table 4. and Table 5.; relative height=.81). Although Yellow-throated Warblers were found at locations with foliage in the ground through subcanopy denser than randomly available, foliage density in the canopy, the stratum most frequently used by Yellow-throated (91%), was in concordance with availability (Figure 24.). In addition, Yellow-throated Warblers foraged in areas with sparse vine foliage, and above areas with switchcane cover less than randomly available (Table 6.). Because they foraged primarily by "gleaning" bark of branches within the distal portion of tree crowns (Table 7., Table 9., and Table 15.), dense vine foliage may have interfered with their search patterns and/or movements.

Other than "gleaning" bark, Yellow-throated Warblers used a variety of behaviors: "sally-gleaning" live leaves, bark, and moss, "probing" and "hang-probing" moss and bark, "hanging" from live leaves and moss, "sally-probing" moss, and "flutter-chasing" falling insects (Table 7. and Table 9.). Eighty-nine percent of all yellow-throated foraging observations occurred in three plant species: baldcypress (41%), willow oak (33%), and Spanish moss (15%).

The Yellow-throated Warbler appears to be a specialist in terms of foraging location, and a generalist in terms of maneuvers employed. This species had the smallest niche breadth value for plant species, the second smallest value for foraging height, and the second largest value for foraging maneuver; overall, it had the third smallest mean value (.138).

American Redstart.- Abundance of American Redstarts varied from rare (1985) to common (1986) during the 6-year study period (Figure 25.). Redstarts were recorded as rare during some years in the flat and oxbow sites; most years they were absent (APPENDIX D and APPENDIX E). Redstart abundance declined steadily during the last 4 years of the study (Figure 25.).

Redstarts foraged with nearly equal frequency in both the subcanopy and canopy layers of the forest (Table 4.). Foraging activity occurred almost exclusively (90%) in trees >10.0 m in height. Redstarts selected locations with foliage denser than at random sites in all strata except the canopy, where foliage density was in concordance to availability (Figure 26.). A large proportion of subcanopy foliage in the forest consisted of vine tangles (Barrow, pers. observ.). Redstart foraging sites had a mean vine density value greater than at random sites (Table 19.).

A variety of foraging maneuvers was used by redstarts: "sally-

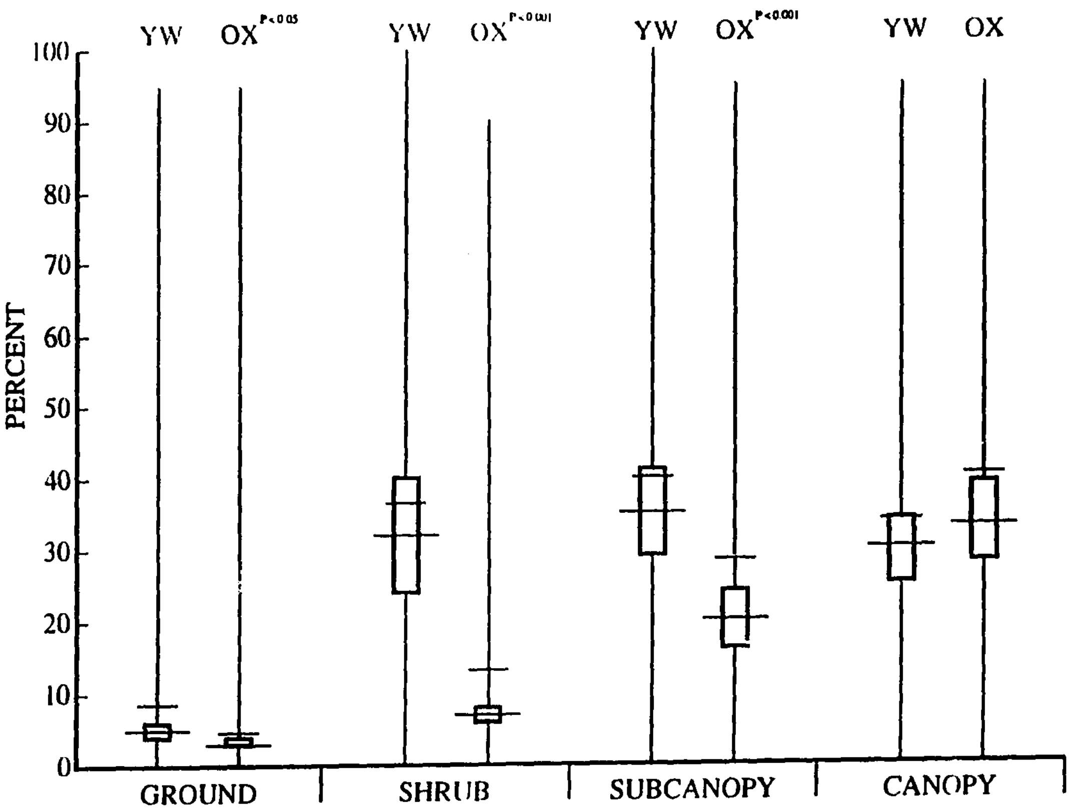
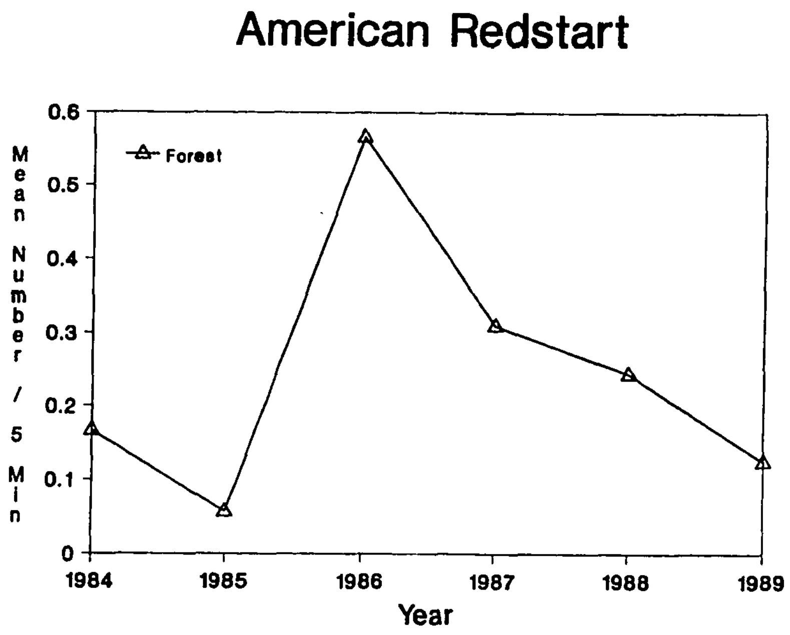


Figure 24. Foliage density use and availability by Yellow-throated Warblers of four height strata in a bottomland hardwood forest.

glean" (51%), "sally" (19%), "glean" (10%), and "flush-pursue" (14%) (Table 7.). The maneuvers were directed almost exclusively toward the lower surfaces of leaves or the air (Table 14. and Table 9.). Redstarts searched for prey mainly along small diameter perches in the outer halves of tree crowns (Table 14. and Table 15.). Almost 50% of redstart foraging activity occurred in two plant species: sweetgum (33%) and water oak (15%). Various species of vines were also used as foraging substrates by redstarts (Table 10. and Table 11.). Redstarts had the third largest niche breadth for foraging maneuver, and the third smallest value for plant species (Table 13.).

Prothonotary Warbler.- The Prothonotary Warbler was common in the flat during all years of the study (Figure 25.). In the oxbow site, the abundance of Prothonotary Warblers ranged from uncommon in 1984 to abundant in 1985, and then fluctuated within the common category from 1986 through 1989. In the forest, they were common in 1984, less common in 1985, and remained consistently uncommon, 1986-1989 (Figure 25.).



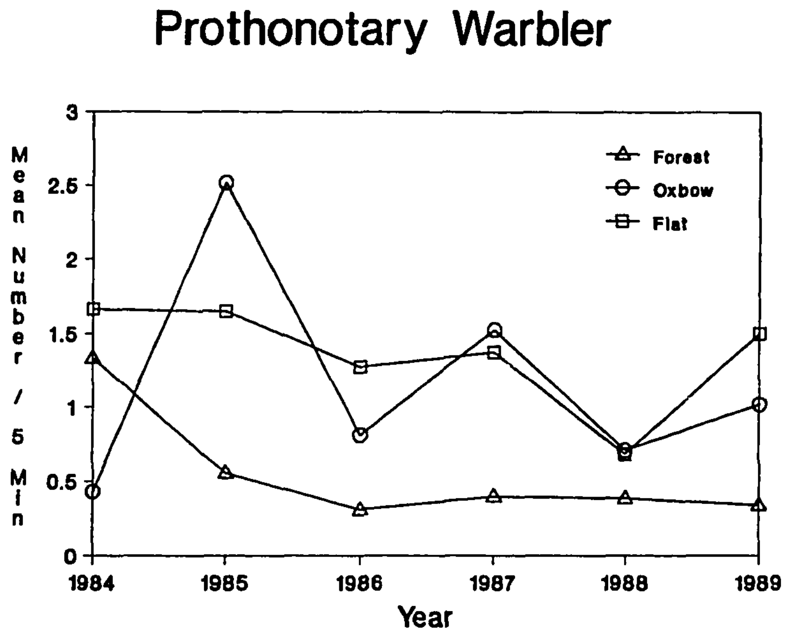


Figure 25. Population trends of two warblers at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

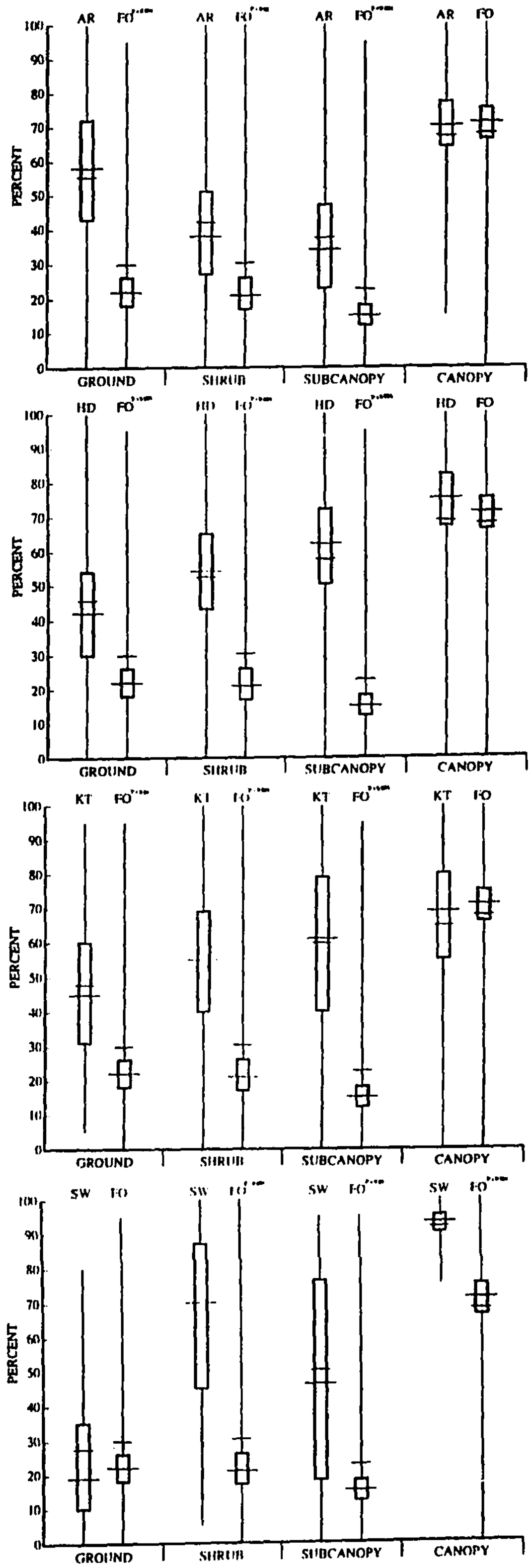


Figure 26. Foliage density use and availability by American Redstarts, Swainson's Warblers, Hooded Warblers, and Kentucky Warblers of four height strata in a bottomland hardwood forest.

At Tensas River NWR, Prothonotary Warblers foraged within all four vegetative strata, although the subcanopy stratum was used most frequently (Table 4.). In the forest, Prothonotary Warblers used foraging sites with greater water cover and less ground litter cover and ground vegetation density than at random sites (Figure 27.). In the subcanopy of the forest site, where 80% of foraging occurred, bird-centered plots had denser subcanopy than randomly available (Figure 27.). Random plots had denser foliage in the canopy stratum than bird-centered plots (Figure 27.). Random sites also had denser palmetto foliage than prothonotary foraging sites (Table 19.). In the forest, Prothonotary Warblers were patchily distributed; they occurred in low-lying areas (old scour-channels) typically devoid of palmetto growth. In the flat, Prothonotary Warblers showed microhabitat use patterns similar to the forest site with regard to water cover, ground litter cover, and canopy foliage density; subcanopy foliage was in concordance to availability (Figure 27.). In the oxbow, Prothonotary Warblers also foraged at sites with greater water cover than randomly available (Figure 27.). However, oxbow-inhabiting prothonotarys foraged at sites with shrub foliage denser than at random sites (Figure 27.). In the oxbow, 50% of all Prothonotary Warbler foraging observations occurred in the shrub stratum. Along the margins of the oxbow lakes, prothonotarys foraged at sites with fewer vine tangles, and less moss density than randomly available (Table 6.).

Prothonotary Warblers searched for prey throughout the crowns of trees and shrubs; they used a variety of perch diameters (Table 14. and Table 15.). Prey were captured primarily by "gleaning" (76%) or "sally-gleaning" (12%) insects from live leaves or bark of tree trunks, branches, and twigs (Table 9.). On several occasions,

prothonotarys were observed "probing" dead leaves or bark substrate (Table 7. and Table 9.). On eight occasions (2%, of total observations), I observed the Prothonotary Warbler use the "gape" maneuver. It was used while searching curled dead leaves and rolled live leaves. Twenty-nine percent of their foraging observations were in two species of shrubs: buttonbush (14%) and swamp privet (15%). A variety of other species accounted for the remaining 71% (Table 10. and Table 11.).

Prothonotary Warblers inhabiting the margins of oxbow lakes foraged differently than those in the flat and forest. Two foraging characteristics were significantly different between the oxbow habitat and each of the other two sites: foraging height and plant height in which foraging occurred. Prothonotarys in the oxbow habitat foraged more frequently in the shrub layer (50.0 vs. 18.9%) and less frequently in the subcanopy (14.1 vs. 58.5%) than flat-inhabiting Prothonotary Warblers (G = 17.9; df = 3; n = 58, 53; p = .0001). Thus, the height of plants most frequently used were shorter in the oxbow site (0.5-2 m: oxbow, 36.2%; flat: 13.2%) and taller in the flat site (>10.0 m; oxbow, 19.0; flat: 30.2%) (G = 9.4; df = 3; n = 58, 53; p = .025). A comparison of the oxbow site and the forest site revealed similar patterns for both foraging height (G = 29.7; df = 3, n = 58, 35; p = .0001 and plant height used (G = 13.1; df = 3, n = 58, 35; p = .005).

Prothonotary Warblers bred in all three macrohabitats and were relatively flexible in their use of foraging locations and plant species used. Prey were captured from live leaf (45%) and bark (34%) substrates with nearly equal frequency. Within the vegetation strata most frequently used in each macrohabitat, there was a wide range of mean foliage densities used (APPENDIX F, APPENDIX G, and APPENDIX H).

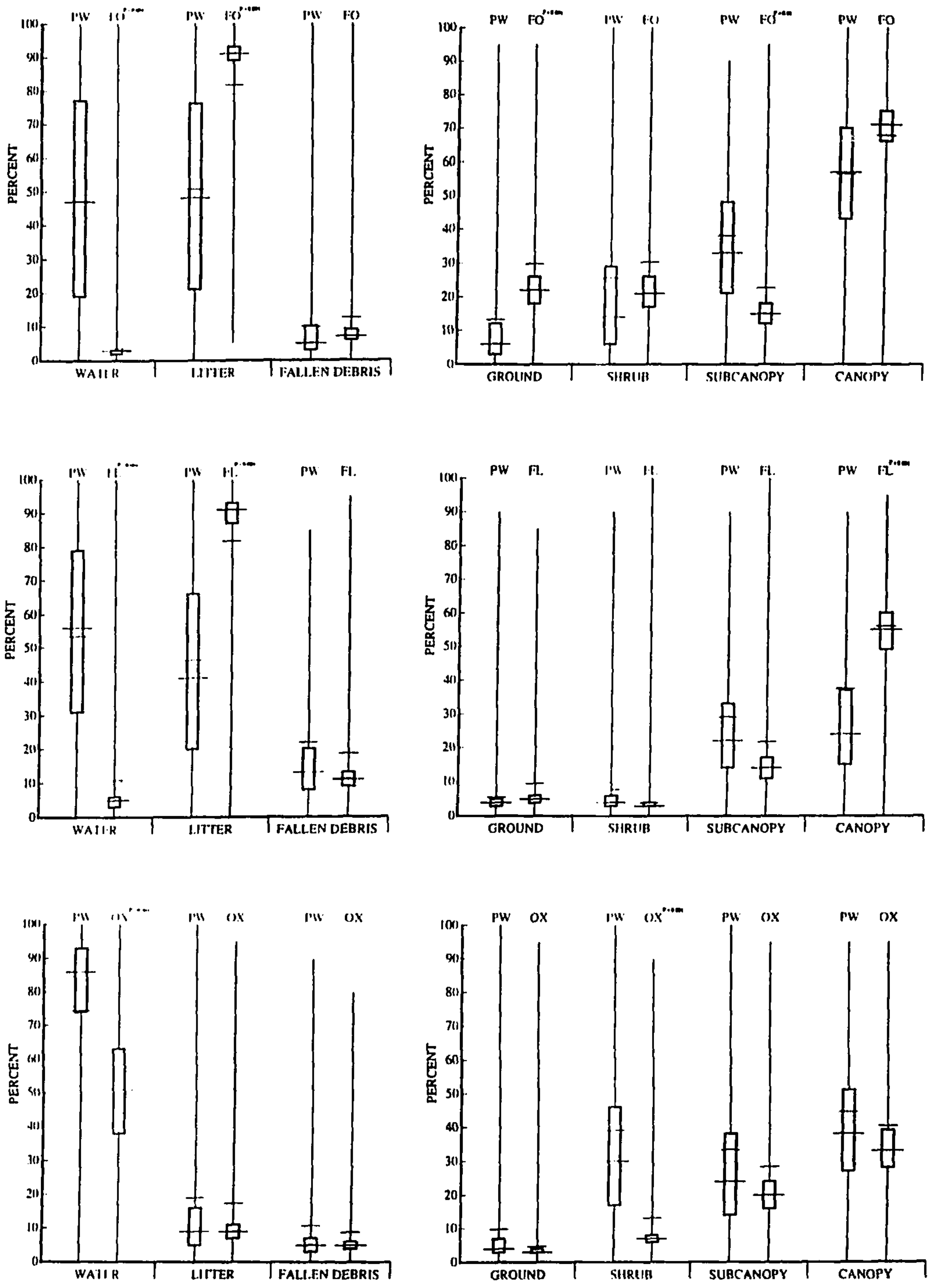


Figure 27. Use and availability of habitat characteristics and foliage density of four height strata by Prothonotary Warblers in a bottomland hardwood forest.

The Prothonotary Warbler had the second largest mean overall niche breadth value (.327) of the 19 species in this study.

Swainson's Warbler.- In the forest site, Swainson's Warblers were common in 1984, rare in 1985 and 1988, and uncommon in all other years of the study (Figure 29.). Swainson's Warblers were rare or uncommon along the margins of oxbow lakes in 1985, 1986, and 1989 (APPENDIX E). On occasion, Swainson's Warblers were observed in the flat, although there was no evidence of breeding (APPENDIX D).

The Swainson's Warbler foraged primarily in the ground stratum (71%); the shrub stratum was also used (29%). The height of substrates used by Swainson's Warblers was evenly distributed among these categories: <0.5 m, 35%; 0.5-2.0 m, 30%; >2.0-10.0 m, 35%. The relative foraging height of the Swainson's Warbler was the lowest of all species (.27). The ground foliage density in Swainson's Warblers feeding cylinders was in concordance with availability (Figure 26.); however, foliage at foraging locations was denser in the shrub through canopy strata than at random sites (Figure 26.). It had the smallest range of canopy foliage density above foraging sites of all 19 species in the study (75-100%). The mean ground litter cover at foraging locations (98%) was greater than at random sites (Figure 28.). In addition, it foraged at sites with greater palmetto density than randomly available (Table 19.). Switchcane, a plant often cited as being a preferred species in Swainson's Warbler's territories, was not significantly denser at foraging sites compared to random sites (Table 19.) (Meanley 1966, 1971). However, switchcane was not a common habitat feature of the forest study area (Table 19.).

Swainson's Warblers foraged primarily by using "flake" maneuver in ground leaf litter (Table 7. and Table 9.). The "glean" maneuver

was the second most common behavior used by this species (Table 7.). Fallen debris (large branches and logs) was used as foraging substrates more often by this species than any other (Table 9.). Palmetto and small hackberries (<15.9 cm dbh) accounted for 53% of the plant species used by foraging Swainson's Warblers (Table 10., Table 11., and Table 17.).

Thus, it appears that the Swainson's Warbler is a closed canopy (>75%) ground foraging specialist. In addition, a narrow range of maneuvers is used while foraging on a few substrate types (Table 13.). The Swainson's Warbler had the smallest mean overall niche breadth of the 19 species in this study (.130).

Kentucky Warbler.- Kentucky Warblers were uncommon in the forest and oxbow during the 6 years of this study, except 1984, when they were common in the forest. Although no evidence of breeding was found, Kentucky Warblers were occasionally observed in the flat (APPENDIX D).

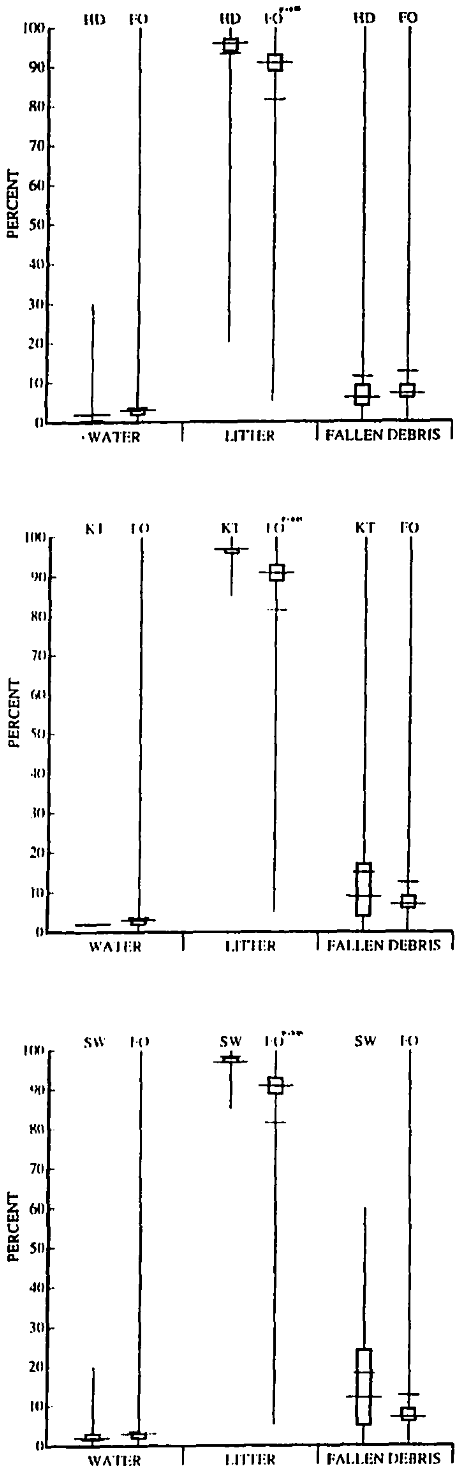
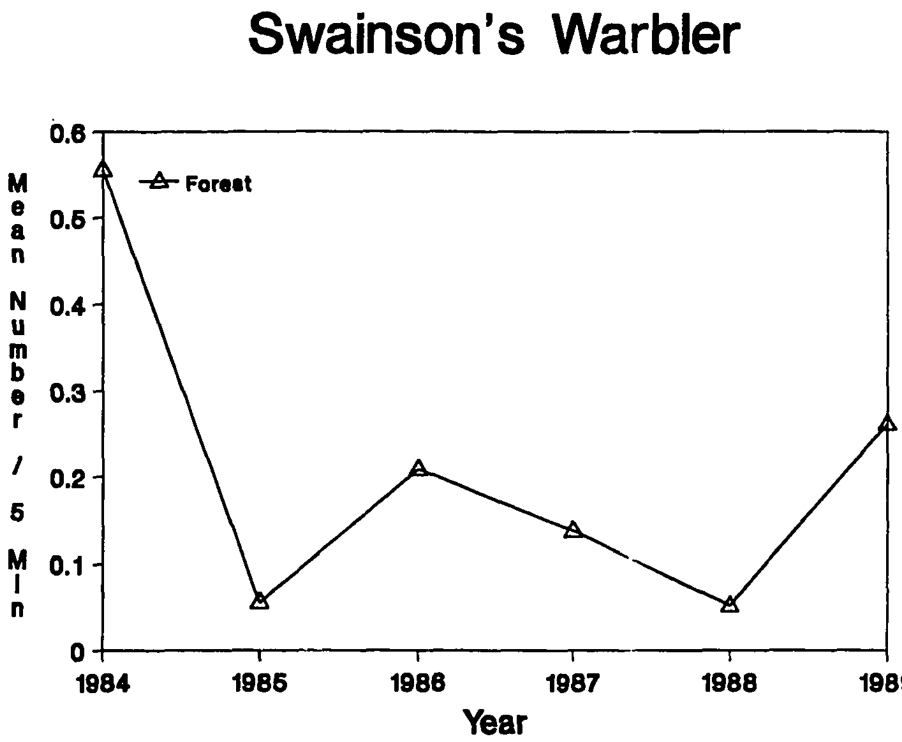


Figure 28. Use and availability of habitat characteristics by Swainson's Warblers, Kentucky Warblers, and Hooded Warblers in a bottomland hardwood forest.



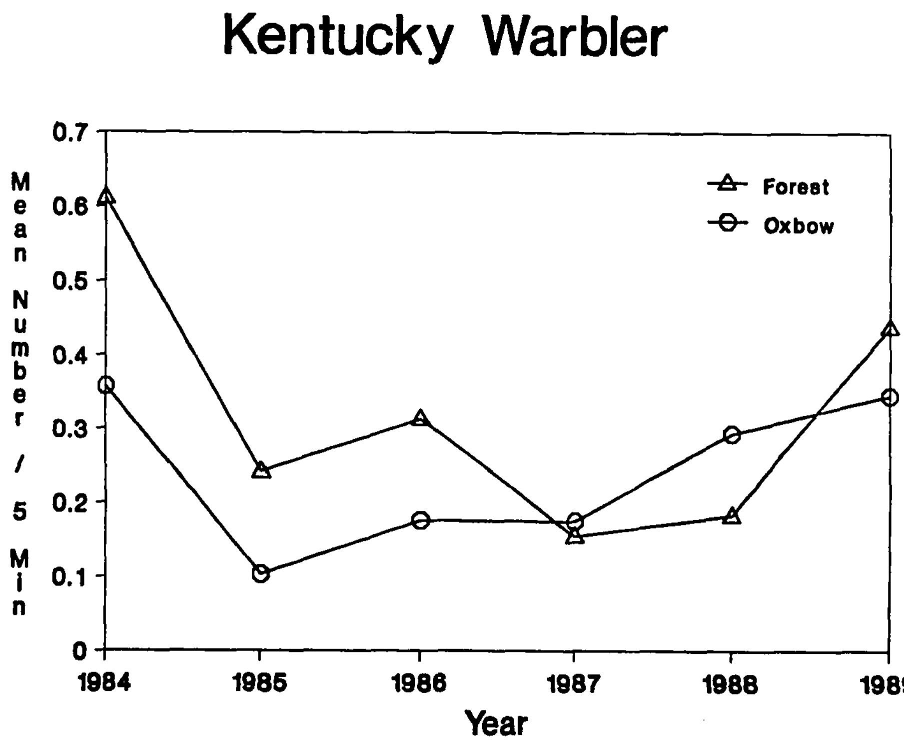


Figure 29. Population trends of understory warblers at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

Table 19. Mean and standard deviations of special habitat features available and at bird foraging locations in the "forest" study site of the Tensas Basin.

		Palmetto[1]		Vine		Moss		Cane	
Species	N	x	sd	x	sd	x	sd	x	sd
Acadian Flycatcher	92	2.8	1.9	2.4	2.1	0.6	1.3	0.1	0.6
Carolina Chickadee	47	3.5	1.9	2.8	2.1	0.3	0.9	0.0	0.0
Tufted Titmouse	38	3.5	1.8	2.5	2.2	0.3	1.1	0.0	0.0
Carolina Wren	38	3.6	1.6	3.8	2.0**	0.3	0.8	0.0	0.0
Ruby-crowned Kinglet	17	2.8	2.2	3.2	2.0	0.3	0.9	0.4	1.4
Blue-gray Gnatcatcher	36	1.9	2.2	2.3	2.3	0.0	0.0	0.1	0.7
White-eyed Vireo	73	3.2	1.8***[2]	3.4	1.9**	0.1	0.5	0.0	0.0
Yellow-throated Vireo	25	3.4	2.0	2.2	1.9	0.1	0.5	0.1	0.6
Red-eyed Vireo	42	3.3	1.6	2.0	1.9	0.0	0.0	0.2	1.0
Tennessee Warbler	14	2.9	2.1	2.0	2.0	0.6	1.1	0.0	0.0
Northern Parula	93	3.4	1.4***	3.1	2.0	1.6	1.9***	0.1	0.4
Yellow-rumped Warbler	28	3.3	2.3	2.1	1.8	1.0	1.8	0.1	0.7
American Redstart	49	3.2	1.5	3.5	1.8**	0.0	0.0	0.2	0.9
Prothonotary Warbler	35	1.8	2.0***	1.9	2.3	0.2	0.7	0.2	0.9
Swainson's Warbler	17	4.4	0.9*	2.8	2.4	0.0	0.0	0.0	0.0
Kentucky Warbler	43	3.1	1.7	4.2	1.6***	0.2	0.9	0.0	0.0
Hooded Warbler	90	3.8	1.6	3.6	1.9***	0.1	0.4	0.1	0.5
Availability	225	4.0	1.5	2.4	2.2	0.4	1.2	0.1	0.2

1. Vegetative density of the special habitat features were estimated for each plot on a subjective scale from 0 to 5. A value of 0 indicates no vegetative density of the habitat feature within a 5 m radius circular plot and a value of 5 indicates a density of 90-100%.
2. The percent density of bird-centered plots vs. random plots (availability) are followed by significance levels for a G-test (for homogeneity of distribution, classes 0 to 5): * = P <= .05; ** = P <= .01; *** = P <= .001.

The abundance pattern of the Kentucky Warbler appears to be relatively stable over the 6 years (Figure 29.).

The Kentucky Warbler foraged from the ground stratum through the subcanopy and rarely into the canopy layer (Table 4.). The majority (54%) of foraging activity occurred in the shrub stratum. A variety of plant heights was used, although 74% had a dbh less than 7.5 cm (Table 5. and Table 17.). The ground litter cover at all Kentucky Warbler foraging locations ranged from 85-100%, and averaged 97%; this was significantly greater than available at random sites (Figure 28.). The mean foliage density in the ground through subcanopy strata, where 98% of all foraging occurred, ranged between 47.9 and 59.7%; the foliage in all three strata was denser than randomly available (Figure 26.). In addition, vine foliage was denser at foraging locations than at random sites (Table 19.). Apparently, vines are an important requirement for Kentucky Warblers; 32% of all prey-attacks were directed toward a vine leaf.

Kentucky Warblers foraged primarily within the proximal portion of tree crowns, mostly of saplings or subcanopy height trees (Table 15. and Table 5.). Kentuckys employed a variety of maneuvers while foraging: "gleaning" or "flaking" ground litter or fallen debris, "leaping" from the ground to snatch insects from the lower surfaces of leaves (usually herbs), and "gleaning" or "sally-gleaning" live leaves and bark (Table 7. and Table 9.).

Hooded Warbler.- In the forest, the Hooded Warbler was common in all years except 1989, when it was uncommon (Figure 30.). In the oxbow site, Hooded Warblers were not observed until 1986, where they were rare until 1989, when they became uncommon (Figure 30.). Hooded Warblers were occasionally observed in the seasonally flooded flat (1987 and 1989); although I do not believe they were breeding

individuals (at least not at this site).

The Hooded Warbler foraged at all heights, from on or near the ground to the top of the canopy (Table 4.). Ninety-five percent of the foraging observations occurred in plants >2.0 m in height (Table 5.). Foliage density at foraging cylinders was denser in the ground through subcanopy strata than at random sites (Figure 26.). Mean ground litter cover was also greater at foraging locations compared to random sites (Figure 28.). Mean foliage density in the shrub and subcanopy ranged between 52.3 and 57.4%; 76% of prey-attacks occurred in these strata. The foliage of vines was also denser at foraging locations compared to random plots (Table 19.). Like the Kentucky Warbler, hoodeds frequently directed foraging at vine leaves (39%).

Hooded Warblers searched for prey primarily in the proximal portion of tree crowns among the smaller branches and twigs (Table 14. and Table 15.). Hoodeds usually "sally-gleaned" or "gleaned" prey from the lower surfaces of live leaves (Table 7., Table 14. and Table 9.). Like the American Redstart and Blue-gray Gnatcatcher, hoodeds also used the "flush-pursue" maneuver (Table 7.). The Hooded Warbler had the second largest niche breadth value in the foraging height category (Table 13.).

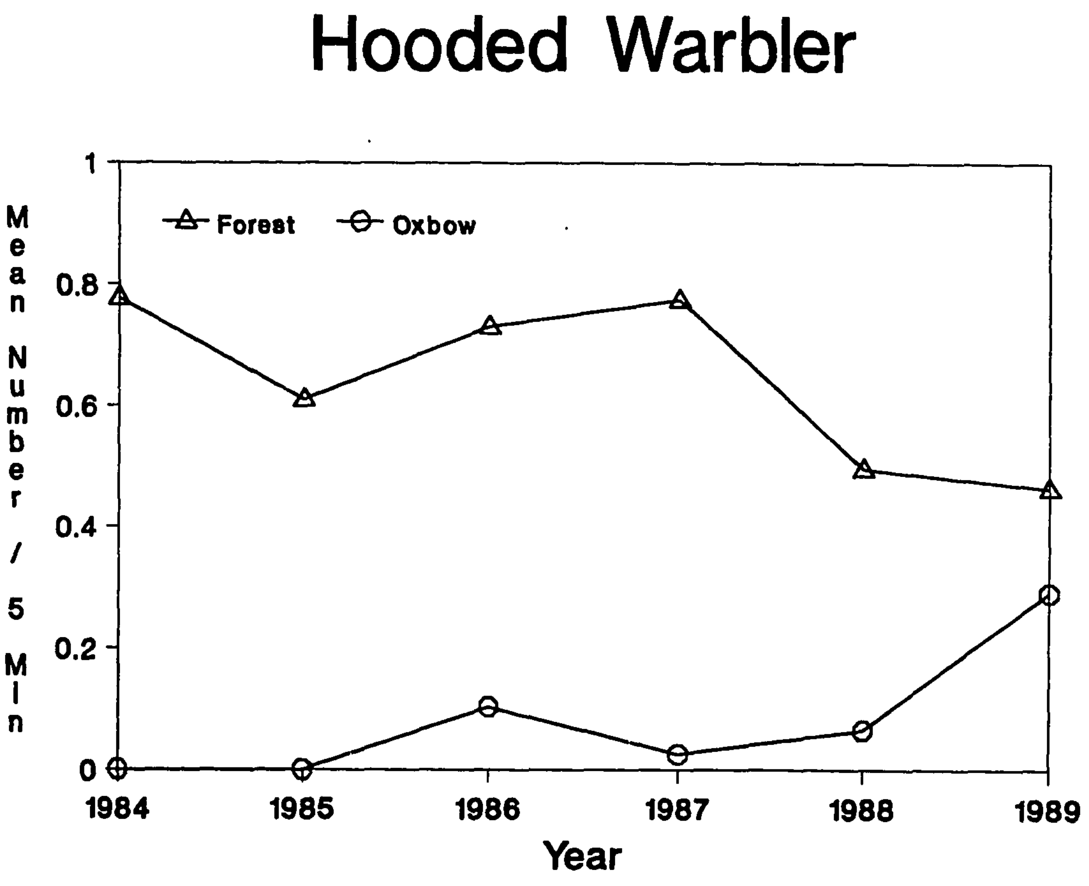


Figure 30. Population trend of Hooded Warblers at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

DISCUSSION

MACROHABITAT USE

Bird distribution in a bottomland hardwood forest.- The mean number of birds per 5 minutes was recorded for each species in three habitat types during the breeding season, 1984-1989. Of the 16 breeding species studied in the Tensas River Basin, four (15%) primarily used only one type of habitat. Two species (12.5%) primarily used two of the three habitat types. Ten species (62.5%) used all three of the major forested habitat types available in the Tensas River Basin. Fifteen of the 16 study species (94%) bred in the non-flooded forest site. Thirteen of the 16 species (81%) consistently bred in the oxbow study area. Only 10 (62.5%) species were found consistently in the seasonally-flooded flat during the 6-year period.

The Yellow-throated Warbler was the most specialized species in terms of macrohabitat. It was consistently found along the margins of oxbow lakes. In 1988-89 a pair of Yellow-throated Warblers nested in an old, moss-covered baldcypress along transect 2 in the seasonally-flooded flat. Apparently, the presence of baldcypress (Moser et al. 1989) and Spanish moss (Bent 1953) are requirements for nesting Yellow-throated Warblers in the Tensas River Basin.

The Hooded Warbler, Swainson's Warbler, and American Redstart primarily bred in the non-flooded oak-gum forest. All three species occurred rarely to uncommonly in the other two habitats during some, but not all, years. The Hooded Warbler probably avoided the seasonally-flooded flat because of its tendency to nest low in dense foliage (Bent 1953, Brittingham and Temple 1980, Mossman and Lange 1982); the reason for its avoidance of oxbow lake margins is less clear. Hooded Warblers are generally regarded as a forest-interior

species during the breeding season (Powell and Rappole 1986, Robbins et al. 1989). Hoodeds were possibly avoiding the "edge" habitat created by the water-forest interface. Nest parasitism and predation have been shown to be significantly more frequent near the forest edge than in the forest interior (Brittingham and Temple 1983, Robinson 1988).

Swainson's Warblers nested and foraged on or near the ground, and thus could not extensively use flooded forest. Swainson's Warblers have been shown to be closely associated with canebrakes in other parts of its breeding range (Meanley 1966, 1971; Eddleman et al. 1980). Switchcane was denser along the margins of oxbow lakes than the other two sites, thus I expected Swainson's Warblers to be accordingly more abundant in this habitat type. I propose three possible explanations for the rarity of Swainson's Warblers at the margins of oxbow lakes: 1) switchcane patch size and/or stem density was not sufficient, 2) they prefer palmetto thickets in the Tensas River Basin, or 3) Swainson's Warblers avoid "edge" for the same reasons as mentioned above for the Hooded Warbler.

The American Redstart nested and foraged in the subcanopy and canopy strata, and the mean range of foliage density used (38-67%) is certainly available in the oxbow and flat study areas. Why are redstarts absent to rare in these two sites? I offer two possible explanations that are tenuous at best. First, redstarts are relatively uncommon in the Tensas River Basin (Table 3.), and are patchily distributed within the oak-gum forest (Barrow and Hamilton, unpublished data). I suggest that redstarts, at least here at the southern end of their breeding range, may be colonial in their nesting habits. Thus, their dispersion pattern in the forest site

may be dictated by the settling pattern of the early-arriving individuals of the "colony". Sherry and Holmes (1985), however, found redstart territories randomly distributed in a northern hardwood forest in New Hampshire. They suggested that this pattern was the result of tendencies of redstarts to avoid certain parts of their study area and to space themselves evenly within other, preferred parts. In other words, their statistically random pattern was thought to result from strongly non-random processes. Thus, my second explanation is that redstarts are simply selecting for microhabitats that happen to be patchily distributed. In particular, they may be responding to local disturbances, such as single or multiple tree-falls. I will develop this idea more thoroughly in my discussion of microhabitat.

The Northern Parula and Kentucky Warbler bred in both the oxbow lake margin and non-flooded forest habitats. Although parulas were recorded regularly in the flat habitat, these were probably not all breeding individuals. The occurrence of Northern Parulas in the flat may represent an overflow from large populations in different but nearby habitats (oxbow lakes and non-flooded forest with Spanish moss). However, I believe the Northern Parula will be common to abundant in other seasonally-flooded flats in the Tensas River Basin, provided Spanish moss is a common habitat feature. Because the Kentucky Warbler nests and forages on or near the ground in relatively dense foliage, it cannot survive the frequent flood events that occur in the flat habitat.

Nine of the remaining ten species primarily nest in the subcanopy or canopy layers, and forage for insects on bark and leaves in those layers. Apparently, all three habitats provide sufficient resources within these strata for these species survival. The

Carolina Wren primarily uses the shrub stratum for nesting and foraging. Thus, it was somewhat surprising that Carolina Wrens were common in the seasonally-flooded flat. Most individuals recorded in the flat were probably using the ecotone between the flat and forest, or the edge of a road (transect 2) that bisects the flat study area. In addition, patches of microhabitat within the flat were provided by recently fallen trees. There were at least three known tree-falls along transect 1. Carolina Wrens were able to place nests in vine tangles and crotches of branches on the fallen trees; I noted that crevices of upturned root-bases above the flood level were also used. Holmes and Robinson (1988) found Winter Wrens (*Troglodytes troglodytes*) utilizing similar patches of microhabitat in a northern hardwood forest.

Landscape pattern as a determinant of avian distribution and abundance in bottomland hardwood forests.- The "bottomland hardwood forest" is often referred to as a habitat type high in bird species richness (e.g., Holder 1970, Fentress 1986, Harris 1989). However, the term, at least in the Lower Mississippi River Valley, should be considered a complex of three, if not more, habitat types. For the purposes of this study, I define landscape as the mosaic of fluvial landforms and its associated forest stands. Fluvial landforms result from distinctive hydrogeomorphic processes (Hupp and Osterkamp 1985). Among such landforms are active-channel beds, historic-channel beds, depositional bars, backwater basins, and terraces. Vegetation patterns in bottomland hardwood watersheds appear to develop as a result of hydrologic processes associated with each fluvial landform (Hupp and Osterkamp 1985). The three landforms selected as study sites in this study represent the greatest areal extent of available habitat types to forest-inhabiting birds in the Tensas River Basin:

oxbow lake margins (i.e., historic-channel beds), seasonally-flooded flats (i.e., backwater basins), and non-flooded oak-rum forest (i.e., terraces) (U.S. Fish and Wildlife Service 1982).

I conclude that the number, size, and distributional pattern of these landforms will, at least in part, determine the distribution and abundance of birds inhabiting bottomland hardwood forests in the Tensas River Basin. Swift et al. (1984) studied the relationship of breeding bird density and diversity to habitat variables in forested wetlands of Massachusetts. They also found significant correlations between avian community parameters and variables used to quantify hydrologic conditions. Because the hydrologic processes in the Tensas River Basin have radically changed over the past 75 years (Gosselink et al. 1989), the current avifauna is likely different from the one that existed in the 1800's, and from the one that will exist in the middle 21st Century. In addition, new landscape-level habitats have been recently created in the Tensas River Basin: dry agricultural fields, flooded agricultural fields, old fields, pine plantations, and urban development (Gosselink et al. 1989). Presently, only about 15% (157,000 ha) of the original forested area of the basin is in existence. Most of the forest area is highly fragmented. The number of forest patches have been estimated at around 500, most of them <300 ha in size (Gosselink et al. 1989).

In summary, the Tensas River Basin is a mosaic of fluvial landforms. These landforms, in turn, support plant communities with predictable vegetation structure and species composition (Hupp and Osterkamp 1985, Tanner 1986, Dickson 1988). Thus, the distribution and number of bird species found in the Tensas River Basin is probably influenced by the size, frequency, and distributional pattern of fluvial landforms.

MICROHABITAT USE

Role of microhabitat structure and pattern as a determinant of avian community organization.- Moser et al. (1989) used data from this study and correspondence analysis to explore the relationship between foraging behavior and habitat. They showed how these 16 breeding species were ordinated according to a foraging-height gradient (Figure 31.). The Swainson's Warbler was a ground forager. The Kentucky Warbler and Carolina Wren were associated with the shrub stratum. The Prothonotary Warbler was ordinated between the shrub and subcanopy layers. The Hooded Warbler, Tufted Titmouse, Carolina Chickadee, Acadian Flycatcher, and White-eyed Vireo were associated with the subcanopy stratum. The Yellow-throated Vireo, Yellow-throated Warbler, Blue-gray Gnatcatcher, Eastern Wood-Pewee, and American Redstart used the canopy layer, whereas the Northern Parula and Red-eyed Vireo were ordinated between the canopy and subcanopy layers. My analysis (Table 16.) is in agreement with Moser's et al. (1989) ordination.

I classified each species according to degree of foliage density used: sparse (<30%), moderate (30-50%), and dense (>50%). The classification is subjective, based on my familiarity with the species. I used results from Moser et al.'s (1989) foraging-height ordination and data from APPENDIX F, APPENDIX G, and APPENDIX H.

Species that foraged in sparse foliage included both flycatchers, Tufted Titmouse, and Swainson's Warbler. The flycatchers probably prefer such areas because of their need to freely maneuver through air-space (e.g., sally and sally-glean). The Tufted titmouse used bark (trunks, branches, twigs) as a foraging substrate more frequently than live leaves (44 vs. 30%). The Swainson's Warbler foraged in the leaf-litter among palmetto stems.

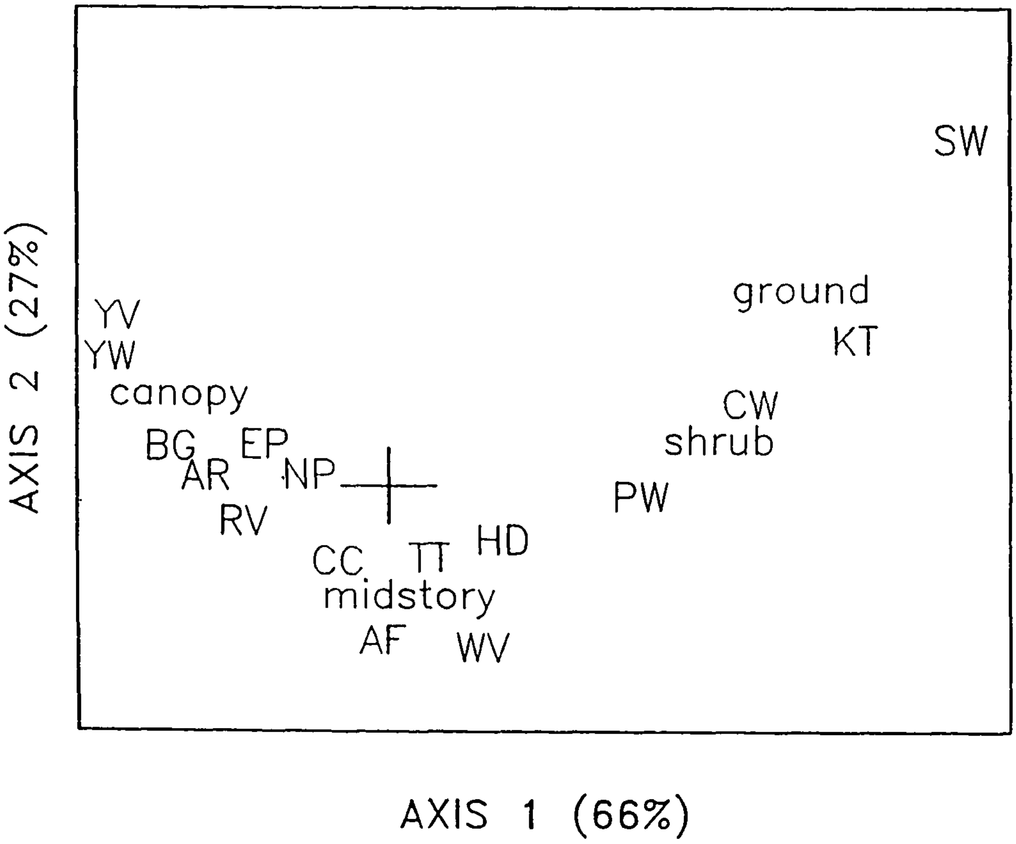


Figure 31. Correspondence analysis of bird species with foraging height class: ground = < 0.5 m, shrub = 0.5-2 m, midstory = 2-10 m, and canopy = > 10 m, as reported by Moser et al. 1989.

Meanley (1971) also reported that Swainson's Warblers preferred foraging sites on the forest floor that were "free of obstructions", such as dense foliage.

Four species were classified as users of dense foliage: Carolina Wren, American Redstart, Kentucky Warbler, and Hooded Warbler. All four species frequently search for insects among the foliage of dense vine tangles. These four species were among the five most frequent users of vine foliage during the breeding season (Table 10. and Table 11.). The remaining species forage in foliage of moderate density.

Most species capture (Table 15., within 1-m diameter sphere surrounding the foraging bird) their prey within foliage less dense than they use to search (2-m diameter cylinder at various height categories) for prey. Ten species captured prey with a mean foliage density value <30%. No species captured prey at locations with a mean foliage density >50%.

Results of this study (see discussion of bird distribution) support MacArthur and MacArthur's (1961) general contention that avian species richness in a habitat increases with the addition of vertical layers. The idea is that with additional vegetative layers there will be additional foraging substrates (e.g., bark, twigs, leaves, epiphytes). More recently, Martin (1985,1986) suggested that nest site availability may be important to site occupation, and therefore, affect bird community composition. Petit and Petit (1988) showed that vegetation densities were greater at nest sites than at corresponding perch sites for Hooded Warblers and Wood Thrushes (*Hylocichla mustelina*).

At Tensas, the non-flooded forest had a more developed ground and shrub layer than the oxbow or flat (Figure 4.). Consequently a

greater number of small, insectivorous birds were found breeding in the forest site. Carolina Wren, White-eyed Vireo, Swainson's, Hooded, and Kentucky Warblers select dense foliage in these strata for nesting and/or feeding. The two species that bred exclusively in the forest site both had a similar pattern of foliage density use in all four vertical strata (Figure 26.). The American Redstart and Hooded Warbler both foraged at sites with denser foliage than available in the ground through subcanopy layers; density of canopy foliage was in concordance with availability. Carolina Wren, White-eyed Vireo and Kentucky Warbler foraging sites showed this same pattern, but they also bred in other habitat types. This pattern of microhabitat use suggests that these species select disturbed sites within the non-flooded forest. Local disturbances, such as single tree falls, are a common occurrence in the Tensas River Basin (Tanner 1986; Barrow, unpublished data). Disturbance rates, in fact, appear to be consistent among temperate, hardwood forests throughout North America; the average rate of disturbance is about 1%/year (Runkle 1985). Canopy gaps allow increased light intensity to reach the forest floor, which in turn, promotes growth of dense foliage, such as herbs, shrubs, saplings, and vine tangles. These four species frequently use vine leaves as a foraging substrate (Figure 12. and Figure 13.). The areas occupied most frequently by these species had denser foliage beneath the canopy than the forest as a whole. Their foraging sites also encompassed vines at a density greater than at randomly located sites (Table 19.). However, such areas occurred where the canopy was nearly complete (Figure 26.), and suggest that the disturbance (e.g., tree-fall) was probably greater than 15 years old (Barden 1989). They have thus been responding, at least in part, to areas of small-scale, local disturbance. Several authors have

found these species inhabiting disturbed areas (i.e., growth of early successional plant species within mature forest) in other parts of their breeding range. Kentucky Warbler: Bent (1953) in Pennsylvania--in swampy thickets and overgrown clearings; Mossman and Lange (1982) in southern Wisconsin--in shrubby openings or edges; Kahl et al. (1985) in Missouri --in dense thickets near forest openings. Hooded Warbler: Blackmore (1895) near New Orleans, Louisiana--in briar patches and edges of openings; Grimes (1935) in Florida--in vine tangles; Mossman and Lange (1982) in Baraboo Hills, Wisconsin--in dense understory of shrubs, brambles, and saplings. American Redstart: Bent (1953 in Maine--in thick growth of small trees; James (1971) in Arkansas--see niche-gestalt illustration p. 219 and photographs of nesting habitat p. 221; Mossman and Lange (1982) in Wisconsin--in thinly timbered shrubby areas and forest edges. I suggest that the frequency and distribution of local disturbances, such as wind-blown trees and selective cutting, can influence the particular abundance and combination of small, insectivorous birds existing in these, and many other, forest habitats.

Relationship between plant species and bird site occupancy.- In the Tensas River Basin, plant species composition and vegetative growth forms may also be important factors in determining community organization. My analysis and Moser et al. (1989) both indicate that the Yellow-throated Warbler was strongly associated with two plant species: baldcypress and Spanish moss. Other investigators have found the Yellow-throated Warbler associated with particular species of plants that include baldcypress (Bent 1953), Sycamore (*Plantanus occidentalis*) (Bent 1953,) mature pines (*Pinus* sp.) (Bent 1953, Jackson 1988,), and coastal palms (Raffaele 1983, Pashley 1989). A correlation appears to exist between Spanish moss and Northern Parula

distribution and abundance (Bent 1953, this study). Species associated with vine tangles, in addition to the four mentioned above, include the Carolina Wren and White-eyed Vireo (Moser et al. 1989, Table 10. and Table 11.). Dead snags in the understory have been shown to be important to Prothonotary Warblers and Carolina Wrens (Moser et al. 1989, Figure 32.). The Swainson's Warbler frequently selected foraging sites with dense palmetto cover (Table 19.). Other studies have documented the importance of plant species composition and growth forms to bird community organization (Bock and Bock 1984, Greenberg 1984, Rice et al. 1984, Robinson and Holmes 1984).

In summary, the abundance and distribution of small, insectivorous bird species found in a particular habitat are influenced by a complex of several microhabitat characteristics. Foraging and nesting opportunities vary with location, both vertically and horizontally, within a forested habitat, at least in part, because of different plant species and morphologies. Responses to local disturbance events (i.e., use of dense vs. sparse foliage) are also important.

FORAGING ECOLOGY

Ecological relations among small avian insectivores in the Tensas River Basin.- Although the use of microhabitat features is important in ecologically separating bird species, partitioning on a finer level is achieved by the bird's differential use of foraging locations, foraging substrates, foraging maneuvers, and the plant species from which prey is obtained (Holmes et al. 1979). Species foraging relationships are illustrated in Figure 33. and Figure 34.. In these dendrograms, species that exploit food in similar ways are

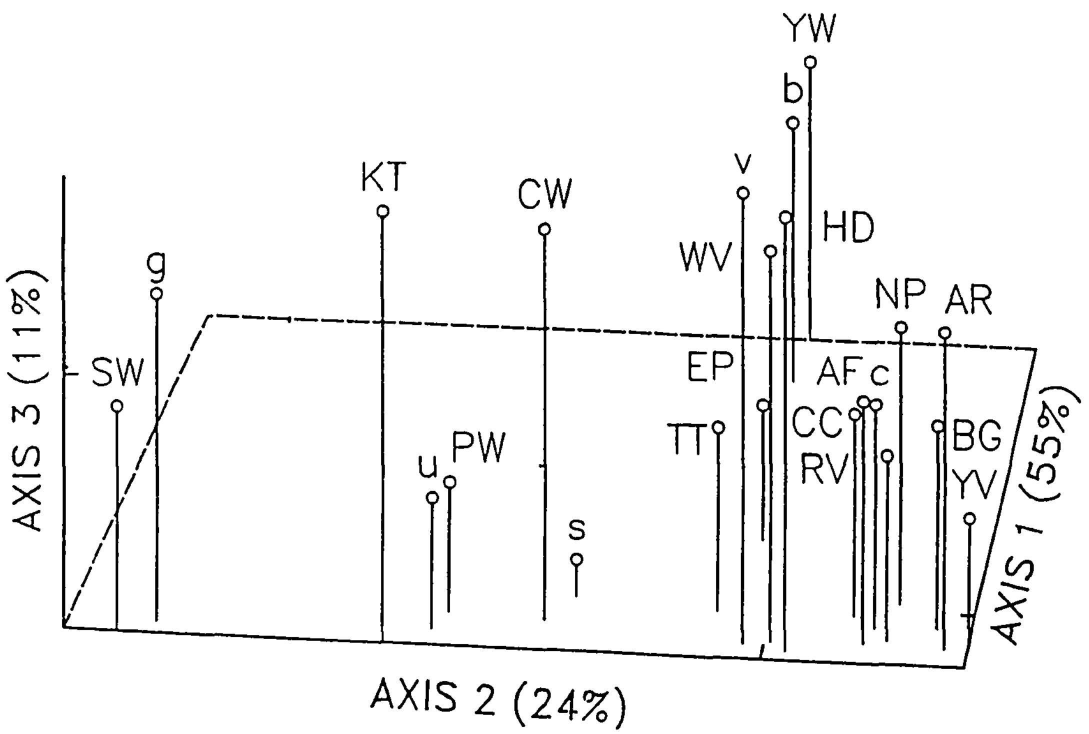


Figure 32. Correspondence analysis of bird species with habitat-management category: b = baldcypress and Spanish moss, g = ground litter, c = overstory, s = snags, u = understory, and v = vines, as reported by Moser et al. 1989.

separated into distinct groupings. Each grouping may be considered a foraging guild (cf. Root 1967) because of its similar food exploitation patterns. For the purpose of this study, these groupings are defined as those species or groups of species separated from one another by Euclidean distances, which are greater than the mean distance between species (*Sensu* Holmes et al. 1979) (breeding species, x = 7.67; all 19 species, x = 7.64).

A heirarchial cluster analysis performed on the 16 study species that breed in the Tensas River Basin identified 6 major patterns of food resource exploitation among the species in this study (Figure 33.). Group I consists of the Acadian Flycatcher and American Redstart, both were primarily "sally-gleaners" of live leaves within the outer portion of tree crowns. Group II contains a single species: the Eastern Wood-Pewee. The pewee foraged almost exclusively by "sallying" insects from the air-space. Perches were frequently located high along the distal portions of branches in baldcypress, bitter pecans, and dead snags. The third group consists of 7 species that fed mainly in the subcanopy and canopy layers. Prey were frequently captured from live leaves or bark and leaves; primarily by the "glean" and "sally-glean" techniques. Group IV contains the Carolina Chickadee, Tufted Titmouse, and Yellow-throated Warbler. These three species gathered their food mainly in the subcanopy and canopy from bark substrates (tree trunks, branches, and twigs), dead leaves, and Spanish moss. All three species employed the "hang" maneuver. Group V is another single species guild. The Carolina Wren foraged almost exclusively in the area proximal to the main stem of shrubs and trees. It foraged relatively low on bark substrates; primarily tree trunks and vine stems. The Carolina Wren frequently used the "probe" maneuver to capture prey at these

locations. The sixth group consists of two species of Warblers, both primarily ground and shrub foragers. Both species used the "glean" and "flake" maneuvers to capture prey from foliage and leaf-litter.

Another cluster analysis, performed on all 19 study species, produced slightly different results (Figure 34.). Seven groups were identified. Five of the groups from the first analysis remained the same: I, II, IV, V, and VI. Three species from Group III formed their own cluster: the Hooded Warbler, White-eyed Vireo, and Prothonotary Warbler. All three species foraged at similar heights and captured prey mainly by "gleaning" and "sally-gleaning" prey from leaves and bark. The Ruby-crowned Kinglet, Yellow-rumped Warbler, and Tennessee Warbler were grouped with two vireos, a gnatcatcher, and a warbler. The two overwintering species, the Ruby-crowned Kinglet and Yellow-rumped Warbler, were clustered together within the group. They are similar in that they both "glean" and "sally-glean" insects from leaves and bark within foliage density of about 23% (within a .5 m radius sphere surrounding the foraging bird). The Tennessee Warbler, a transient migrant, was positioned in the same group, but was more similar to the foliage-gleaning Red-eyed Vireo and Northern Parula.

Thus, resident species and non-breeding species do not form totally distinct foraging guilds. However, it is noteworthy that 2 of the 3 non-breeding species were most similar to each other, as were two of the resident species; the other permanent resident formed its own group. This illustrates how species with similar life-history traits, may respond to a changing environment in a similar manner. Apparently, permanent resident species tend to use bark substrates more frequently than migratory species.

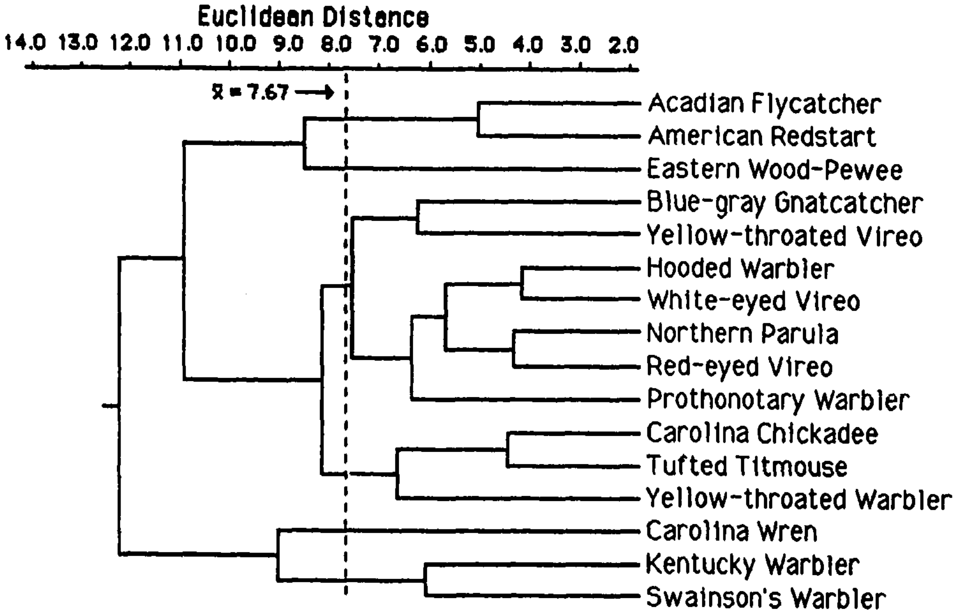


Figure 33. Dendrogram indicating similarities and differences in foraging ecology among 16 breeding bird species at Tensas River NWR.

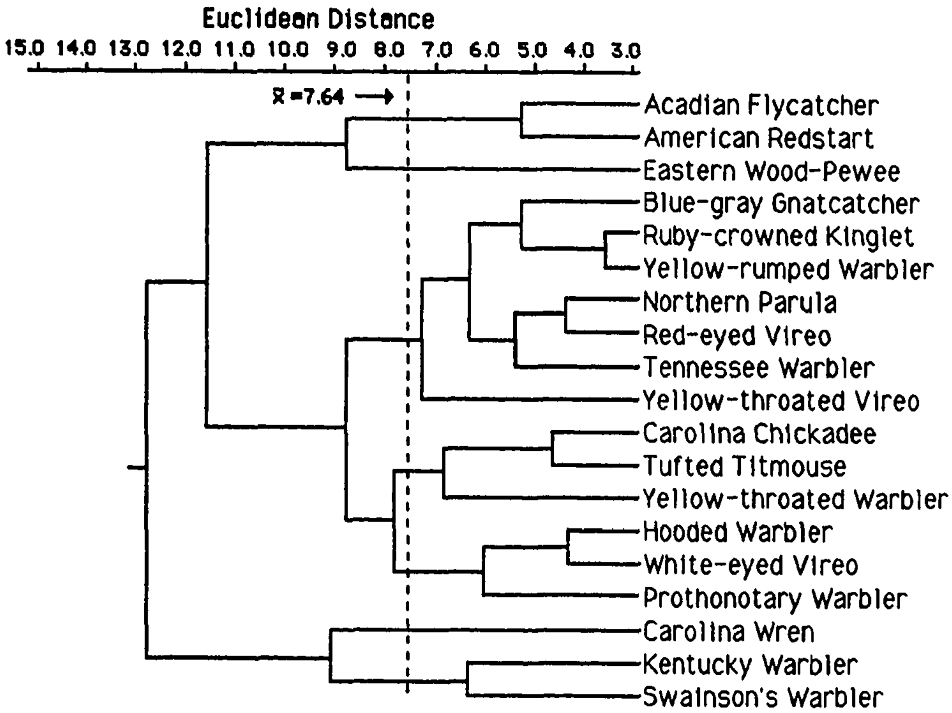


Figure 34. Dendrogram indicating similarities and differences in foraging ecology among 19 bird species at Tensas River NWR.

Niche changes by birds between habitat types in the Tensas River Basin .- Of the 12 breeding species that consistently used more than one of the broad habitat types, six showed either statistically significant or nearly significant changes in some of the foraging variables between habitats. The Eastern Wood-Pewee and Acadian Flycatcher changed in their frequency of use of foraging-height categories. Changes for both of the species can be attributed to a preference for open to sparse foliage density. The Eastern Wood-Pewee could have expanded its use of the subcanopy and in particular, the shrub stratum of the flat vs. the oxbow because the foliage was less dense, thereby facilitating the pewee's need to freely maneuver in the open air-space. The more open canopy in the flat (compared to the forest) may have allowed the Acadian Flycatcher to forage higher. An alternative explanation for the foraging height shift of the Acadian Flycatcher is interspecific interactions with an ecologically similar species. Sherry (1979) provided evidence for interspecific competition between American Redstarts and Least Flycatchers (*Empidonax minimus*) in a northern hardwood forest. Because the Least Flycatcher is an ecologically similar congener of the Acadian Flycatcher (Barrow 1982), release from competition thus appears to be a plausible explanation. The American Redstart was primarily a canopy forager in the forest site, and both species have been shown to be ecologically similar at Tensas (Figure 33.). However, I believe the relatively low abundance and patchy distribution of redstarts precludes interspecific competition as an important factor in this particular niche shift.

The Carolina Chickadee showed several niche differences between the forest and flat sites. In general, chickadees tended to gather food more frequently from the tips of branches in the forest than the

flat. Consequently, foraging maneuvers required to attack prey at such locations were more frequently used (e.g. "hang", "hang-probe", and "sally-glean"). Were preferred prey-items more abundant at these sites in the forest? Unfortunately, I do not have the data to answer this question; however, chickadees did have a significantly faster prey-attack rate in the forest than the flat. Chickadees in the oxbow foraged more frequently in the shrub stratum than chickadees in the flat. Foliage in the shrub stratum was denser than in the flat.

In a comparison of the forest vs. the flat, the Tufted Titmouse changed its foraging behavior in a maneuver similar to the chickadee; they foraged more frequently on leaves from within the distal portions of tree crowns in the forest. Because these two parids occupy nearly identical ecological niches at Tensas (this study, Moser et al. 1989), they are probably responding in a like manner to different prey bases at the two sites.

Blue-gray Gnatcatchers inhabiting the forest also tended to forage more frequently from twigs than those inhabiting the flat. Gnatcatchers are somewhat stereotyped in their use of tree crowns positions; they forage among the outer halves of branches regardless of habitat type. Thus gnatcatchers are either responding in a similar manner as the two parids, or smaller diameter perches are simply more abundant in the forest site.

Prothonotary Warblers foraged lower and utilized shrubs more frequently in the oxbow habitat compared to the other two sites. Although not quantified, Prothonotary Warblers tended to concentrate their activities, including feeding, close to the water-ground interface along oxbow lakes. In the oxbow habitat, nests (n = 24) were typically placed in dead snags, cypress knees, or tree stumps in or adjacent to the lakes (Barrow, unpublished data). Prothonotarys

used bark substrates more frequently at such locations probably because they were more available (e.g. tree buttresses, cypress knees, and fallen branches washed ashore). Petit et al. (1990) found significant intersexual differences in foraging height and substrate height during the prenestling period in Tennessee. During the nestling period, this divergence between sexes also included substrate type. In addition, they showed that males demonstrated significant annual variation in foraging height and substrate height; females showed significant variation across years (1984-87) for foraging height and substrate type, but not substrate height. They also reported that in Tennessee, prothonotarys showed flexibility in other foraging parameters, such as foraging method, perch diameter, substrate species, and crown position. Apparently, Prothonotary Warblers are a behaviorally plastic species with a broad niche that modifies its behavior in response to change in reproductive context as well as to change in foliage structure.

Degree of specialization among foraging birds in the Tensas River Basin.- I define specialization as the breadth of resource utilization, in this case, foraging maneuver, foraging height, foraging substrate, and plant species (Table 13.). Thus, a species may be a specialist for some parameters and a generalist for others.

In terms of foraging maneuvers, the three most specialized species were the Eastern Wood-Pewee, Acadian Flycatcher and Tennessee Warbler. Interestingly, each specialized in a different type of maneuver: "sallying", "sally-gleaning", and "gleaning", respectively. The Blue-gray Gnatcatcher, American Redstart, and Yellow-throated Warbler were the most generalized species.

The two most specialized species in terms of foraging height were the Yellow-throated Vireo and Yellow-throated Warbler, both

canopy foragers. Generalized species included the Prothonotary Warbler and Hooded Warbler, both shrub and subcanopy foragers.

The most specialized species, in terms of substrates used, were the two flycatchers and the Red-eyed Vireo. The acadian red-eyed used live leaves and the pewee used the air-space. The three permanent resident species were the most generalized in the use of substrate types. Because insect abundance and activity is related to basic environmental factors (e.g. temperature, moisture), permanent resident species in temperate regions must exhibit plasticity in their foraging repertoire if they are to survive. Thus, it is not surprising they are generalized in terms of prey capture location.

Three warblers were the most specialized in terms of plant species used: Yellow-rumped Warbler, Yellow-throated Warbler, and Swainson's Warbler. As mentioned above, the Yellow-throated Warbler is closely associated with specific plant species throughout its breeding range, although the particular species of plant varies with habitat type or geographic location. Thus, the Yellow-throated Warbler is a specialist that exhibits plasticity in plant species used, depending on the habitat occupied (Morse 1971). Two of the three permanent residents, the Carolina Chickadee and Tufted Titmouse, were most generalized with respect to usage of particular plant species.

A comparison of mean overall niche breadths revealed that the four specialized foragers at Tensas were long-distance neotropical migrants: the Yellow-throated Vireo, Tennessee Warbler, Swainson's Warbler, and Yellow-throated Warbler. In contrast, the most generalized species, in terms of feeding ecology, were the Prothonotary Warbler and the three permanent resident species: the Carolina Chickadee, Tufted Titmouse, and Carolina Wren.

Does specialization result in restrictions of the range of habitats used (MacArthur and Pianka 1966)? In considering the breeding species at Tensas, results of this study support this generalization. The three permanent residents were able to exploit a wide variety of resources and successfully bred in the three major habitat types of the Tensas River Basin. Foraging habits of these species during the breeding season reflect winter feeding centered on trunks, branches, and twigs, substrates that are available year round. Two of the three specialist species each had specific requirements that restricted its successful exploitation of certain habitat types. For example, the Yellow-throated Warbler required the presence of baldcypress trees and Spanish moss. Because Yellow-throated Warblers primarily used bark as a foraging substrate, the bark of old-growth baldcypress may be what is really important to the birds. All of the plant species typically associated with Yellow-throated Warblers [i.e., baldcypress, sycamore, and longleaf pine (*Pinus palustris*)] have one characteristic in common -- exfoliating bark. A more detailed investigation of this relationship should be considered. The Swainson's Warbler is a ground foraging specialist that requires abundant leaf-litter beneath palmetto thickets at Tensas. It consistently bred only in the non-flooded forest site.

CONSERVATION AND MANAGEMENT IMPLICATIONS

ARE POPULATIONS OF NEOTROPICAL INSECTIVOROUS BIRDS DECLINING ?

Several authors have noted that many neotropical migratory bird species have been declining over the past 40 years (Aldrich and Robbins 1970, Walcott 1974, Criswell 1975, Temple and Temple 1976, Whitcomb et al. 1977, Briggs and Criswell 1979, Robbins 1979, Whitcomb et al. 1981, Ambuel and Temple 1982, Hall 1984, and Askins et al. 1989). Because most of these reports were based on small-scale local studies, Hutto (1988) suggested that they do not provide definitive evidence that migrants everywhere are declining. However, a recent analysis of the U. S. Fish and Wildlife Service's Breeding Bird Survey (Robbins et al. 1989) demonstrates a general decline in neotropical migratory birds throughout eastern North America.

Are the small insectivorous bird species that breed at Tensas declining? Robbins et al. (1989) analyzed population trends of two different periods: 1966-1978 and 1978-1987 (Table 20.). During the first period, 4 species (25%) had negative trends, of which 2 were significant ($P<.01$). Positive trends occurred in 12 species (75%), of which 5 were significant. In contrast, during the second period (1978-1987) 9 of the species (56%) showed negative trends with 4 significant, and only 5 had positive trends (38%), of which only one was significant. The Swainson's Warbler showed no trend during the years 1978-1987.

Because more than 50% of the bottomland hardwood forests of the Lower Mississippi River Valley had been cleared and converted to other land use practices prior to 1966 (MacDonald et al. 1979), Robbins et al.'s (1989) conclusions may underestimated potential problems of birds associated extensively with these forests.

Table 20. Population index trends of 17 bird species for 1966-1978 and 1978-1987, as reported from Robbins et al. 1989.

Species	Trend, %/Year	
	1966-1978	1978-1987
Eastern Wood-Pewee	-2.1**	-0.7
Acadian Flycatcher	1.2*	-1.3*
Carolina Chickadee	0.0	-0.5
Tufted Titmouse	-2.0**	3.5
Carolina Wren	1.2**	5.4**
Blue-gray Gnatcatcher	0.5	1.4
White-eyed Vireo	0.3	-1.2*
Yellow-Throated Vireo	-0.2	-0.9
Red-eyed Vireo	2.8**	0.2
Tennessee Warbler	18.6	-11.6*
Northern Parula	1.2	-2.1**
Yellow-throated Warbler	2.0*	-0.4
American Redstart	1.3	-1.2
Prothonotary Warbler	4.4**	1.1
Swainson's Warbler	6.6*	0.0
Kentucky Warbler	-0.3	-1.6
Hooded Warbler	0.9	0.4

* = $P < 0.05$
** = $P < 0.01$

Swainson's and Hooded Warblers are considered to be primarily species of the Lower Mississippi River Valley and associated drainages (Remsen and Parker 1983). If, for example, the abundance of one of these species drastically declined in concordance with removal of these forests in the late 40's through the mid 60's, then a population trend of 0.0 or 0.4, as in the case of the Hooded Warbler, may cause conservationists to overlook these species, that, in fact, may be in serious trouble. The main point here is that historical events, especially those on a regional scale, must be considered in the design of conservation strategies.

POPULATION TRENDS OF SMALL INSECTIVOROUS BIRDS DURING SIX YEARS IN THE TENSAS RIVER BASIN

To determine the abundance trends during the past 6 years at Tensas, I classified each of the 16 breeding species as either permanent residents or neotropical migrants (Table 3.) and plotted its mean number per five minutes against the 6 years of the study. A fitted line through these data points showed that the three resident species have an increasing population trend, whereas neotropical migrants had a slightly declining trend (Figure 35.).

The number of neotropical migrants recorded per five minutes appeared to be relatively stable during the study period, whereas the residents tended to fluctuate widely between years. In fact, if not for the high numbers of migrants recorded in 1984, migrants probably would have showed no trend. It is possible that the large numbers recorded in 1984 were a result of massive overflow from adjacent areas cleared during 1983 and the spring and summer of 1984. Approximately 16,200 ha of forest were cleared within a 18 km radius of the study during these 2 years.

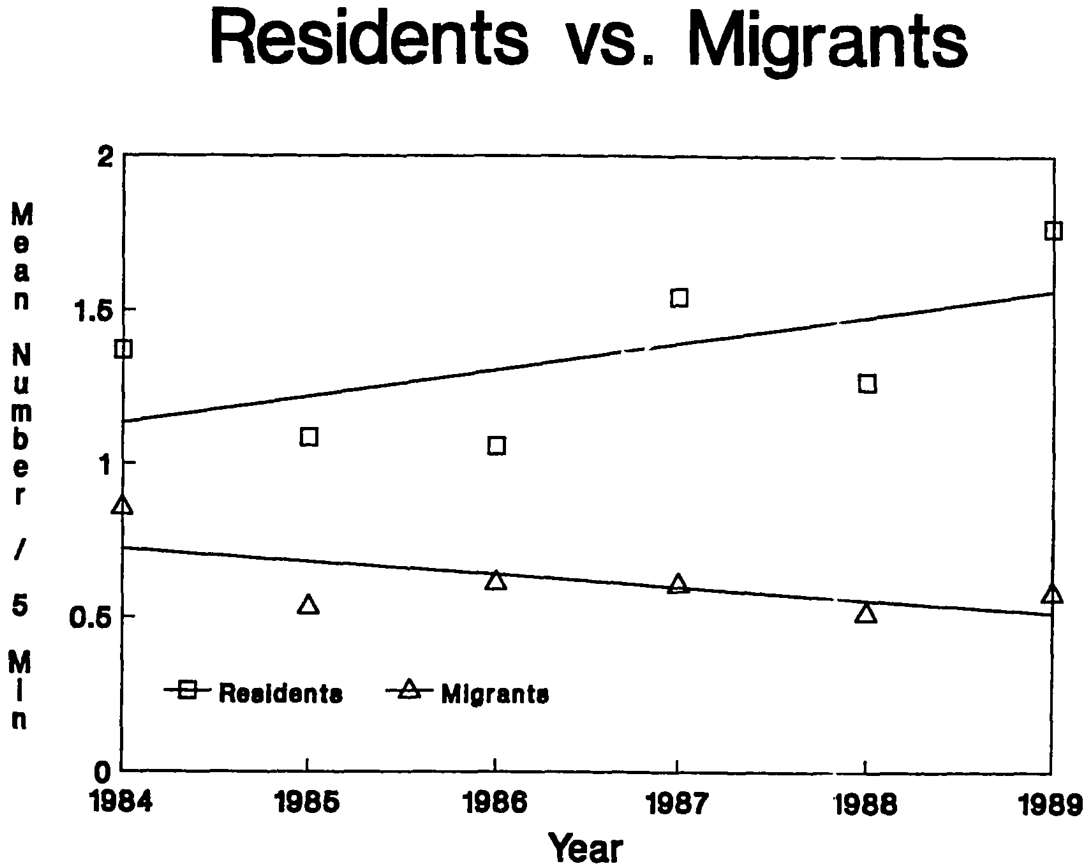


Figure 35. Population trends of migratory and resident bird species at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

The abundance of both migrants and residents declined in 1985 and 1988. Both years were considered drought years in the Tensas River Basin (Figure 1.). Abnormally low levels of precipitation during the Spring and Summer months could have had a negative effect on food supply and/or microclimate at some nest sites. For neotropical migrants, I cannot rule out the possible effects of events occurring on their wintering grounds or along migration routes (e.g., deforestation). The further decline of permanent residents between the summers of 1985 and 1986 coincided with an extremely cold winter that year (Figure 2.). Graber and Graber (1979) provided evidence of winter mortality of permanent residents in southern Illinois during severe winter weather. The increase in abundance of both migrants and residents in 1989 may be attributable to a tent caterpillar outbreak during early Spring of that year (Barrow and Hamilton, pers. observ.). Irruptions of defoliating Lepidoptera, an important food resource, have been shown to influence bird population at Hubbard Brook, New Hampshire (Holmes et al. 1986). It is likely that six years is not a sufficient period of time to confidently reveal true changes in abundances of birds breeding at Tensas, or any other site (Holmes et al. 1986). I recommend monitoring of avian abundances at these study sites be continued for as long as possible.

MANAGEMENT IMPLICATIONS

Because many of these small insectivorous birds tend to select certain configurations of vegetation, timber management practices will likely effect avian distribution and abundance at Tensas. Results from this study (see p.51) indicate that five species will probably have a positive response to selective cutting operations: White-eyed Vireo, American Redstart, Swainson's Warbler, Kentucky Warbler, and Hooded Warbler. However, negative responses may result

from large canopy openings (e.g., group selection or patch clear-cutting); all five species used sites with a relatively closed canopy. Thus, I recommend single-tree selection with a long-term rotation (i.e., > = 100 yrs.). Local populations of the Acadian Flycatcher, however, will probably decline as a result of selective cutting; they require a closed canopy with a relatively open understory. Selective removal of large, old-growth trees, particularly baldcypress, may negatively impact Eastern Wood-Pewees, Yellow-throated Vireos, and Yellow-throated Warblers. Furthermore, removal of dead snags will likely cause declines in abundance of Eastern Wood-Pewees and Prothonotary Warblers. Northern Parulas and Yellow-throated Warblers are sensitive to changes in distribution and density of Spanish moss, thus managers should be attentive to harvest operations in areas where moss is concentrated. Species that used vegetation density in concordance with availability and/or were flexible in their foraging behavior will probably be least effected by timber harvesting operations. These species include the Carolina Chickadee, Tufted Titmouse, and Red-eyed Vireo. Because the Blue-gray Gnatcatcher uses foraging sites with canopy less dense than available, they may respond favorably to cutting activities as well. Land management operations must be designed with accurate knowledge about habitat requirements of each species, and management activities may need to be modified to avoid local population declines or extirpation.

The recent history of the Tensas biota reflects the impact man-induced changes to the landscape can have on the fauna of a forested watershed. Several species that once included the basin as part of their original range that are now absent, include the red wolf (*Canis rufus*), florida panther (*Felis concolor*), Ivory-billed Woodpecker,

Carolina Parakeet (*Conuropsis carolinensis*), Bachman's Warbler (*Vermivora bachmanii*), and Cerulean Warbler (*Dendroica cerulea*) (Oberholser 1938, McKinley 1988, Burdick et al. 1989). Except for the Carolina Parakeet and Bachman's Warbler, the disappearance of these species from the watershed was probably directly related to the loss and degradation (e.g., fragmentation) of forest habitat in the basin. At the current rate of bottomland hardwood forest clearing and fragmentation in the Tensas River Basin (10,000 ha/yr., Gosselink et al. 1989), I predict the occurrence of future losses of interior forest breeding species, especially long-distance neotropical migratory birds.

The primary conservation action needed is habitat protection and restoration. A critical step in this process is consultation with public agencies involved in management of refuges (Grumbine 1990) throughout the Lower Mississippi River Valley. The amount of forest edge should be minimized because predation and brood parasitism rates are substantially higher in such areas (Askins et al. 1989). As Askins et al. (1989) stated, "Preserves with long narrow shapes, embedded open areas, and wide roads and power line corridors are likely to be less effective in preserving populations of forest-dwelling neotropical migrants.". At the landscape-level, managers must consider the proximity of nonforested habitats to a particular forested area. Mayfield (1965) documented the increased abundance of Brown-headed Cowbirds (*Molothrus ater*) in eastern North America over the last three centuries. It is encouraged by changed land use, in particular, the conversion of extensive forests into a fragmented landscape of forest patches interspersed with agricultural fields. This is precisely the situation that has occurred in the Tensas Watershed over the last 50 years. During the 6 years of this study,

cowbirds have shown a markedly positive population trend (Figure 36.). Thus, large-scale reforestation efforts are recommended. At the local level, timber harvesting operations will reshape the distribution of microhabitat availability, and hence, influence the resulting bird community. If such activities are deemed necessary, long-term rotation is desirable. I recommend the selection cutting system, particularly single-tree selection, due to its resulting resemblance to natural treefall gaps. The most effective way to ensure the long-term survival of native birds is to protect intact bottomland hardwood ecosystems from further degradation and restore them as nearly as possible to their natural state. Priority acquisition sites should be situated as to provide linkage between existing preserves, thereby increasing the size of contiguous blocks of forest. Efforts should also be made to restore the natural hydrologic regimes of watersheds. Additionally, conservationists must be concerned with circumstances where these species winter (see Keast and Morton 1980). A more thorough discussion of winter-related issues can be found in Chapters 3 and 4.

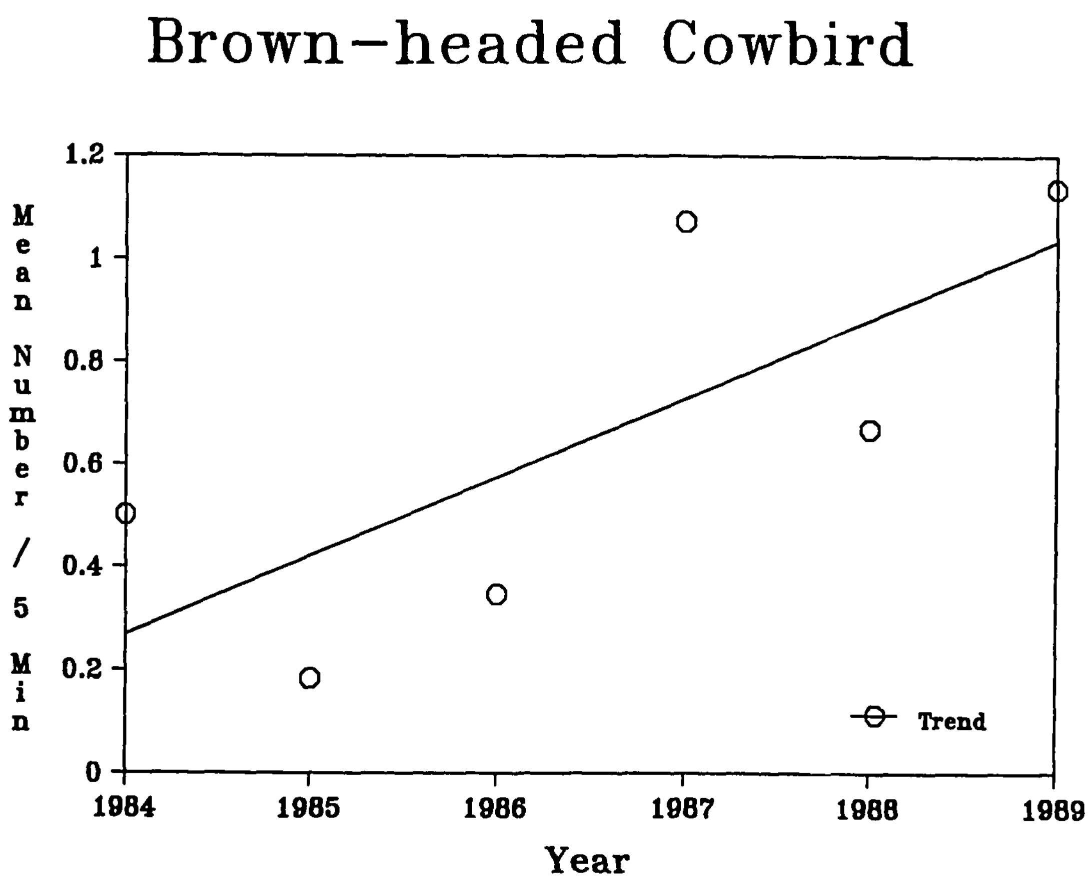


Figure 36. Population trend of Brown-headed Cowbirds at Tensas River NWR, 1984-1989. Data represent the mean number of individuals recorded per five minutes in the breeding season.

LITERATURE CITED

Aldrich, J. W., and C. S. Robbins. 1970. Changing abundance of migratory birds in North America. Smithsonian Contr. Zool. 26:17-26.

Ambuel, B., and S. A. Temple. 1982. Songbird populations in southern Wisconsin forests: 1954 and 1979. J. Field Ornith. 53:149-158.

Askins, R. A., J. F. Lynch, and R. Greenburg. 19 . Population declines in migratory birds in eastern North America. Pp. 1-57, Current Ornithology. Vol. .

Barden, L. S. 1989. Repeatability in forest gap research: studies in the Great Smoky Mountains. Ecology 70:546-547.

Barrow, W. C. 1982. Comparative ecology of two sympatric *Empidonax* flycatchers coexisting in an eastern deciduous forest. M.S. Thesis West Virginia Univ., Morgantown, W.V.

Bent, A. C. 1953. Life Histories of North American Wood Warblers. U. S. Govt. Printing Office, Washington, D. C.

Blackmore, A. B. 1895. The Hooded Warbler. Oologist 12:119-121.

Bock, C. E., and J. H. Bock. 1984. Importance of sycamores to riparian birds in Southeastern Arizona. J. Field Ornithol. 55:97-103.

Briggs, S. A., and J. H. Crisswell. 1979. Gradual silencing in Washington. Atlantic Naturalist 32:19-26.

Brittingham, M. C., and S. A. Temple. 1980. Hooded Warblers nesting in the Baraboo Hills, Sauk County, Wisconsin. Passenger Pigeon. 41:128-130.

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

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

Dickson, J. G. 1988. Bird communities in oak-gum-cypress forests. Pp. 51-62 *in* Bird Conservation no. 3, J. A. Jackson (ed). Univ. of Wisconsin Press, Madison.

Eddleman, W. R., K. E. Evans, and W. H. Eldes. 1980. Habitat characteristics and management of Swainson's Warbler in southern Illinois. Wildl. Soc. Bull. 8(3):228-233.

Eyre, F. H., Ed. 1980. Forest cover types of the United States and Canada. Soc. of Am. For., Washington, D. C. 148 pp.

Fentress, C. D. 1986. Wildlife in bottomlands: species and status. Pp. 37-57, *in* Bottomland Hardwoods in Texas, (C. A. McMahan and R. G. Frye, eds.), Parks and Wildlife Div., Res. Rep. 7100, Nacogdoches Texas.

George, W. C. 1971. Vanished and endangered birds of Illinois: a new 'black list' and 'red list'. Audubon Bull. 157:2-11.

Gosselink, J. G., G. P. Shaffer, L. C. Lee, D. M. Burdick, D. L. Childers, N. Taylor, S. C. Hamilton, R. Boumans, D. Cushman, S. Fields, M. Koch, and J. Visser. 1989. Cumulative impact assessment and management in a forested wetland watershed in the Mississippi River Floodplain. Coastal Ecology Inst., LSU, Baton Rouge, La. 131 pp.

Graber, J. W., and R. R. Graber. 1979. Severe winter weather and bird populations in southern Illinois. Wilson Bull. 91:88-103.

Greenberg, R. 1984. The winter exploitation systems of Bay-breasted and Chestnut-sided Warblers in Panama. Univ. Calif. Publ. in Zoology Vol. 116, Univ. of Calif. Press, Berkeley, Calif.

Grimes, S. A. 1935. The Hooded Warbler in Florida. Fla. Natur. 8:16-22.

Grumbine, R. E. 1990. Viable populations, reserve size, and federal lands management: a critique. Conserv. Biol. 4: 127-134.

Hall, G. A. 1984. Population decline of neotropical migrants in an Appalachian forest. Am. Birds 38:14-18.

Harris, L. D. 1989. The faunal significance of fragmentation of southeastern bottomland forests. Pp. 126-133, *in* The Forested Wetlands of the Southern United States, (D. D. Hook and L. Russ, eds.), Gen. Tech. Rep. SE-50, For. Serv., U.S.D.A., Asheville, North Carolina.

Holder, T. H. 1970. Disappearing wetlands in eastern Arkansas. Arkansas Planning Commission, Little Rock. 72 p.

Holmes, R. T., R. E. Bonney, Jr., and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: A multivariate approach. Ecology 60:512-520.

Holmes, R. T., and S. K. Robinson. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwood forest. Wilson Bull. 100(3):377-394.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperature deciduous forest: long-term trends at Hubbard Brook. Ecol. Monogr. 56:201-220.

Hupp, C. R., and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology 66:670-681.

Hutto, R. L. 1988. Is tropical deforestation responsible for the

reported declines in Neotropical migrant populations? Amer. Birds 42:375-379 .

Jackson, J. A. 1988. The southeastern Pine forest ecosystem and its birds: past, present, and future. Pp. 119-160, *in* Bird Conservation, J. A. Jackson (ed), University of Wisconsin Press, Madison, Wisconsin.

James, F. C. 1971. Ordination of habitat relationships among breeding birds. Wilson Bull. 88:215-236.

Kahl, R. B., T. S. Baskett, J. A. Ellis, and J. N. Burrough. 1985. Characteristics of summer habitats of selected nongame birds in Missouri. Res. Bull. 1056, Missouri Agric. Expt. Stat., Columbia, Missouri.

Keast, A., and E. S. Morton (eds). 1980. Migrant birds in the Neotropics: ecology, behavior, distribution and conservation, Washington, D.C., Smithsonian Inst. Press.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacArthur, R. H., and E. R. Pianka. 1966. An optimal use of a patchy environment. Am. Natur. 100:603-609.

Morse, D. 1971. The insectivorous bird as an adaptive strategy. Pp. 177-200 *in* Annual Review of Ecology and Systematics, (R. F. Johnston, P. W. Frank, and C. D. Michener, eds.), Vol. 2, Annual Reviews, Inc. Palo Alto, Calif.

MacDonald, P. O., W. E. Frayer, and J. K. Clauser. 1979. Documentation Chronology, and Future Projections of Bottomland Hardwood Habitat Loss in the Lower Mississippi Alluvial Plain 2 fools. U. S. Fish and Wildlife Service, Washington, D. C.

Martin, T. E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. Pp. 181-210, *in* Current Ornithology, R. F. Johnston (ed), Vol. 4, Plenum Press, New York.

Martin, T. E. 1985. Habitat effects on structure of forest bird assemblages: is predation an important underlying influence? Paper presented at the 103rd Am. Ornithol. Union meeting, Tempe, Arizona (abstract) p. 28.

Mayfield, H. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4:13-28.

McKinley, D. 1988. The Carolina Parakeet in Louisiana: a history. J. of La. Ornith. Vol. 1(1):1-13.

Meanley, B. 1971. Natural History of Swainson's Warbler. U. S. Dept. of Interior, Bur. of Sport Fish and Wild., N. A. Fauno no. 69, Washington, D. C.

Meanley, B. 1966. Some observations on habitats of the Swainson's Warbler. Living Bird, Vol. 5:151-165.

Moore, H. 1987. Monthly occurrence of birds in Warren county, Mississippi and Madison Parish, Louisiana, 1969-1986. Vicksbirder Newsletter 1987, Vicksburg, Miss.

Morrison, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. Condor 86: 146-150.

Moser, E. B., W. C. Barrow, and R. B. Hamilton. 1989. An exploratory use of correspondence analysis to study relationships between avian foraging behavior and habitat, Pp 309-317, *in* Avian Foraging Theory, Methodology, and Applications, M. S. Morrison C. J. Ralph, and J. Verner and J. R. Jehl, Jr. (eds.), Studies in Avian Biology, No. 13, Cooper Ornith. Soc., Allen Press, Lawrence, Kansas.

Mossman, M. J., and K. I. Lange. 1982. Breeding Birds of the Baraboo Hills, Wisconsin: Their History, Distribution, and Ecology. Dept. of Nat. Res. and Wisconsin Soc. for Ornith., Madison.

Oberholser, H. C. 1938. The Bird Life of Louisiana. Dept. of Conserv. Bull. no. 28, New Orleans.

Pashley, D. N. 1989. A distributional analysis of the warblers of the West Indies. Ph.D. Dissertation, Louisiana State University, Baton Rouge, La., 679 pp.

Petit, K. E., D. R. Petit, and L. J. Petit. 1988. On measuring vegetation characteristics in bird territories: nest sites vs. perch sites and the effect of plot size. Am. Midl. Nat. 199:209-215.

Petit, L. J., D. R. Petit, K. E. Petit, and W. J. Fleming. 1990. Annual variation in foraging ecology of Prothonotary Warblers during the breeding season. Auk 107:146-152.

Petit, L. J., D. R. Petit, K. E. Petit, and W. J. Fleming. 1990. Intersexual and temporal variation in foraging ecology of Prothonotary Warblers during the breeding season. Auk 107:133-145.

Powell, G. V. N., and J. H. Rappole. 1986. The Hooded Warbler. Pp. 827-853 *in* Audubon Wildlife Report 1986, R. L. Disilvestro (ed), Nat. Aud. Soc., New York.

Raffaile, H. A. 1983. A Guide to the Birds of Puerto Rico and the Virgin Islands. Fondo Educativo Interamericano, San Juan, Puerto Rico, 253 pp.

Remsen, Jr., J. V., and S. K. Robinson. 1989. A classification scheme for foraging behavior of birds in terrestrial habitats. Pp. 144-160, *in* Avian Foraging: Theory, Methodology, and Applications, M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. (eds), Studies in Avian Biology No. 13, Cooper Ornith. Soc., Allen Press, Lawrence, Kansas.

Remsen, J. V., Jr., and T. A. Parker, III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15:223-231.

Reynolds, R. T. and E. C. Meslow. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. Auk 101: 761-799.

Rice, J., B. W. Anderson, and R. D. Omhart. 1984. Comparison of the importance of different habitat attributes to avian community organization. J. Wildl. Manage. 48:895-911.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. Proc. Natl. Acad. Sci., Vol. 86:7658-7662.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918-1931.

Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672-684.

Robinson, S. K. 1988. Reappraisal of the costs and benefits of habitat heterogeneity for nongame wildlife, *in* Transactions of the Fifty-Third North American Wildlife and Natural Resource Conference, pp. 145-155.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecological Monographs 37:315-350.

Runkle, J. R. 1985. Disturbance regimes in temperature forests. Pp. 17-22 *in* The Ecology of Natural Disturbance and Patch Dynamics, S. T. A. Pickett and P. S. White (eds). Academic Press, New York.

Sampson, F. B. 1979. Lowland hardwood bird communities. Pages 49-66 *in* R. M. DeGraaf and K. E. Evans (eds), Management of north central and northeastern forests for nongame birds. USDA For. Serv. Gen. Tech. Rep. NC-51.

Sherry, T. W., and R. T. Holmes. 1985. Dispersion patterns and habitat responses of birds in northern hardwoods forests. Pp. 283-310 *in* Habitat Selection in Birds, M. L. Cody (ed), Academic Press, Inc., New York.

Sherry, T. W. 1979. Competitive interactions and adaptive strategies of American Redstarts and Least Flycatchers in a northern hardwoods forest. Auk 96:265-283.

Soil Conservation Service. 1982. Soil Survey of Madison Parish, Louisiana. U. S. Dept. ,Agric., Soil Conserv. Serv., Washington, D.C.

Swift, B. L., J. S. Larson, and R. M. DeGraaf. 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. Wilson Bull. 96:48-59.

Tanner, J. T. 1942. The Ivory-billed Woodpecker. Nat. Aud. Soc. Res. Rep. No. 1. 99 pp.

Tanner, J. T. 1986. Distribution of tree species in Louisiana bottomland forest. Castanea 51(3):168-174.

Turner, R. E., and N. J. Craig. 1980. Recent areal changes in Louisiana's forested wetland habitat. La. Acad. Sci. 42:61-68.

U. S. Fish and Wildlife Service. 1984. Blue ribbon panel for bottomland hardwoods. U. S. Dept. of Interior, Fish and Wild. Serv., Vicksburg, Miss.

U. S. Fish and Wildlife Service. 1982. Tensas River Project, Louisiana. Fish and Wildl. Coord. Act Rep., Jackson Area Office, Jackson, Miss.

U. S. Fish and Wildlife Service. 1988. Forest habitat management plan, Tensas River National Wildlife Refuge. Tensas River National Wildlife Refuge, (Draft Copy), Tallulah, La.

Walcott, C. F. 1974. Changes in bird life in Cambridge, Massachusetts from 1860-1964. Auk 91:151-160.

Whitcomb, B. L., R. F. Whitcomb, and D. Bystrak. 1977. Island biogeography and "habitat islands" of eastern forest. III. Long-term turnover and effects of selective logging on the avifauna of forest fragments. Am. Birds 31:17-23.

Chapter 3. THE HOODED WARBLER (*Wilsonia citrina*): NONBREEDING DISTRIBUTION AND COMPARISONS OF ECOLOGY AT SUMMER AND WINTER SITES

INTRODUCTION

Each autumn, most of North America's forest-dwelling passerine bird species migrate to wintering grounds in the Neotropics. This provides opportunities to study habitat use patterns and foraging strategies of birds at different places (Baker and Baker 1973; Greenberg 1979, 1984, 1989; Rabenold 1980; Hutto 1984). I compare here Summer and Winter habitat use and foraging ecology of the Hooded Warbler, *Wilsonia citrina* (Parulinae).

The Hooded Warbler is a migratory insectivore that encounters a variety of plant communities and habitat structures throughout the year. Its breeding range extends from the Atlantic Coast west to eastern Texas and Oklahoma, north to southern Ontario and central New York, and south to the Gulf Coast and northern Florida (Oberholser 1974, American Ornithologists' Union 1983, Wood and Schnell 1984, Peck and James 1987). Its non-breeding range has not been hitherto precisely determined but has been roughly delineated by Cooke (1904) and Rappole et al. (1983).

BREEDING RANGE

The habitat requirements of Hooded Warblers on their breeding grounds have rarely been described quantitatively. In a multivariate analysis of habitat relationships of birds in Arkansas, James (1971) concluded that Hoodeds "occur in upland and lowland situations but only in the most mature mesic forests." Anderson and Shugart's (1974) univariate and multivariate analysis of habitat selection of

birds in Tennessee found seven variables that categorize the Hoodeds' distribution; all were associated with dense shrub and understory cover. In another Arkansas study, Smith's (1977) multivariate analysis found that Hooded Warblers favored large trees in moist situations. He concluded that the Hooded Warbler was an "obligatory" moist-forest species. In a study of vertical distribution of birds in a Louisiana bottomland hardwood forest, Dickson and Noble (1978) found > 75% of sightings of Hooded Warblers in the midstory (0.6 - 7.6 m) stratum of the forest. More recently, Robbins et al. (1989) identified several variables that were significant predictors of Hooded Warbler relative abundance in the Middle Atlantic states (listed in decreasing order of significance): mean canopy height, percent of forest within 2 km of counting point, foliage density between 0.3 and 1 m, and percent ground cover. In Louisiana, Moser et al. (1989 in press) used correspondence analysis to study the relationships between avian foraging behavior and habitat of small insectivorous birds. Hoodeds were associated with the midstory (2 - 10 m) of non-flooded forest, particularly in areas with dense vine cover.

General habitat descriptions are more numerous. In the Mississippi and Ohio River floodplains and the Southeastern Coastal Plain, Hooded Warblers occur in mature bottomland hardwood forests (Audubon 1831, Dawson 1903, Howell 1924, Grimes 1935, Oberholser 1938, Sprunt and Chamberlain 1949, Stewart and Robbins 1958), cypress-tupelo forests (Burleigh 1958), and in the deciduous understory of southern pine forests (Hamel et al. 1982). In the Ozark Mountains and Southern Appalachian region, Hoodeds are found in oak-hickory forests (Smith 1977, Hall 1983), mixed pine/hardwoods (Brooks 1940, Mengel 1965), and northern hardwoods (Brooks 1940). In

New England and southern Ontario, Hoodeds nest in upland deciduous or mixed forests (Eaton 1914, Cadman et al. 1987) and beech-maple forests (Eaton 1914, Bent 1953).

Unique habitat features consistently in the Hooded Warblers' territories include vine tangles (Audubon 1827, Grimes 1935, Bent 1953, Sprunt 1954); cane brakes (Wilson 1808, Ridgway 1878, Davie 1898, Howell 1924, Arthur 1931, Bent 1953, Meanley 1971); forested ravines (Arthur 1931, Odum 1931, Bent 1953, Burleigh 1958, Hall 1983); rhododendron and laurel thickets (Forbush 1929, Todd 1940, Mengel 1965); briar patches, stump sprouts, or other thickets in small forest openings (Blackmore 1895, Bailey 1925, Brooks 1940, Bent 1953, Mossman and Lange 1982, Cadman et al. 1987, Peck and James 1987); and large tracts of forest (Mengel 1965, Powell and Rappole 1985, Robbins 1989). Mature trees and dense undergrowth appear to be common characteristics throughout the breeding grounds.

WINTER RANGE

Winter habitat of Hooded Warblers has generally been reported to be undergrowth of humid forests. On the Yucatan Peninsula, males used closed-canopy forests of moderate to full stature, whereas females held territories in areas with more shrubs, fewer and smaller trees, and a lower canopy (Lynch et al. 1985). In the Los Tuxtlas area, birds (apparently mostly males) occurred in primary forest and seemed to center their activities around structures such as fallen trees or brush piles (Rappole and Warner 1980).

Others have made general references to Winter habitat requirements: Wetmore (1943) in southern Veracruz -- in lowland forest and thickets; Berrett (1962) in Tabasco -- in humid wooded sections, predominantly in the rain forest belt; Binford (1989) in Oaxaca -- in tropical evergreen forest; Alvarez del Toro (1958) in

Chiapas -- in humid forests; Waide (1981) in Campeche -- along edges; Griscom (1926) in Quintana Roo -- in forests; Paynter (1955) in the Yucatan Peninsula in woodland, particularly in the more humid southern forest.

In Central America Hoodeds occur: in Belize, in undergrowth of tall forest and second growth (Russell 1964); in Guatemala, in humid forest, plantations, and second growth (Land 1970), in rain forests and bushy areas (Land 1963), and in the dense undergrowth of humid forest borders (Smithe 1966); in Honduras, at low levels in rain forests and second growth (Monroe 1968); and in Costa Rica, in second-growth and on forest borders in shrub and leafy thickets (Slud 1960, 1964).

There have been Winter sightings in mangroves from Tabasco (Berrett 1962), Cuba (Barbour 1943), Puerto Rico (Raffaele 1983), and Venezuela (Meyer de Schauensee and Phelps 1978). Other Caribbean reports are from gardens and stream banks in Cuba (Barbour 1943), forest undergrowth in Puerto Rico (Raffaele 1983), and in heavy undergrowth of the moist forest of St. John in the Virgin Islands (Robertson 1962).

If I are to conserve migrant insectivorous birds in the near future, I must know the ranges and habitats of each species and how each uses various habitats seasonally. In this paper I will provide such information for the Hooded Warbler. My objectives are to (1) delineate as precisely as possible the Hooded Warblers' nonbreeding geographic range, (2) to describe quantitatively its habitat and foraging behavior during the Winter and Summer, and (3) to discuss how the above information affects its conservation and management needs.

STUDY AREAS AND METHODS

WINTER AND MIGRATORY DISTRIBUTION

To obtain data from extant specimens, Pashley (1988c, unpubl. ms.) examined specimens (or received data) from 39 museums in the United States, Canada, and Europe; he obtained information on 374 Hooded Warbler specimens. I used this information plus location information gathered by Pashley from literature reports of sightings, nettings, photographs, and unlocated specimens. Pashley prepared distribution maps for four seasons: (1) early Fall -- August, September; (2) late Fall, -- October, November; (3) Winter -- December, January, February; and (4) Spring -- March, April, May.

LOUISIANA STUDY SITE

Hooded Warbler data were collected as part of a long-term study of the distribution and ecology of birds of bottomland hardwood forests in the Tensas River Basin, Louisiana. For this study, habitat and foraging data were collected from late March to late July 1984 - 1989 in a 260 ha stand of bottomland hardwood forest located on the Tensas River National Wildlife Refuge, Madison Parish, Louisiana (91° 22′ W, 32° 21′ N). This study area is in the interior of an approximately 40,470 ha block of bottomland hardwood forest; the nearest man-created edge is 2.2 km away. The study area is a second-terrace flat of the lower Mississippi River Floodplain and does not flood seasonally, except for small depressions of parallel scour channels approximately 25 m wide. The forest is relatively mature (> 75 yrs old); the canopy is dominated by sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), willow oak (*Q. phellos*), and various species of elm (*Ulmus* spp.). The understory

consists primarily of saplings, swamp palmetto (*Sabal minor*), deciduous holly (*Ilex decidua*), and numerous vines such as *Rhus radicans*, *Berchemia scandens*, and *Ampelopsis arborea*.

The study area is in a subtropical, transitional climatic region. Mean monthly minimum and maximum temperatures have ranged between -7.8°C and 36°C (Soil Conservation Service 1982). The average annual precipitation was 1306 mm over a 10-year period. During the breeding season (April - July), the average annual precipitation for 10 yrs. was 447 mm (Soil Conservation Service 1982).

MEXICO STUDY SITES

Habitat measurements, foraging observations, and bird counts were made during the Winter in the Sierra de Los Tuxtlas of southern Veracruz, Mexico (95° 04' W, 18° 34' N) as a part of a 3-year study of the Winter distribution and ecology of small, insectivorous birds in the Sierra de Los Tuxtlas, Mexico. I began collecting foraging data during the Winter of 1983-84 (13 - 27 January). I collected additional data from 19 September 1984 to 16 March 1985, and from 29 October 1985 to 2 February 1986. I sampled along trails or small dirt roads in five study areas that contained three habitat types: (1) mature, evergreen rain forest (Miranda and Hernandez 1963) at the Estacion de Biologia Los Tuxtlas, a 700-ha forest preserve connected with a 10,000-ha block of rain forest surrounding the San Martin Volcano (5.61 km of trails); (2) disturbed forest/fields -- found at three sites that included 3.25 km of trails from the biological station to Playa Escondida, 2.07 km of trails through an "ejido" (rural settlement) located near the station, and 2.76 km of trails from the station to the village of Balzapote on the Gulf of Mexico; (3) Savanna -- sampled along 3.29 km of trails near the village of La Palma. The study sites ranged in altitude from 10 m to 450 m and

small watercourses meandered through each of them.

Tree species of the rain forest canopy were diverse, and included dominants such as: *Nectandra ambigens* (Lauraceae), *Brosimum alicastrum*(Moraceae), and *Poulsenia armata* (Moraceae). Co-dominants and subcanopy trees included *Pseudolmedia oxyphyllania* (Moraceae) and *Stemmadenia donell-smithii* (Apocynaceae). *Astrocaryum mexicanum* (Palmae) and *Faramea occidentalis* (Rubiaceae) were common in the understory.

The disturbed forest/field area consisted of young and old shrub and forest patches scattered among cattle pastures and agricultural plots (usually corn, coffee, or oranges). Vegetation in these areas included *Cecropia obtusifolia* (Moraceae), *Bursera simaruba* (Burseraceae), *Heliocarpus appendiculatus* (Tilaceae), *Neurslaena macrocephala* (Compositae), *Carica papaya* (Caricaceae), *Phytolacca rivinoides* (Phytolacaceae), *Hampea nutricia* (Malvaceae), and *Heliconia bihaii* (Musaceae). Numerous species of vines and epiphytes occurred on all sites.

The savanna area consisted of single, sparsely distributed trees in a grass/sedge wetland with gallery forest occurring along several watercourses. The area had originally been rain forest, but because of past clear-cutting, it had become savanna-like.

The climate in the Sierra de Los Tuxtlas is warm and humid with mean monthly minimum and maximum temperatures of 17°C and 29°C, respectively. The average annual precipitation was 4950 mm over a 10-year period (1972-80). There is a long wet season from June to February and a shorter dry season lasting from March to May (Coates-Estrada et al. 1985).

FIELD METHODS

I sampled by regularly and repeatedly traversing the study

areas and recording foraging data as I encountered birds. I recorded species, sex, time of day, type of foraging maneuver, foraging height, height of the substrate, spherical vegetation density (estimated vegetation volume [in %] within an imaginary 1-meter sphere centered on the foraging bird), foraging rate, and foraging-flock status. I used the scheme of Remsen and Robinson (1989) to classify foraging maneuvers. I occasionally needed to use compound names; otherwise, my terminology is almost the same as theirs. I lumped Remsen and Robinson's (1989) "sally-strike" and "sally-hover" maneuvers into "sally-glean" where a flying bird takes prey from a substrate. I also included their "lunge" and "reach" categories within my "glean"; for ground-foraging birds, "reach" was included in "flutterchase" or "flush-pursue". The substrates were litter, herbs, fallen debris (trees, logs, or branches), tree trunk, branch (> 1 cm), twig (< 1 cm), leaf (dead or live), air, and other (rock, epiphyte, etc.). If discernable, the leaf surface (upper or lower) at which a maneuver was directed was recorded. Foraging heights were grouped into four categories: ground (< 0.5 m), shrub (0.5 - 2 m), subcanopy (2.1 - 10 m), and canopy (> 10 m). Each warbler was followed until it performed 10 foraging maneuvers or until lost from sight. For each foraging sequence longer than 20 seconds (*sensu* Robinson and Holmes 1982) (maximum = 10 maneuvers), I calculated foraging rate (number of prey-attacking maneuvers/min.). To prevent serial correlation problems, one observation from each observation sequence was randomly selected and used for statistical analysis or foraging data (see Morrison 1984).

Habitat use was investigated at two spatial scales: (1) macrohabitat (among types) and (2) microhabitat (within vegetative types). In Mexico, macrohabitat use was compared among the three

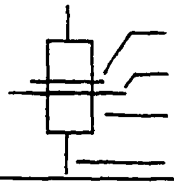
habitat types described above. I recorded the location of all Hooded Warbler sightings within the three habitat types and the time of initial observation. Later, I calculated #/hr., by hr., from the times of observation and compared the rates among the habitats.

If a Hooded Warbler was observed on 40 percent or more of visits at the same location (within 20 m of a particular point), the location was classified as a "territory." Through the course of our field work, I found that Hooded Warblers frequently used areas that included recent tree or branch falls; therefore, I recorded the presence of such structures in territories. All but two of the territories were occupied by unmarked birds, and it is possible that they were not always occupied by the same birds. In the two cases with marked birds, only the marked birds occupied the territory; one did change location once during the Winter (moved from one territory to another). Hoodeds frequently and consistently used these locations that are important habitats whether they represented "exclusive" territories or not. Therefore, I compared territory use among habitats.

I also compared microhabitat use and availability at both the Louisiana and Mexico study areas. Notations used in graphs throughout the chapter are described in Table 21.. Microhabitat was sampled at the site where an individual's first foraging maneuver was observed. An imaginary cylinder with a diameter of 2 m and centered on the bird was divided into the four height categories described earlier (the diameter of the cylinder in the canopy layer was expanded to 10 m). The relative volume (in %) of vegetation was estimated in each strata; the canopy height was measured with a range finder. I used the same methods at randomly located points to determine "availability" of microhabitat.

Table 21. Notations used in box plot figures in Chapter 3.

Notation	Definition
HL	Hooded Warbler in Louisiana
HM	Hooded Warbler in Mexico
RL	Availability in Louisiana
RM	Availability in Mexico



I recorded species composition of all mixed-species flocks and army-ant swarm flocks encountered as I traversed the study sites. A flock was defined as an association of birds moving in concert within an approximately 20 m diameter circle (Greenberg 1984). All flocks were followed as long as necessary to determine species composition, if possible.

DATA ANALYSIS

I used Student's *t*-test (SAS 1988) to compare means (use vs availability). Most of the variables were recorded as percents and deviated from normal distributions; therefore, I used logit transformation on microhabitat variables. Untransformed means, transformed means, confidence limits, and range are shown in all relevant figures; probability values are based on transformed variables.

I used the G-statistic to test differences in use of forage-related variables (Sokal and Rohlf 1969) and Chi-square tests to compare distribution of "territories" among habitat types and to compare seasonal use.

I compared behavior with Schoener's (1968) index:

$$O_{hj} = 1-\frac{1}{2}\sum(P_{ih} - P_{ij})$$

where P_{ih} is the proportion of behavior *i* at site *h* and P_{ij} is the proportion of behavior *i* at site *j* with *i* being 1 of *n* behaviors; summation is from 1 to *n*. O_{hj} varies from 0 with no correspondence to 1 with complete overlap.

Exact probabilities are given throughout; I used a = 0.05 when I specifically refer to a significant difference.

RESULTS

DISTRIBUTION

The core of Hooded Warbler Winter distribution is the Gulf Coast and Caribbean slope from south-central Veracruz south to Honduras (Figure 37., Figure 38., Figure 39., and Figure 40. ; Table 23.). The species occurs very irregularly in Costa Rica (Slud 1964) and Panama (Wetmore et al. 1984), and is accidental in Colombia (Hilty and Brown 1986) and Venezuela (Meyer de Schauensee and Phelps 1978). It is unclear whether the infrequent specimen and sight records from throughout the West Indies (Pashley 1988 a, b; 1989; Pashley and Hamilton ms.) are from small over-wintering populations or are records of relatively frequent accidental visitors.

Position of migratory routes is uncertain. Locations varied slightly by season, but are not numerous enough to elucidate migratory pathways clearly. Most individuals apparently move north and south over the mainland of eastern Mexico or the adjacent Gulf of Mexico (Figure 37., Figure 38., and Figure 40.). Trans-Gulf migration, particularly of birds wintering on the Yucatan Peninsula and in Honduras, cannot be ruled out. Cooke (1904) provided evidence that Hooded Warblers may use the Mississippi River Valley as their main migration route during the Spring.

RELATIVE ABUNDANCE AMONG HABITATS

Wintering Grounds.- During the 2 Winters of this study, I observed 256 Hooded Warblers that made up 12.5 percent of the wintering warbler observations; Hoodeds ranked third in abundance (Barrow and Pashley, unpubl. data). The mean observation rate (birds/hr) ranged from 0.63 in 1985-86 to 0.72 in 1984-85, and averaged 0.65 (Table22); it varied most in Fall migration (15

Table 22. Number (n) and observation rate, number observed per hour (r), of Hooded Warblers observed in Mexico in Fall and Winter 1984-85 and 1985-86, by habitat type.

Habitat	1984-85						1985-86						Both	
	Fall		Winter		Total		Fall		Winter		Total		Total	
	n	r	n	r	n	r	n	r	n	r	n	r	n	r
Forest	49	.82	33	1.33	82	.97	8	.27	50	.72	58	.58	140	.76
Disturbed Forest/Field	38	.63	18	.58	56	.61	3	.37	52	.69	55	.66	111	.63
Savanna	1	.08	2	.31	3	.16	--	--	2	.13	2	.13	5	.15
Total	88	.67	53	.85	141	.72	11	.29	104	.65	115	.63	256	.65

Table 23. Number of Hooded Warbler specimens located, by region, by month; as reported by Pashley (1989, unpubl. ms.).

Region	A	S	O	N	D	J	F	M	A	M
MEXICO										
Sonora						1				
Durango										1
San Luis Potosi	1							1		
Tamaulipas				1					3	
Veracruz	11	11	12	11	11	7	8	20	7	
Tabasco				1			2	7	1	
Oaxaca		5	4	1		2	3	8	2	
Chiapas		5		1	3	4		5		
Campeche		2		2	3	1	1			
Yucatan		3	3	5		2	4	6	4	
Quintana Roo	1		2	5	6	14	2	3		
BELIZE	1	1			7	3	4	16	8	
GUATEMALA		3	9		2	4	10	4	2	
EL SALVADOR					1			1		
HONDURAS		6		2	1	2	8	8	3	1
NICARAGUA							1	3	1	
COSTA RICA			1	1						
PANAMA			3					1		
COLUMBIA						1				
BERMUDA	1	2								
BAHAMAS			1			1				
CUBA								1	1	
W. CARIBBEAN								1		
HISPANIOLA				1						
PUERTO RICO				1						
VIRGIN ISLANDS								2	1	
LESSER ANTILLES			1				1	1		

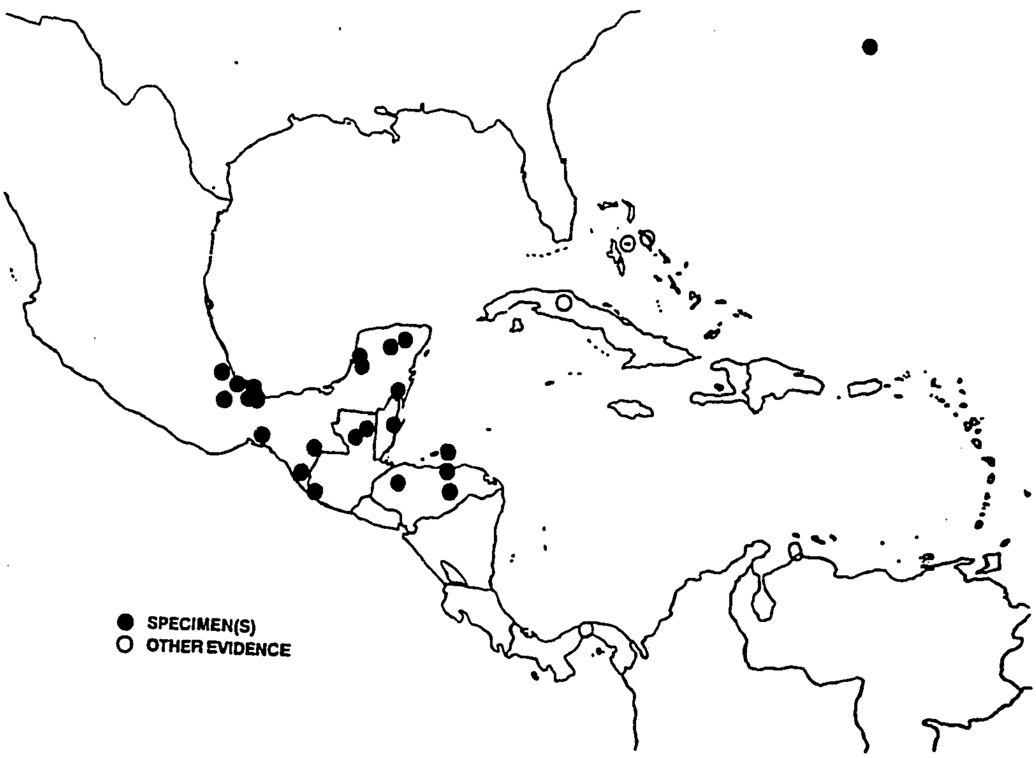


Figure 37. Nonbreeding range of Hooded Warbler in the Neotropics during early fall (August, September).

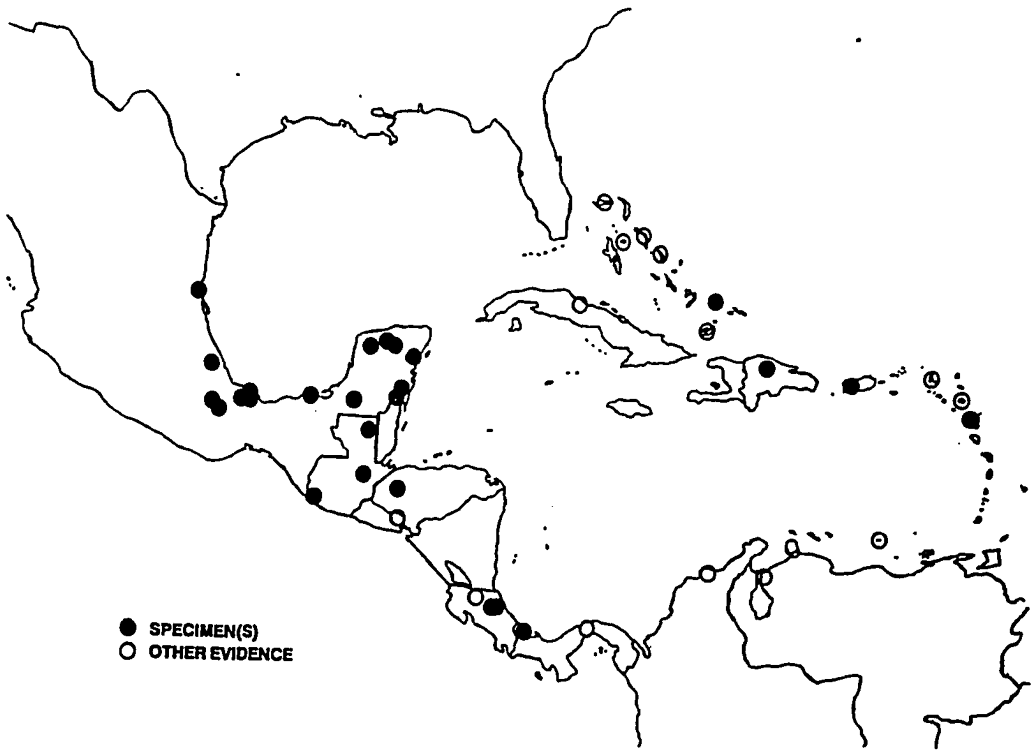


Figure 38. Nonbreeding range of Hooded Warbler in the Neotropics during late fall (October, November). Other evidence includes literature reports of sightings, nettings, photographs, and unlocated specimens.

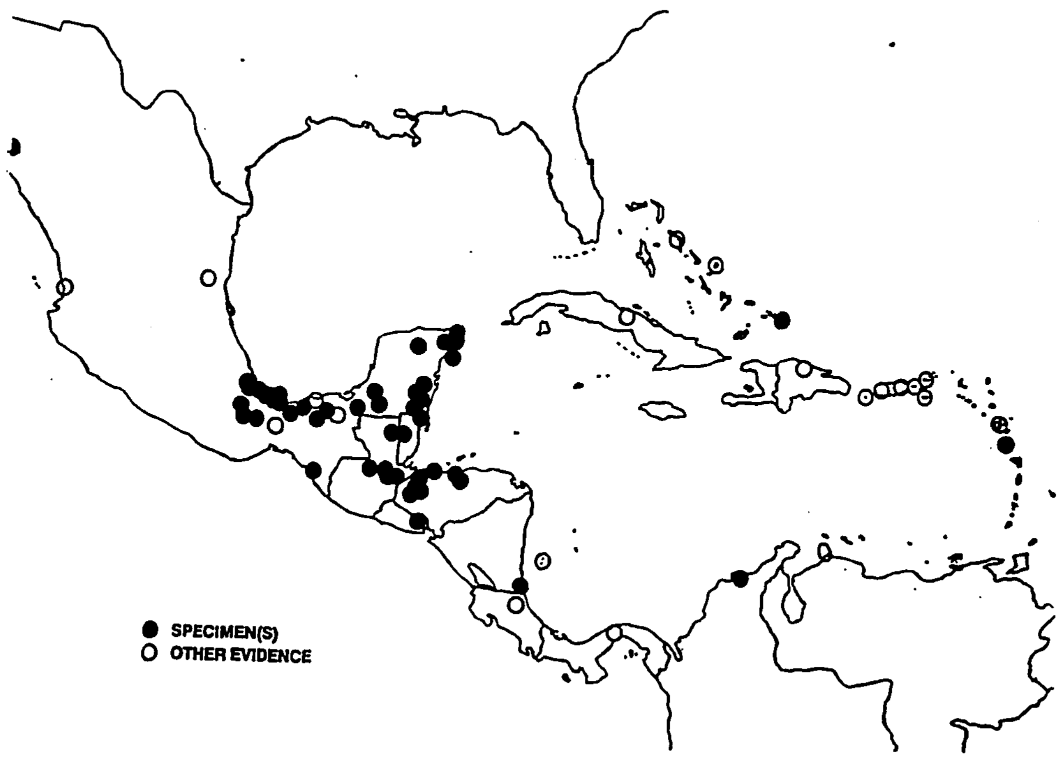


Figure 39. Nonbreeding range of Hooded Warbler in the Neotropics during winter (December, January, February). Other evidence includes literature reports of sightings, nettings, photographs, and unlocated specimens.

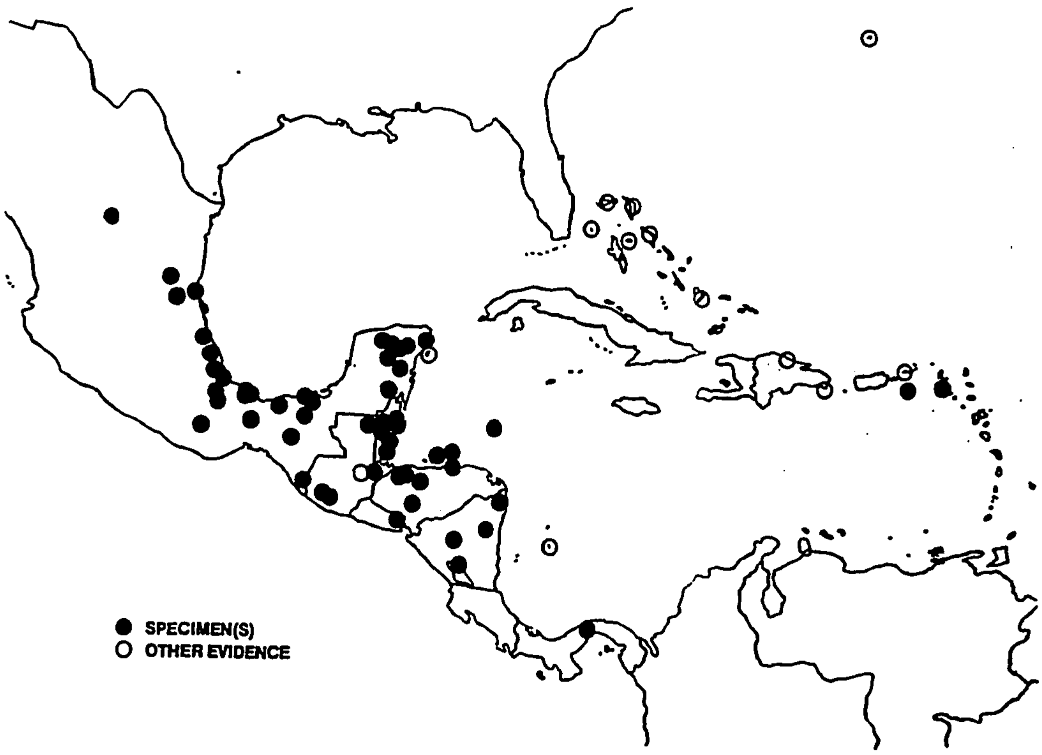


Figure 40. Nonbreeding range of Hooded Warbler in the Neotropics during Spring (March, April, May). Other evidence includes literature reports of sightings, nettings, photographs, and unlocated specimens.

September - 15 November). The time span of our study in Mexico (2 yrs.) and precision of our data are insufficient for analysis of temporal numerical trends, but I can test for differences in relative abundance among habitats. The observation rate was highest in the forest in 1984-85, and highest in the disturbed forest/field habitat in 1985-86 (Table 22.). The two sites differed in their foliage height profiles. In the rain forest, foliage was denser in the canopy and subcanopy strata (Figure 41.); the foliage in the ground stratum was denser in the disturbed forest/field sites (Figure 42.). Warblers were easier to see in the open fields or savanna than the dense forest; they were observed in savanna only on five occasions (Table 22.). The young second-growth, and the mosaic of forest patches that existed in the fields, especially along watercourses, supported a large number of Hooded Warblers and were important habitats, but relative numbers were high because of an observational bias in these relatively open habitats.

Hooded Warblers have been found defending territories on their wintering grounds (Rappole and Warner 1980, Lynch et al. 1985) and the relative abundance of these varied among habitats; I had attempted to search all study areas with equal effort. For this analysis, I subdivided forest into edge (< 30 m from a field) and interior (>30 m from field border). Territories were disproportionately common within the forest interior (2 yrs. pooled data; $X^2 = 22.3$, $df = 2$, $n = 49$, $p = .005$) (Table 24.). Disturbed forest/field did not contain "territories" in proportion to its abundance, but much of the area was field and not suitable habitat. I found a majority of Hooded Warbler "territories" in the disturbed [or *'man-altered'* forested] landscape over the 2 years of this study, but those were the most frequently sampled habitats

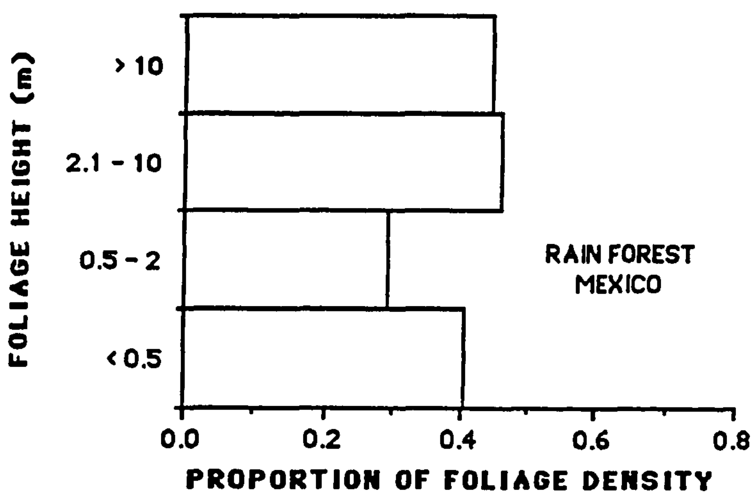


Figure 41. Mean foliage-height profile of Mexico rain forest study site.

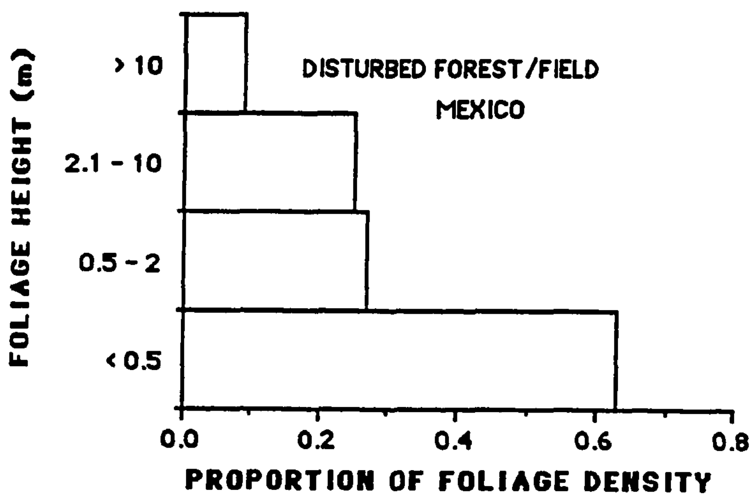


Figure 42. Mean foliage-height profile of Mexico disturbed forest/field study site.

(Table 24.)and birds were easier to find near the trail and in openings.

Rappole and Warner (1980) stated that many Hooded Warblers seemed to have 'favorite' areas, such as fallen trees or brush piles within their territories. I concur and suspect that such areas are important to wintering Hooded Warblers (as well as other migrants, pers. obs.) and are used preferentially in the Los Tuxtlas region. In 1984-85, 35 percent of all territories contained a slash pile, fallen tree or branch; in 1985-86, 37 percent (Table 24.). During the two Winters, 27 percent of all forest interior territories contained fallen trees or branches (Table 24.). In the fields and forest patches, slash piles were more frequently utilized by foraging birds throughout the Winter; 40 percent of all territories within this habitat type had such structures (Table 24.).

The "territorial" birds were predominantly males. Of 17 territory holders in 1984-85, only 2 were known to be females. In 1985-86, 3 of 35 territory occupants were identified as females. I carefully observed all individuals to ascertain sex (see Lynch et al. 1985). Rappole and Warner (1980) found a similar sex ratio (8:1) in mature forest of the Sierra de Los Tuxtlas. Both of our female "territory" holders were in second-growth forest or disturbed areas. Sample size was not large enough to test habitat preference of females, but Rappole and Warner (1980) also found females more abundant in second growth forest and Lynch et al. (1985) found females inhabiting shrubby old fields and low-stature woodlands in the Yucatan Peninsula.

Breeding Grounds.- In the bottomland hardwood forest of the Tensas River Basin, three habitats were sampled: (1) oxbow lake edges (mostly bald cypress [*Taxodium distchum*] forest with buttonbush

Table 24. Distribution of Hooded Warbler territories during the Winter of 1984-85 and 1985-86, by habitat type.

Habitat	Trail Length(km)	1984-85 n	1985-86 n	Total Obs.	Total Exp.
Forest Interior		6	10	16	--
At 'tree fall'*		1	5	6	--
Total	3.16	7	15	22	9.5
Forest Edge		2	1	3	--
At "tree fall"		2	2	4	--
Total	2.45	4	3	7	7.3
Disturbed Forest/Field		2	10	12	--
At "tree fall"		3	5	8	--
Total	11.37	5	15	20	34.1
Buildings		1	1	2	--
At "tree fall"		0	1	1	--
Total	0.38	1	2	3	1.1
Total	17.36	17	35	52	52

* Slash pile, fallen tree or branch located within the territory and frequently utilized by bird.

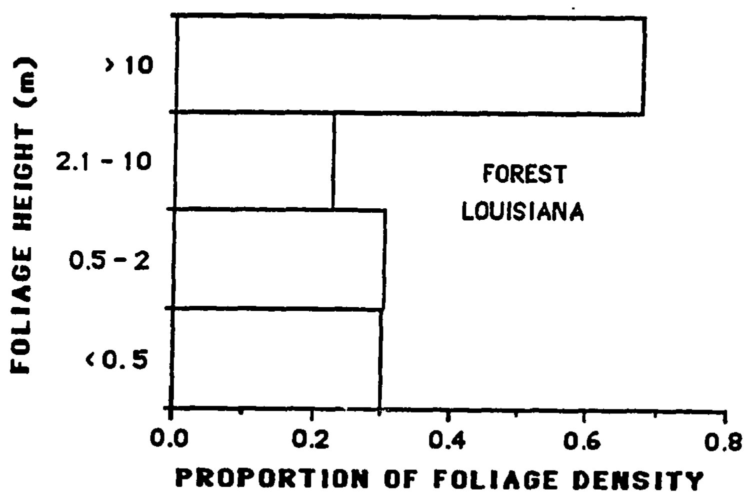


Figure 43. Mean foliage-height profile of Louisiana bottomland hardwood forest study site.

[*Cephalanthus occidentalis*] understory), (2) seasonally flooded forest (overcup oak [*Quercus lyrata*]-water hickory [*Carya aquatica*]), and (3) non-flooded forest (sweetgum-willow oak). Hoodeds were found only in the nearly mature, non-flooded forest (Moser et al. 1989)(Figure 43.). Within this forest type, Hoodeds concentrated in areas of dense understory vegetation.

MICROHABITAT USE

Wintering Grounds.- In the virgin rain forest, Hooded Warblers used areas of dense foliage in the ground layer (< 0.5 m) (47.3%, SD = 24.7) with a relatively sparse canopy cover above (> 10 m) (33.1%, SD = 22.6). The means of these layers were significantly different than similar layers in random plots (Figure 44.; t = 2.94, df = 572, p = .003; t = 4.51, df = 572, p = .001, respectively). The foliage density used in the shrub (0.5 - 2 m) and subcanopy (2.1 - 10 m) strata, the ones frequently used by Hoodeds, ranged from 32.5% (SD = 23.1) to 45.0% (SD = 23.3) and were not different than random plot means (Figure 44.; shrub: t = 1.27, df = 572, p = .205; subcanopy: t = .20, df = 572, p = .840).

In disturbed forest/fields, the mean foliage density for the ground stratum (used, 60.1%, SD = 23.4; random, 62.7%, SD = 24.8) was nearly identical for bird-centered and random plots (Figure 45.; t = 1.11, df = 801, p = .267). The mean foliage density used by Hoodeds in the shrub and subcanopy strata ranged from 41.5% (SD = 27.7) to 44.1% (SD = 29.4), respectively, and was significantly greater than available foliage density in the same layers (Figure 45.; shrub [26.9%, SD = 25.7]: t = 5.30, df = 801, p = .0001; subcanopy [25.3%, SD = 26.6]: t = 6.24, df = 801, p = .0001). Mean foliage density in the canopy stratum was also denser in bird-centered plots than random plots (Figure 45.; t = 4.75, df = 801, p = .0001).

Breeding Grounds.- The average foliage density of the shrub and subcanopy used by Hoodeds in Louisiana ranged from 52.3% (SD = 31.7) to 57.4% (SD = 31.5), respectively. In contrast, the average density available in the shrub (30.3%, SD = 30.4) and subcanopy layers (27.7%, SD = 26.9) was significantly less (Figure 46.; t = 5.57, df = 306, p = .0001; t = 8.89, df = 287, p = .0001, respectively). Foliage used by Hoodeds in the ground stratum was also denser than in random plots (Figure 46.; t = 3.52, df = 293, p = .0005).

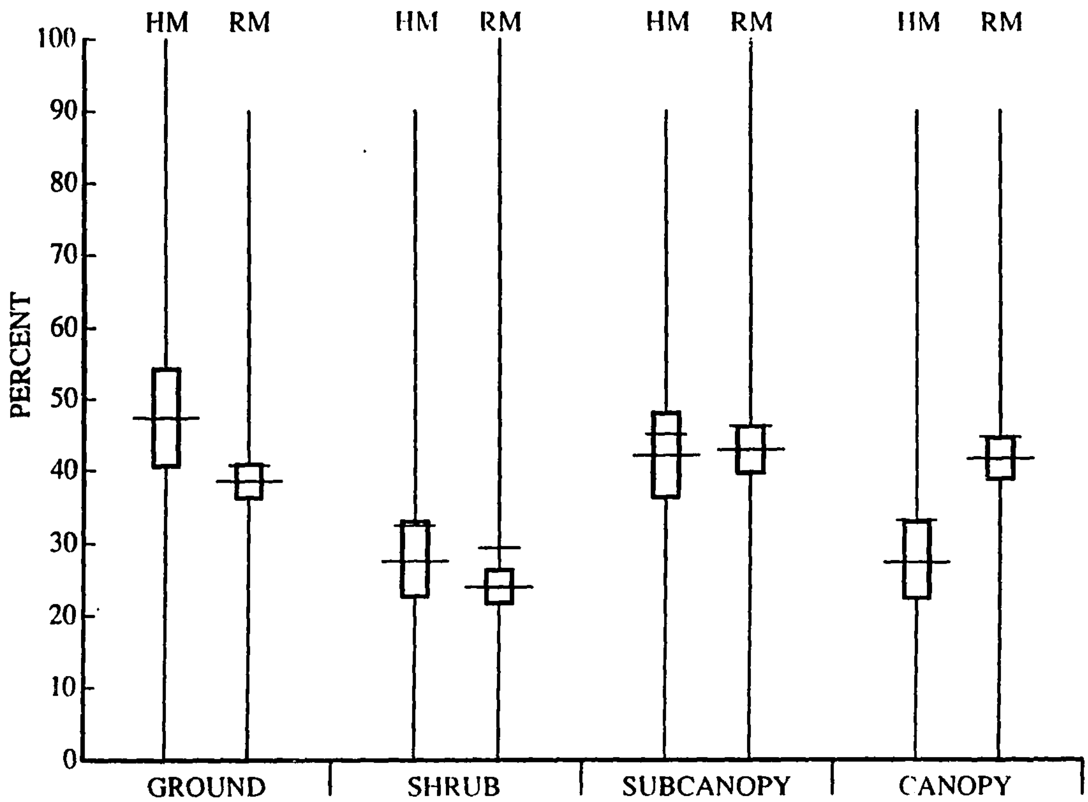


Figure 44. Foliage density use and availability by Hooded Warbler of four height strata in a Mexican rain forest.

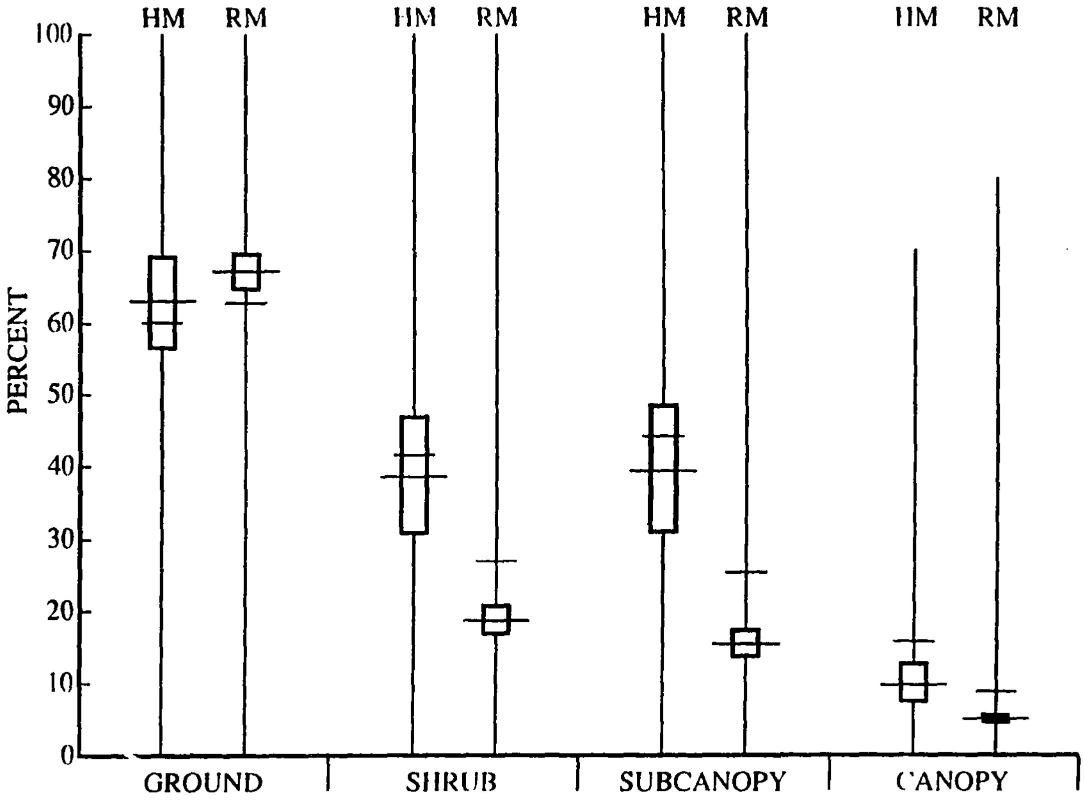


Figure 45. Foliage density use and availability by Hooded Warbler of four height strata in a Mexican disturbed forest/field.

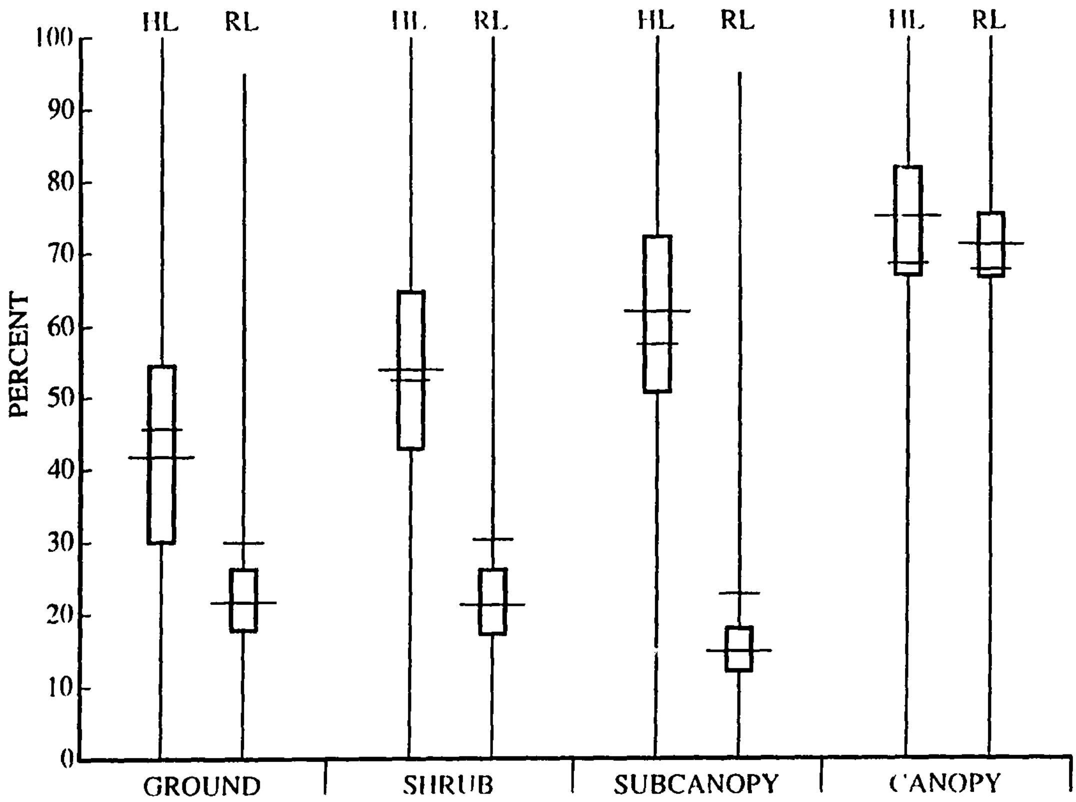


Figure 46. Foliage density use and availability by Hooded Warbler of four height strata in Louisiana bottomland hardwood forest.

Geographical Comparison of Habitat Structure and Seasonal Use.- The structure of the two forests differed significantly in all but one stratum (Figure 49.). Ground and subcanopy foliage were denser in Mexico (Figure 49.; $t = 7.19$, $df = 691$, $p = .0001$; $t = 11.57$, $df = 691$, $p = .0001$; respectively), but canopy foliage was denser in Louisiana (Figure 49.; $t = 10.88$, $df = 691$, $p = .0001$).

On the breeding grounds, Hooded Warblers used areas with denser foliage in the shrub ($t = 4.47$, $df = 187$, $p = .0001$), subcanopy ($t = 3.34$, $df = 168$, $p = .001$), and canopy strata ($t = 8.87$, $df = 189$, $p = .0001$) than similar strata on the forested wintering grounds (Figure 47.). The foliage density used ranged from 45.6% (SD = 35.7) to 57.4% (SD = 31.5) in the ground through subcanopy in Louisiana. In Mexican rain forest at the sites, the foliage density used ranged from 32.5% (SD = 23.1) to 47.3% (SD = 24.7) in the same three strata. The average canopy density at foraging locations was 68.5% (SD = 28.4) at the Louisiana site and 33.1% (SD = 22.6) in the rain forest of Mexico (Figure 47.).

The density of foliage used by Hoodeds in the ground layer and subcanopy was greater in the disturbed forest/field of Mexico than in the Louisiana forest (Figure 48., $t = 3.14$, $df = 161$, $p = .002$; $t = 3.08$, $df = 155$, $p = .002$, respectively), but foliage density used in shrub and canopy strata was greater in the Louisiana study area (Figure 48., $t = 2.20$, $df = 174$, $p = .029$; $t = 13.37$, $df = 176$, $p = .0001$, respectively).

FORAGING ECOLOGY

Foraging Behavior.- The foraging behavior of the Hooded Warbler differed significantly between breeding and non-breeding seasons (Figure 50.; $G = 13.14$, $df = 5$, $p = .022$). During both seasons the most frequent behavior was the "sally-glean" (Figure 50.).

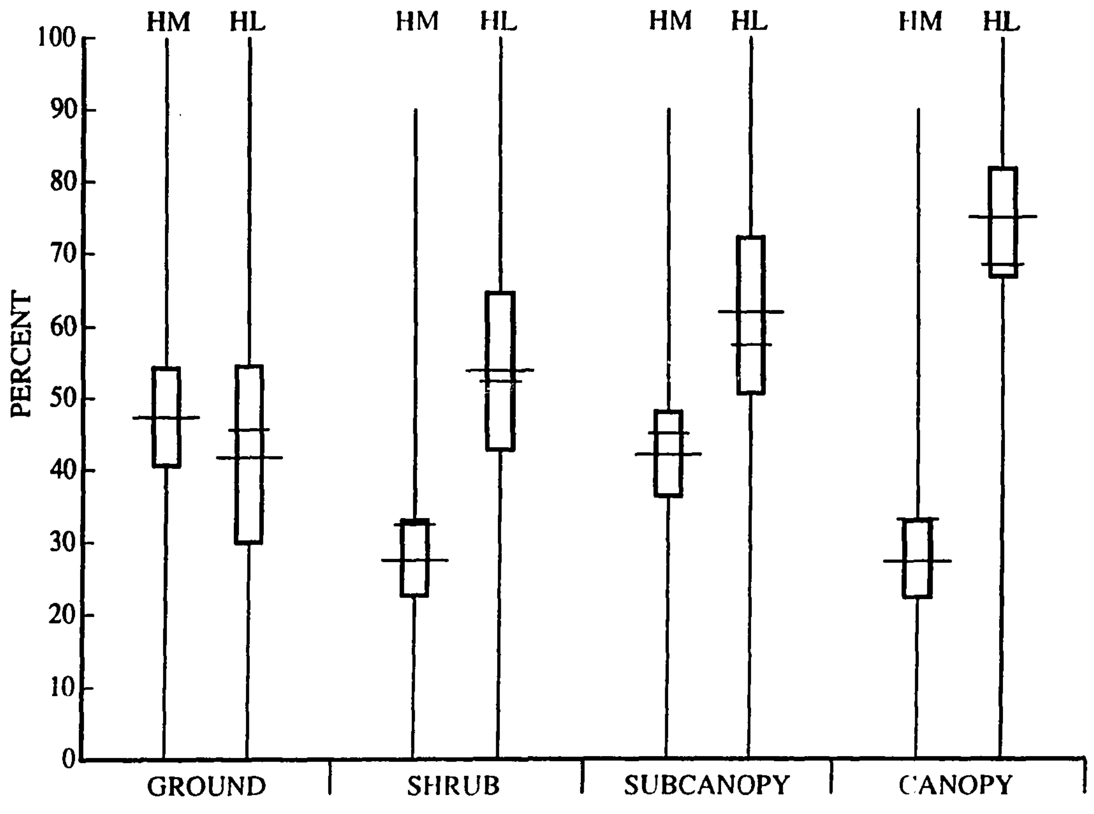


Figure 47. Foliage density use by Hooded Warblers in forest of Louisiana and rain forest of Mexico.

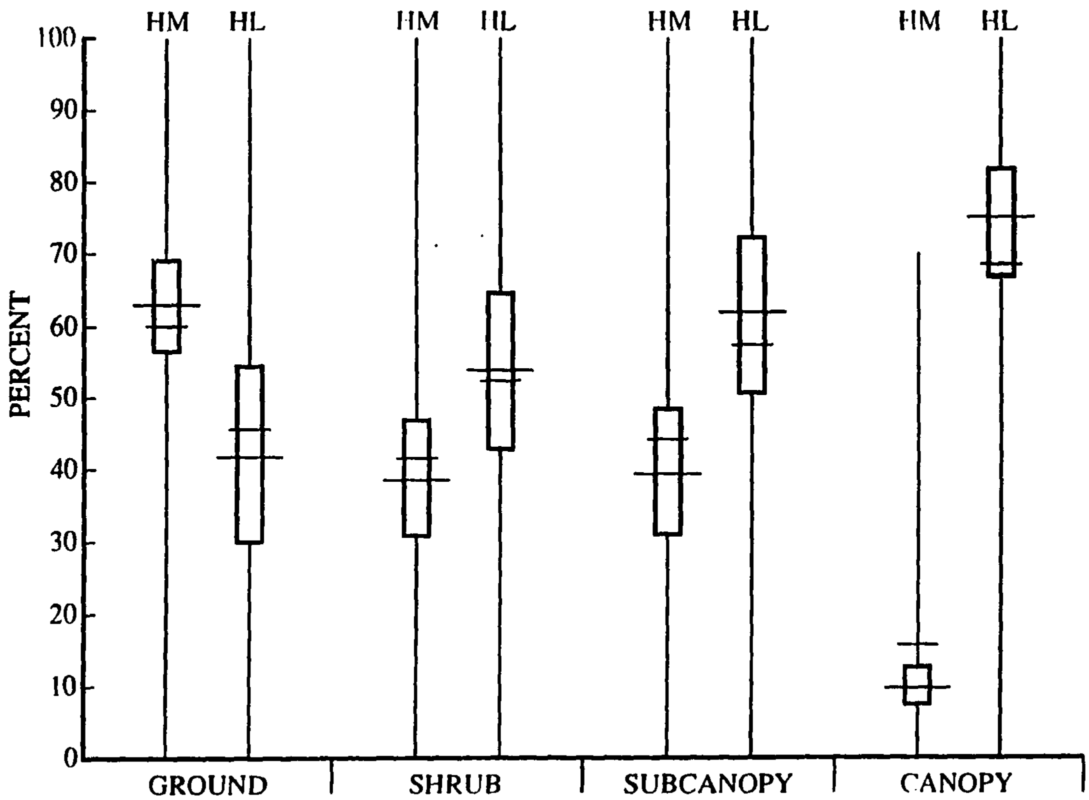


Figure 48. Foliage density use by Hooded Warblers in Louisiana forest and Mexico disturbed forest/field.

"Sallying" was relatively frequent in Winter, whereas "flush-pursuits" and "gleaning" were move prevalent in summer. Results were similar when data only from forest sites were used. I found a significant difference in the relative proportion of maneuvers employed in the two Mexican habitats ($G = 26.38$; $df = 5$; $n = 29, 93$; $p = .0001$). The "sally" maneuver was used more often in the disturbed forest/field area (40 vs 19%) than in the rain forest, but the "sally-glean" comprised 48 percent of the maneuvers in the forest and only 23 percent in the more open areas.

The mean foraging rate of feeding birds during the breeding season (2.9 attempts/min., $SD = 1.7$, Range = 0.6 - 8.4, min. = 82.01, n [sequences] = 58) was not significantly different ($t = 1.25$, $df = 157$, $p = .213$) from that during the Winter (3.3 attempts/min., $SD = 2.1$, Range = 0.7 - 9.6, min. = 155.28, $n = 101$). On the wintering grounds my impression was that Hooded Warblers seemed to spend a greater proportion of their day foraging (Barrow and Hamilton, pers. obs.), but I did not quantify time-activity budgets.

Foraging Substrates.- Substrate use differed between seasons (Figure 51.; $G = 25.11$, $df = 7$, $p = .001$). Hooded Warblers foraged primarily from live leaves (57%) in Summer (Figure 51.). Branches, twigs, and air accounted for an additional 34 percent of the substrates used. During the Winter, however, foraging attempts were more evenly distributed among available substrates (Figure 51.). Slash, litter, herbs, and air were used more frequently on the wintering grounds (Figure 51.).

Frequencies of substrate use differed significantly at the Mexican ($G = 31.92$; $n = 29, 93$; $df = 7$; $p = .0001$) and Louisiana forest sites ($G = 17.29$; $n = 70, 93$; $df = 7$; $p = .016$). The almost exclusive use of slash and herbs in Mexico accounted for much of the

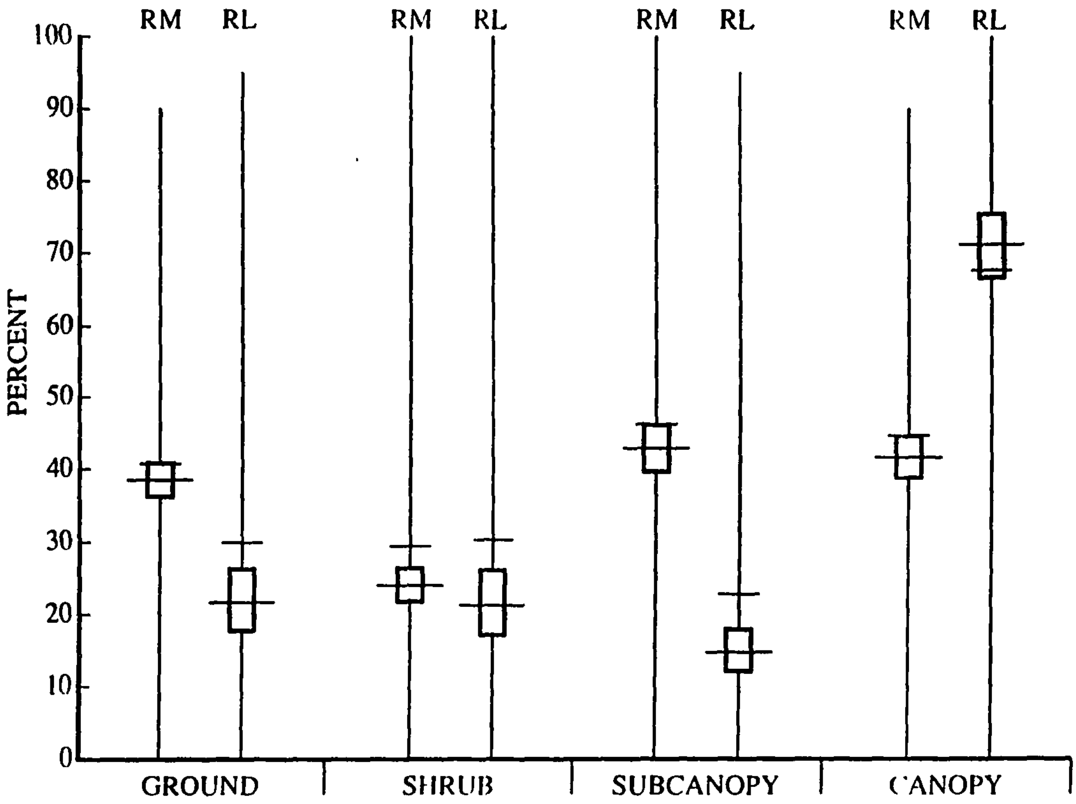


Figure 49. Forest foliage density of four height strata in Louisiana and Mexico.

difference (17 vs 1%). Litter (11 vs 4%) and air (44 vs 22%) were frequently used in the disturbed forest/field, and leaves (11 vs 42%) were used more in the interior rain forest.

When foraging from leaves, Hooded Warblers usually used the lower surfaces, but did so in Louisiana more than in Mexico (Winter: lower = 68%, upper = 32%; Summer: lower = 88%, upper = 12%; $G = 8.52$; $n = 117, 116$; $df = 1$; $p = .004$]).

Several insectivorous bird species in the Neotropics, including migrants, use dead leaves as a foraging substrate (Remsen and Parker 1984, Greenberg 1987). Dead-leaf clumps often become suspended in understory palms and shrubs, and are readily available to birds searching for arthropods. I found that Hooded Warblers used dead leaves infrequently (Winter: live = 89%, dead = 11%; Summer: live = 95%, dead = 5%) ($G = 1.36$, $n = 140, 127$; $df = 1$; $p > .05$).

Foraging Height Distribution.- Hoodeds foraged higher at the Louisiana site (5.4 m, $SD = 3.9$) than at the Mexico site (2.0 m, $SD = 3.0$) (Figure 52.; pooled: $G = 52.52$, $df = 3$, $p = .0001$; forest: $G = 40.82$; $n = 122, 90$; $df = 3$, $p = .0001$). Substrate height (mostly slash piles, shrubs, and trees) also differed significantly (Figure 53.; pooled: $G = 71.63$, $df = 3$, $p = .0001$; forest: $G = 55.40$; $n = 122, 90$; $df = 3$; $p = .0001$); higher substrates were used more frequently at Tensas (12.2 m, $SD = 7.6$) than Mexico (4.8 m, $SD = 6.7$).

In Mexico, foraging height distributions in the forest differed significantly from those in disturbed forest/field ($G = 12.73$; $n = 93, 29$; $df = 3$; $p = .005$). The average foraging height in the forest was 2.1 m (SD = 3.0), whereas the mean foraging height in the disturbed forest/field was 1.7 m (SD = 3.0). however, there was no significant difference in the distributional use of substrate heights

between the two habitats (G = 4.01; n = 93, 29; df = 3; p = .260).

Spherical Vegetation Density.- Hooded Warblers foraged within denser foliage (as measured in the imaginary 1-m sphere surrounding a bird) in Louisiana (31.2%, *SD* = 23.3) than in both Mexican habitats (15.7%, *SD* = 17.5) (Figure 54.; *G* = 18.28, *df* = 2, *p* = .0001) and in rain forest alone (18.0%, SD = 17.2) (*G* = 15.13; *n* = 93, 90; *df* = 2; *p* = .001). In Mexico, the mean vegetation density at foraging sites was greater in forest (18.0%, *SD* = 17.2, *n* = 93) than in the more open, patchy disturbed area (8.6%, *SD* = 16.8, *n* = 29) (G test not valid, 33% of cells have expected counts less than 5).

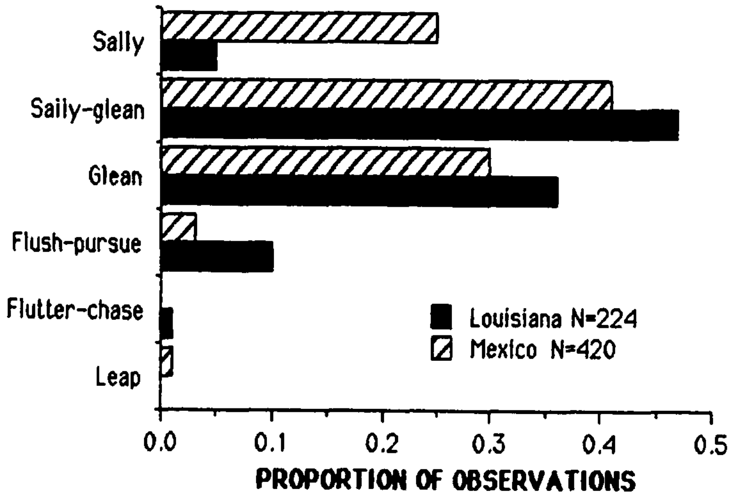


Figure 50. Relative frequency of foraging maneuvers of Hooded Warblers in Louisiana and Mexico.

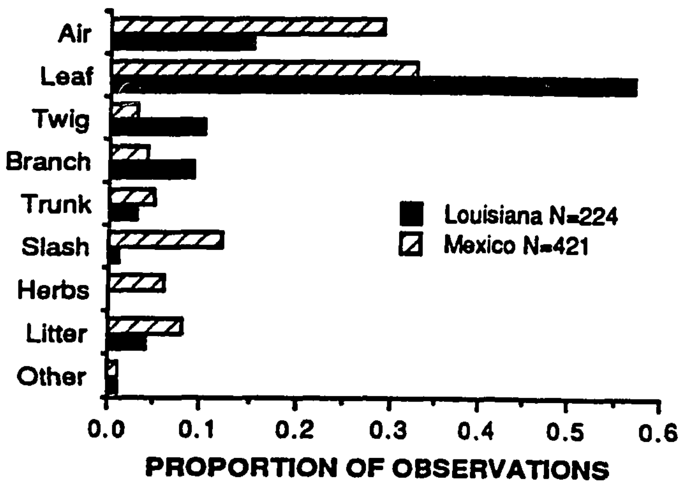


Figure 51. Relative frequency of foraging substrates of Hooded Warblers in Louisiana and Mexico.

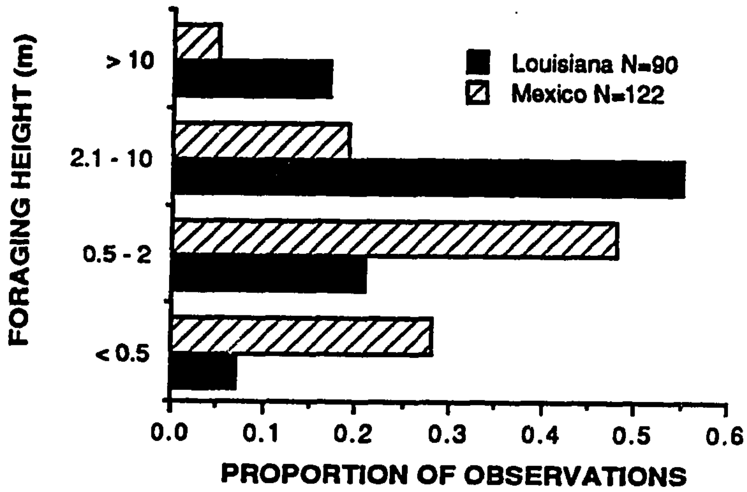


Figure 52. Relative frequency of foraging heights of Hooded Warblers in Louisiana and Mexico.

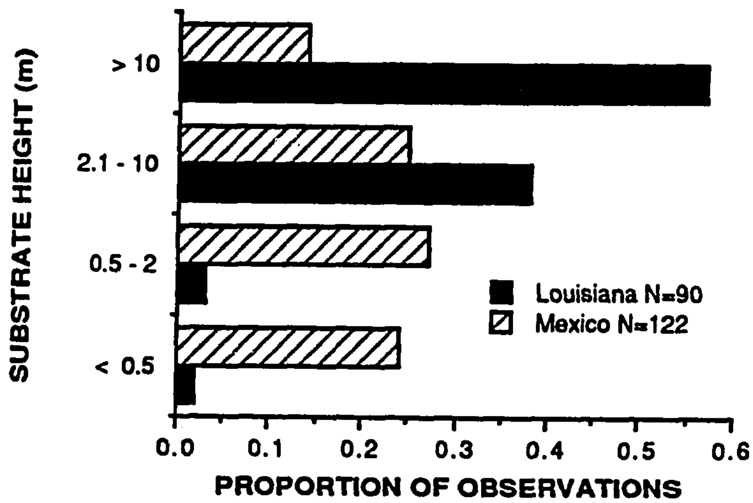


Figure 53. Relative frequency of substrate heights of Hooded Warblers in Louisiana and Mexico.

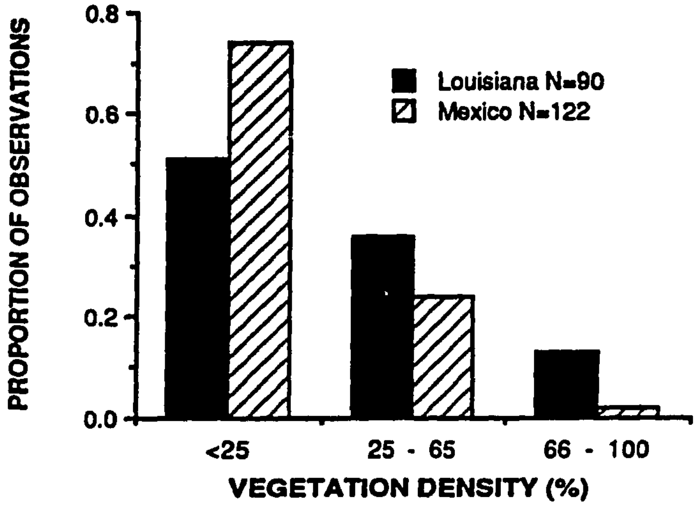


Figure 54. Relative frequency of spherical vegetation density of Hooded Warblers in Louisiana and Mexico.

Geographical and Seasonal Comparison of Foraging Behavior.- Foraging behavior of the Hooded Warbler in Mexico differed from that in Louisiana. I found that foraging height and foraging substrate were the variables that differed most between Summer and winter (Table 25.) as did Hutto (1981) in his comparison of foraging among four western warblers. The mean foraging overlap for the four species of western warblers that Hutto (1981) studied was 0.94, whereas our value for the Hooded Warbler was 0.80. Thus, relative to these four warblers, Hoodeds demonstrate greater seasonal plasticity in their use of foraging maneuvers. Vegetation variables (vegetation density surrounding a foraging bird and canopy cover) were not as variable seasonally (Table 25.).

FLOCK ATTENDANCE

Mixed-species Flocks.- Powell (1980:478) did not report that Hooded Warblers join mixed-species flocks, however, I found them in the Sierra de Los Tuxtlas, where they were present in 23% of the 96 mixed-species flocks observed (Table 26.). Thirty-one percent of all Hoodeds encountered on walks through forest were in a mixed-species flock. Hoodeds usually joined flocks as the flocks moved close to or through the Hoodeds' territories (Rappole and Warner 1980, pers. obs.). I do not know if "floaters" joined flocks more frequently than "territory" holders.

Six species were associated with Hooded Warblers in flocks (Table 26.) more than expected. All are considered understory species in the Sierra de Los Tuxtlas. Thus, Hoodeds apparently attended those flocks that used understory vegetation.

Table 25. Overlap of foraging variables between Summer and Winter study sites of the Hooded Warbler. Overlap values vary from 0 (no correspondence) to 1 (complete correspondence).

Variable	Overlap value
Foraging maneuver	.80*
Foraging substrate	.64**
Foraging height	.52**
Substrate height	.54**
Vegetation density	.85**
Canopy Cover	.77*

* = $p < 0.05$, G tests.

** = $p < 0.001$, G tests.

Table 26. Occurrence of common flocking species (> 0.10 frequency) in all mixed-species flocks (n = 96), in flocks with Hooded Warblers (n = 22), and expected number in flocks with Hooded Warbler.

Species	Number in all flocks	Number with Hooded Warbler(s)	Expected with Hooded Warbler(s)
Golden-fronted Woodpecker	9	0	2.1
Olivaceous Woodcreeper	14	1	3.2
Eye-ringed Flatbill	22	6	5.0
Stub-tailed Spadebill	15	4	3.4
Sulphur-rumped Flycatcher	9	0	2.1
Band-backed Wren	10	2	2.3
Spot-breasted Wren	12	2	2.8
White-breasted Wood-Wren	12	8	2.8
Blue-gray Gnatcatcher	28	4	6.4
White-eyed Vireo	12	3	2.8
Yellow-throated Vireo	11	3	2.5
Tawny-crowned Greenlet	12	3	2.8
Lesser Greenlet	32	5	7.4
Northern Parula	8	0	1.8
Magnolia Warbler	44	11	10.1
Black-throated Green Warbler	41	5	9.4
Black-and-White Warbler	44	9	10.1
American Redstart	32	7	7.3
Worm-eating Warbler	13	5	3.0
Kentucky Warbler	5	4	1.2
Wilson's Warbler	46	13	10.5
Golden-crowned Warbler	46	12	10.5
Yellow-throated Euphonia	10	0	2.3
Red-crowned Ant-Tanager	9	1	2.1
Red-throated Ant-Tanager	8	2	1.8
Habia Sp.	11	2	2.5
Summer Tanager	8	0	1.8

Table 27. Frequency of occurrence of common flocking species (> 0.10 frequency) attending all army ant swarms (n = 15), and attending swarms with Hooded Warblers (n = 11).

Species	Frequency at all swarms	Frequency at swarms with Hooded Warblers
Tawny-winged Woodcreeper	.33	.27
Olivaceous Woodcreeper	.13	.18
Barred Woodcreeper	.20	.27
Ivory-billed Woodcreeper	.27	.27
Eye-ringed Flatbill	.13	.18
Stub-tailed Spadebill	.20	.27
Bright-rumped Attila	.20	.09
Spot-breasted Wren	.33	.45
White-breasted Wood-Wren	.67	.82
Wood Thrush	.20	.27
White-throated Robin	.13	.18
Black-and-White Warbler	.20	.27
Ovenbird	.20	.18
Kentucky Warbler	.60	.73
Golden-crowned Warbler	.60	.64
Gray-headed Tanager	.27	.36
Red-throated Ant-Tanager	.73	.73

Army Ant Flocks.- Hooded Warblers were recorded attending 11 of the 15 army ant (*Eciton burchelli* and *Labidus praedator*) swarms observed. The White-breasted Wood-Wren (*Henicorhina leucosticta*), Golden-crowned Warbler (*Basileuterus culicivorus*), Red-throated Ant-Tanager (*Habia fuscicauda*), and Kentucky Warbler (*Oporornis formosus*) also frequently attended army ant swarms (Table 27.).

Flocking Birds, Foraging, and Microhabitat.- In rain forest habitat of Mexico, the foraging behavior ($G = 1.03$; $n = 226, 71$; $df = 5$; $p = 0.960$) and substrate use ($G = 6.03$; $n = 227, 71$; $df = 7$, $p = 0.536$) of Hooded Warblers attending flocks was not significantly different than that of Hoodeds foraging solitarily. We observed Hoodeds foraging on live bark substrate (trunk, branch, and twig) (21%) and leaf-litter (17%) more in flocks than when alone (10 and 6%, respectively); solitary birds used dead bark substate (slash) more frequently (13 vs. 4%). Flock-attending birds also used leaf litter on the ground more (17 vs 3 %) than did solitary foraging birds.

Hooded Warblers in flocks may have tended to forage more often in the ground layer (0 - 0.5 m) (45 vs 27%), and solitary foraging birds may have utilized the shrub layer (0.5 - 2 m) more often (48 vs 18%) ($G = 6.80$; $n = 71, 22$; $df = 3$; $p = .08$), but substrate heights were similar ($G = 0.54$; $n = 71, 22$; df = 3; $p = .91$). The vegetation density (within a 1-m diameter sphere) did not differ significantly with flocking ($G = 2.92$; $n = 71, 22$; $df = 2$; $p = 0.23$); however, there was a significant difference in canopy cover ($G = 11.51$; $n = 71, 22$; $df = 2$; $p = .003$); those in flocks used our densest cover class (66 - 100%) more frequently (82 vs 49%). Perhaps the affinity of solitary foraging birds for fallen debris within the forest (i. e., canopy gaps) can account for the difference, or army ants might prefer areas with dense canopy cover.

DISCUSSION

MACROHABITAT USE

Our study was conducted within the core areas of the Hooded Warbler's Winter (Figure 39.) and breeding ranges (Remsen and Parker 1983:226), and took place in typical, if not optimal, habitat.

Long-distance migratory birds, especially small insectivores, that breed in mature forest are also generally thought to be restricted to interior forest on their wintering grounds (Terborgh 1980, Rappole and Morton 1985). Hooded Warblers predominantly occurred in mature forest during the Winter, but also consistently used disturbed habitats. These findings concur with those of Lynch (1989) in the Yucatan Peninsula and Waide(1980) in southern Campeche, where Hoodeds routinely used secondary habitats in addition to mature tropical forest. Green et al. (1987) reported that in the Yucatan Peninsula, Hoodeds begin to colonize regenerating old fields that are 3 to 4 years in successional age. Robbins et al. (1987) surveyed numerous sites in the West Indies, Central America, and northern South America, and found that overwintering North American migrants restricted to extensive forests during the breeding season are just as common in small fragments as in extensive forests in Winter. Rappole and Morton (1985) examined the effects of disturbance on a mature forest tract in the vicinity of our study sites, and found that the number of Hooded Warblers declined from 22.5 captures before partial clearing to 17.5 captures after logging (Powell and Rappole 1986). This is not a drastic decline, and perhaps not a real decline at all. however, they presented evidence that many of the Hoodeds in the disturbed area in 1980-81 were "nomads" and thus may have had lower survival rates. I also found that mature forest had more "territorial" individuals than forest edge birds (3.5/km vs. 1.4/km)

or disturbed forest/field birds (0.9/km). The relationship between survival rates and habitat is an important question and should be the focus of future studies.

Within both forested and disturbed habitats, Hooded Warblers frequently used specific habitat features. On the wintering grounds, slash piles, fallen trees, and fallen branches were heavily used. Forest gaps created by small-scale disturbances are natural features of forests in the tropics (Whitmore 1978) and temperate regions (Runkle 1985). Presumably because of high primary productivity and a rich supply of fruits and arthropods, treefall gaps have been shown to attract migrant, as well as resident birds (Willson et al. 1982, Martin and Karr 1986). Hoodeds frequented slash piles and treefalls in the gaps as well as in cleared fields near forest edges; fallen debris seems to be an important habitat feature.

MICROHABITAT USE

In the rain forest of Mexico, Hooded Warblers foraged in the shrub and subcanopy strata in foliage with densities in concordance with availability; 65% of foraging observations were in these strata (Figure 52.). Hoodeds do not appear to be very selective in their Winter microhabitat. The increased use of the ground stratum in Winter may be in response to foraging in proximity to army ant swarms, as opposed to a preference for a particular foliage density. That Hoodeds preferred denser foliage than the average available in the disturbed areas is not surprising because of the mosaic of open and wooded areas there. Hoodeds seemed to prefer between 30 and 45% foliage density in the shrub and subcanopy strata and foraged in areas with those densities no matter where they occurred: closed forest or mixed areas with the proper foliage densities available.

On the breeding grounds, Hoodeds are highly selective, and prefer

denser foliage than randomly available in the ground through subcanopy layers. The foliage density used by Hoodeds in the shrub and subcanopy strata ranged from 52 to 57%; over 93% of Hooded Warbler foraging observations were in these two strata. These densities must be optimum in the places where I studied Hoodeds because there was a much wider range available and Hoodeds apparently selected them (Hilden 1965, James 1971).

A representation of the "niche-gestalt" of the microhabitat of Hoodeds in Arkansas is illustrated in James (1971:219). This graphic representation seems to us to match the configuration of a single treefall gap approximately 4 - 10 yrs old and is consistent with many previous references [see Introduction]. Because microhabitat data for Hoodeds in Louisiana also fit this pattern of dense foliage in the ground through subcanopy of mature forests, I propose that Hooded Warblers routinely use "old" treefall sites in mature forest. Most treefall locations in our bottomland hardwood forest study area are the result of "tree-snaps" from high winds (Barrow unpubl. data). In these areas, fallen debris usually consists of large branches, tree-tops, or entire trees. Canopy closure results from lateral expansion of the existing, adjacent canopy, or upward growth of saplings. After several years, the understory vegetation in these gaps consists of briar patches and young sapling thickets, and the subcanopy is often dominated by fast growing vines that respond to the increased light intensity. In Louisiana, 39% of all foraging attempts (n = 224) were directed at vines, mostly *Berchemia scandens* and *Rhus radicans* (Barrow unpubl. data). In 8-yr. old gaps of the Smoky Mountains National Park, replacement trees averaged 10 m tall (the upper limit of our subcanopy strata) and were beginning to close the canopy (Barden 1989). Because gaps used by Hoodeds at Tensas

were usually closed, most gap-induced "thickets" used by Hoodeds in the Tensas River Basin were probably 8-yrs. old or older. Blackmore (1895) was perhaps the first to note the association of small gaps and Hooded Warbler distribution:

> "... these woods are thickly filled with a low growth of common cane, and here in the more open spots are immense, impenetrable thickets of blackberries. Although the Hooded Warbler seems to prefer the deeper woods for feeding and song, nearly all nests are built on the edge of an opening or clearing just within the shadow of the trees, possibly because the undergrowth is thicker in such spots and affords better concealment for the mother bird and her home."

Mossman and Lange (1982) described Hooded Warbler habitat in a northern section of its breeding range (Wisconsin):

> "In all cases this species was found in or near a brushy opening, created by logging or the 2-lined chestnut borer, within extensive woods. These openings varied in size from ca 0.03 - 1 ha. Every locality had thinly scattered trees with a dense understory of shrubs, brambles, and saplings. In large, mesic woods almost every such opening was included in a Hooded Warbler territory...". [Also see other references given in introduction.]

The preference for dense thickets within mature forests may be related to nest-site selection. All nests observed in the Tensas River Basin were located in dense thickets within extensive forest. The affinity for dense foliage may also be related to foraging efficiency. Population eruptions of lepidopteran larvae in the Spring may cause Hoodeds to spend more time searching dense foliage, as opposed to using ground or aerial feeding methods. In addition, Hoodeds may be most efficient (sally-gleaning) in vegetation of that thickness.

FORAGING ECOLOGY

Hooded Warblers differed in their foraging behavior between

Tensas and Los Tuxtlas. At Tensas they capture prey primarily from the lower surfaces of leaves in dense foliage of shrubs and subcanopy. In Los Tuxtlas, they become more generalized and capture prey from air and leaves in almost equal proportion and use a variety of other substrates as well as forage in more-open portions of the lower strata of the forest. In Veracruz, Keast(1980) observed Hoodeds foraging in creek-edge vegetation, low shrubs, and sometimes from the ground. Blackburnian (*Dendroica fusca*) and Black-throated Green (*D. virens*) Warblers are also more generalized in their foraging behavior during the Winter (Chipley 1980, Rabenold 1980).

My results are consistent with those reported from Bennett's (1980:328-9) comparative study between Tennessee and Chiapas, Mexico . In Tennessee, Hoodeds "sally- or perched-gleaned" leaves 82% of the observations (n = 63) and no "aerial-hawking" was observed. Over 65% of the observations were above 3.1 m. In Mexico, Hoodeds captured prey in the air 35% of the time (n = 96), and 95% of observations were below 2.8 m. It is possible that the Winter season has played an important role in shaping certain aspects of Hooded Warbler morphology (bill width and rictal bristles, e. g.).

I have demonstrated that Hooded Warblers use small-scale natural disturbances in forest interiors as well as secondary habitats in Mexico. In addition, Hoodeds also attended army ant swarms regularly, and occasionally joined mixed-species flocks. Willis (1966) also observed Hoodeds foraging in low vegetation and capturing prey from the ground while attending army ant swarms in Belize. Thus the Hooded Warbler utilizes a larger proportion of the habitat in Winter and is more flexible in the habitat used

then. I suggest that the observed differences in foraging behavior between seasons are in response to structural differences in microhabitats used by Hoodeds, Winter social behavior, and possibly a change in prey abundance, distribution, or visibility; although I do not have data to support the latter. The switch to nonfoliage insects (aerial and ground) may also be related to low arthropod abundance associated with understory foliage during the Winter (Greenberg 1984). Hoodeds capture 33 percent of their prey from foliage in winter and more than 55 percent from foliage in the Summer, and also had a high seasonal overlap value (0.85) in the density of vegetation used in Summer and Winter. The distribution and density of foliage must be important habitat variables for Hooded Warblers (Morton 1980).

LITERATURE CITED

Alvarez del Toro, M. 1958. Lista de las especies de aves que habitan en Chiapas: Endemicas, emigrantes y de paso. Revista de la Soc. Mex. de Hist. Nat. 19: 73-113.

American Ornithologists'Union. 1983. Checklist of North American Birds, Sixth Ed. Amer. Ornithol. Union, Washington, D. C.

Anderson, S. H., and H. H. Shugart, Jr. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55: 828-837.

Arthur, S. C. 1931. The Birds of Louisiana. Louisiana Dept. of Conservation, New Orleans.

Audubon, J. J. 1831. Ornithological Biography. A. Black, Edinburgh.

Bailey, H. H. 1925. The Birds of Florida. Williams and Wilkins Co., Baltimore.

Barbour, T. 1943. Cuban ornithology. Memoirs of the Nuttall Ornithol. Club 9: 1-144.

Barden, L. S. 1989. Repeatability in forest gap research: studies in the Great Smoky Mountains. Ecology 70: 546-547.

Bennett, S. E. 1980. Interspecific competition and the niche of the American Redstart (*Setophaga ruticilla*) in wintering and breeding communities. Pp. 319-335 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S. Morton (eds.). Smithsonian Inst. Press, Washington, D. C.

Bent, A. C. 1953. Life Histories of North American Wood Warblers. U. S. Nat. Mus. Bull. no. 203, U. S. Govt. Printing Office, Washington, D. C.

Berrett, D. G. 1962. The birds of the Mexican State of Tabasco. Ph. D. dissertation, Louisiana State Univ., Baton Rouge.

Binford, L. C. 1989. A Distributional Survey of the Birds of the Mexican State of Oaxaca. Ornithol. Monogr. 43, Amer. Ornithol. Union, Washington D. C.

Blackmore, A. B. 1895. The Hooded Warbler. Oologist 12: 119-121.

Brennan, L. A., W. M. Block, and R. J. Gutierrez. 1987. Habitat use by Mountain Quail in northern California. Condor 89: 66-74.

Brooks, M. 1940. The breeding warblers of the central Allegheny mountain region. Wilson Bull. 52: 249-266.

Burleigh, T. D. 1958. Georgia Birds. Univ. of Oklahoma Press, Norman.

Cadman, M. D., P. F. J. Eagles, and F. M. Helleiner. 1987. Atlas of the Breeding Birds of Ontario. Univ. of Waterloo Press, Ontario.

Chipley, R. M. 1980. Nonbreeding ecology of the Blackburnian Warbler. Pp. 309-317 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S. Morton (eds.). Smithsonian Inst. Press, Washington, D. C.

Coates-Estrada, R., A. Estrada, D. Pashley, and W. Barrow. 1985. Lista de los Aves de la Estacion de Biologica, Los Tuxtlas. Instituto de Biologia, Direccion General de Publicaciones de la Universidad Nacional Autonomia de Mexico, Mexico, D. F.

Cooke, N. W. 1904. Distribution and Migration of North American Warblers. USDA, Biol. Surv. Bull no. 18, Govt. Printing Office, Washington, D. C.

Davie, O. 1898. Nests and Eggs of North American Birds, 5th ed. David McKay, Philadelphia.

Dawson, W. L. 1903. The Birds of Ohio. The Wheaton Publ. Co., Columbus, Oh.

Dickson, J. G., and R. E. Noble. 1978. Vertical distribution of birds in a Louisiana bottomland hardwood forest. Wilson Bull. 90: 19-30.

Eaton, E. H. 1914. Birds of New York. Univ. of the State of New York, Albany.

Forbush, E. H. 1929. Birds of Massachusetts and Other New England States. Mass. Dept. of Agric., Part III, Norwood Press, Norwood, Mass.

Gomez-Pompa, A. 1987. Tropical deforestation and Maya silviculture: an ecological paradox, Pp. 19-37 *in* Tropical Forests: Conservation and Uses. Tulane Studies in Zoology and Botany, Vol. 26, no.1, Tulane Univ., New Orleans.

Graber, J. W., R. R. Graband E. L. Kirk. 1983. Illinois Birds: Wood Warblers. Ill. Nat. Hist. Surv. Biol. Notes no. 118, Dept. of Energy and Nat. Res., Champaign, Ill.

Greenberg, R. 1979. Body size, breeding habitat, and Winter exploitation systems in *Dendroica*. Auk 96: 156-766.

Greenberg, R. 1987. Seasonal foraging specialization in the Worm-eating Warbler. Condor 89: 158-169.

Grimes, S. A. 1935. The Hooded Warbler in Florida. Fla. Natur. 8: 16-22.

Griscom, L. 1926. The ornithological results of the Mason-Spinden expedition to Yucatan. I. Introduction: Birds of the winland of eastern Yucatan. Amer. Mus. Novitates 235:1-19.

Hall, G. A. 1983. West Virginia Birds. Carnegie Museum of Natural History Spec. Publ. no. 7, Pittsburgh.

Hamel, P. B., H. E. LeGrand, Jr., M. R. Lennartz, and S. A. Gouthreaux. 1982. Bird-habitat Relationships. USDA, For. Serv. Gen. Tech. Rep. SE-22, Asheville, North Carolina.

Hilden, O. 1965. Habitat selection in birds: a review. Ann. Zool. Fenn. 2: 53-75.

Hilty, S. L., and W. L. Brown. 1986. A Guide to the Birds of Colombia. Princeton Univ. Press., Princeton, New Jersey.

Howell, A. H. 1924. Birds of Alabama. Alabama Dept. of Fish and Game, Montgomery.

Howell, A. H. 1932. Florida Bird Life. Fla. Dept. of Game and Freshwater Fish, Concord-McCaan, New York.

Hutto, R. L. 1981. Seasonal variation in the foraging behavior of some migratory western Wood Warblers. Auk 98: 705-777.

James, F. C., R. F. Johnston, N. O. Wamery, G. J. Niemi, and W. J. Boecklen. 1984. The Grinnellian niche of the Wood Thrush. Am. Natur. 124: 17-34.

James, F. C. 1971. Ordination of habitat relationships among breeding birds. Wilson Bull. 88: 215-236.

Keast, A. 1980. Spatial relationships between migratory Parulid warblers and their ecological counterparts in the Neotropics. Pp. 109-132 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S.. Marton (eds.). Smithsonian Inst. Press, Washington, D. C.

Land, H. C. 1963. A collection of birds from the Caribbean lowlands of Guatemala. Condor 65: 49-65.

Land, H. C. 1970. Birds of Guatemala. Livingston Publ. Co., Wynnewood, Penn.

Lynch, J. F., E. S. Morton, and M. E. Van der Voort. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (Wilsonia citrina). Auk 102: 714-721.

Lynch, J. F. 1989. Distribution of over wintering Nearctic migrants in the Yucatan Peninsula, I: general patterns of occurrence. Condor 91: 515-544.

MacDonald, P. O., W. E. Frayer, and J. K. Clauser. 1979. Documentation Chronology, and Future Projections of Bottomland Hardwood Habitat Loss in the Lower Mississippi Alluvial Plain, 2 fools. U. S. Fish and Wildlife Service, Washington, D. C.

Martin, T. E., and J. R Karr. 1986. Patch utilization by migrating birds: resource oriented? Ornis Scand. 17: 165-174.

Meanley, B. 1971. Natural History of Swainson's Warbler. U. S. Dept. of Interior, Bur. of Sport Fish. and Wild., N. A. Fauna no. 69, Washington, D. C.

Mengel, R. M. 1965. The Birds of Kentucky. Ornith. Monogr. no 3, Amer. Ornithol. Union, Washington, D. C.

Meyer de Schauensee, R., and W. H. Phelps, Jr. 1978. A Guide to the Birds of Venezuela. Princeton Univ. Press, Princeton, N. J.

Miranda, F., and E. Hernandez. 1963. Los tipos de vegetation de Mexico y su clasificacion. Bol. Soc. Bot. Mex. 29: 29-179.

Monroe, B. L., Jr. 1968. A Distributional Survey of the Birds of Honduras. Ornithol. Monogr. 7, Amer. Ornithol. Union, Washington, D. C.

Morse, D. H. 1980. Population limitation: breeding or wintering grounds? Pp. 505-516 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S. Morton (eds.), Smithsonian Inst. Press, Washington, D. C.

Moser, E. B.., W.C. Barrow, and R. B.. Hamilton. In Press. An exploratory use of correspondence analysis to study relationships between avian foraging behavior and habitat, Pp.309-319 *in* Food Exploitation by Terrestrial Birds, M. L.. Morrison, C. J. Ralph, and J. Verner (eds), Studies in Avian Biology, Cooper Ornith. Soc., Allen Press, Lawrence, Kansas.

Mossman, M. J., and K. I. Lange. 1982. Breeding Birds of the Baraboo Hills, Wisconsin: Their History, Distribution, and Ecology. Dept. of Nat. Res. and Wisconsin Soc. for Ornith., Madison.

Nations, J. D. 1987. Mesoamerica's tropical rain forest conflicts and conservation. Pp. 59-75 *in* Tropical Forests: Conservation and Uses, Tulane Studies in Zoology and Botany, Vol. 26, no.1, Tulane Univ., New Orleans.

Oberholser, H. C. 1974. The Bird Life of Texas. Vol. 2, Univ. of Texas Press, Austin.

Oberholser, H. C. 1938. The Bird Life of Louisiana. Dept. of Conserv. Bull. no. 28, New Orleans.

Odum, E. P. 1931. Notes on the nesting habitats of the Hooded Warbler. Wilson Bull. 43: 316-317.

Pashley, D. N. and R. B. Hamilton. 1989. Warblers of the West

Indies III. The Lesser Antilles. Carib. J. Sci. In Press.

Paynter, R. A., Jr. 1955. The ornithogeography of the Yucatan Peninsula. Bull. Peabody Mus. Nat. Hist., Yale Univ. 9: 1-347.

Peck, G. K., and R. D. James. 1987. Breeding Birds of Ontario: Nidiology and Distribution, Vol. 2, Passerines. Misc. Publ., Royal Ontario Museum, Ontario.

Powell, G. V. N., and J. H. Rappole. 1985. The Hooded Warbler. Pp. 827-853 *in* Audubon Wildlife Report 1986, R. L. Disilvestro (ed), Nat. Aud. Soc., New York.

Rabenold, K. N. 1980. The Black-throated Green Warbler in Panama: geographic and seasonal comparison of foraging. Pp. 297-307 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S.. Morton (eds.). Smithsonian Inst. Press, Washington, D. C.

Raffaele, H. A. 1983. A guide to the birds of Puerto Rico and the Virgin Islands. Fondo Educativo Interamericano, San Juan.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pp. 353-394 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S. Morton (eds.), Smithsonian Inst. Press, Washington, D. C.

Rappole, J. H., E. S. Morton, T. E. Lovejoy, III, and J. L. Ruos. 1983. Nearctic Avian Migrants in the Neotropics. U. S. Dept. of Interior, U. S. Fish and Wildlife Service, Washington, D. C.

Rappole J. H., and E. S. Morton 1985. Effects of habitat alteration on a tropical avian forest community. Pp. 1013-1023 *in* Neotropical Ornithology, P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (eds.). Ornith. Monogr. no. 36, Amer. Ornithol. Union, Washington, D. C.

Remsen, J. V., Jr., and T. A. Parker, III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15: 223-231.

Ridgway, R. 1878. Notes on birds observed at Mount Carmel, southern Illinois, in the Spring of 1878. Nutt. Ornith. Club Bull. 3: 162-166.

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

Robertson, W. B., Jr. 1962. Observations on the birds of St. John, Virgin Islands. Auk 79: 44-76.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63: 1918-1931.

Runkle, J. R. 1985. Disturbance regimes in temperature forests.

Pp. 17-33 *in* The Ecology of Natural Disturbance and Patch Dynamics, S. T. A. Pickett and P. S. White (eds.). Academic Press, New York.

Russell, S. M. 1964. A Distributional Study of the Birds of British Honduras. Ornithol. Monogr. 1, Amer. Ornithol. Union, Washington, D. C.

SAS Institute, Inc. 1988. SAS/STAT User's Guide Release 6.03 Edition. SAS Inst., Cary, N. C.

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patch habitats. Ecology 51: 408-418.

Slud, P. 1964. The birds of Costa Rica, distribution and ecology. Bull. Amer. Mus. Nat. Hist. 128: 1-430.

Slud, P. 1960. The birds of Finca "La Selva" Costa Rica: a tropical wet forest locality. Bull. Amer. Mus. Nat. Hist. 121: 49-148.

Smith, K. G. 1977. Distribution of Summer birds along a forest moisture gradient in an ozark watershed. Ecology 58: 810-819.

Smithe, F. B. 1966. The birds of Tikal. Natural Hist. Press, New York.

Soil Conservation Service. 1982. Soil Survey of Madison Parish, Louisiana. U. S. Dept. Agric., Soil Conserv. Serv., Washington, D. C.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H.. Freeman, San Francisco.

Sprunt, A. Jr., and E. B. Chamberlain. 1949. South Carolina Bird Life. Univ. South Carolina Press, Columbia.

Sprunt, A. Jr. 1954. Florida Bird Life. Coward-McCoan, New York.

Stewart, R. E., and C. S. Robbins 1958. Birds of Maryland and the District of Columbia. U.S. Dept. of Interior, Fish and Wildlife Service, North American Fauna no. 62, Washington, D. C.

Tanner, J. T. 1986. Distribution of tree species in Louisiana bottomland forest. Castanea 51(3): 168-174.

Todd, W. E. C. 1940. Birds of Western Pennsylvania. Univ. Pittsburgh Press, Pittsburgh.

U.S. Fish and Wildlife Service. 1984. Blue ribbon panel for bottomland hardwoods. U. S. Dept. of Interior, Fish and Wild. Serv., Vicksburg, Miss.

Waide, R. B. 1981. Interactions between resident and migrant birds in Campeche, Mexico. Tropical Ecology 22: 134-154.

Wetmore, A., R. F. Pasquiand S. L. Olson. 1984. The Birds of the Republic of Panama. Part 4 - Passeriformes: Hirundinidae (swallows) to Fringillidae (finches). Smithsonian Misc. Coll. 150. Smithsonian Inst. Press, Washington, D. C.

Wetmore, A. 1943. The birds of southern Veracruz, Mexico. Proc. U. S. Nat. Mus. 93: 215-340.

Whitmore, T. C. 1978. Gaps in the forest canopy. Pp. 639-655 *in* Tropical Trees as Living Systems, P. B. Tomlinson and M. H. Zimmermann (eds.). Cambridge Univ. Press, London.

Willson, M. F., E. A. Porter, and R. S. Condit. 1982. Avian frugivore activity in relation to forest light gaps. Carib. J. Sci. 18: 1-6.

Wilson, A. 1808. American Ornithology. Bradford and Inskeep, Philadelphia.

Wood, D. S., and G. D. Schnell. 1984. Distribution of Oklahoma Birds. Univ. of Okla. Press, Norman.

CHAPTER 4. CONCLUSION AND MANAGEMENT NEEDS

CONCLUSION

In order to identify the determinants of avian community organization in the Tensas River Basin, or at any site, one must consider many interacting factors operating at different scales of resolution. Insectivorous birds occupying forest stands at Tensas are dynamic, species appear and disappear within local areas; and abundance of some species fluctuate widely.

Each species appears to use its habitat in a unique fashion. Habitat use patterns of Tensas forest birds are a response to historical occurrences, landscape-level events (e.g., tree falls and logging operations), plant species composition, and avian biogeographic origins (Sabo and Holmes 1983) (i.e., palearctic or permanent residents vs. neotropical or Summer residents). Other important factors, although not directly investigated in this study, that influence the mix of bird species in a particular habitat undoubtedly include the spatial and temporal patterns of occurrence of other species, such as predators, prey,and competitors (Sabo and Holmes 1983).

I acknowledge that many of these relationships are correlational and will require verification. A more complete understanding of why certain combinations of birds occur in a particular habitat will nessitate experimental habitat manipulations (e.g., cooperation with timber harvest operations). Additionally, opportunities exist to benefit from "natural manipulations" of habitat structure; tornadoes and wind-throws are common occurrences in the Tensas Basin. To accurately asses the effects of climate, land use changes, periodic disturbance, and hydrological processes on birds at Tensas, long-term monitoring at

a variety of spatial scales is recommended.

MANAGEMENT NEEDS

Much of the forested land on important breeding and wintering areas has been recently cleared. Remsen and Parker (1983) considered the lowland forest of the Lower Mississippi River Valley to be the Hooded's primary breeding habitat; the species is able to utilize similar situations outside the main drainage. In 1937, there were 5.2 million hectares of forested land in the Mississippi alluvial floodplain south of Kentucky and Missouri. Only 2.9 million hectares remain today (MacDonald et al. 1979). The total annual clearing rate of bottomland hardwood forests in the Lower Mississippi River Valley is about 44,600 ha/yr (U.S. Fish and Wildlife Service 1984). I have shown that southern Mexico lies within the core Winter range of the Hooded Warbler. In Mexico, as of 1981, intact natural vegetation covered less than 40% of Mexico's land area. Tropical evergreen forest had been reduced to half of the original size (Flores-Villela and Fernandez 1989). Myers (1980) estimated the deforestation rate to be about 16,000 km^2/yr. Many bird communities in which Hoodeds occur may continue to face drastic habitat loss under current land use practices (Rappole 1974, Terborgh 1980, Wilcove and Whitcomb 1983, Rappole and Morton 1985, Dickson 1988). Several authors have indicated that local breeding populations of migrant birds are declining in North America (Briggs and Criswell 1979, Robbins 1979, Ambuel and Temple 1982, Lynch and Whigham 1984, Robbins et al. 1989). Steinhart (1984) speculated that declines in numbers of temperate forest breeding migrants is primarily due to tropical deforestation. Rappole and Morton (1985) provided information to support this hypothesis. However, several other investigators

(Willis 1966, Moreau 1972, Karr 1976, Hutto 1980, 1989) have suggested that many migratory species in the tropics do not make heavy use of extensive primary forests, but instead tend to utilize patches of original forests, second growth, and edge habitats. More recently, authors have recognized that some species use a range of both disturbed and undisturbed habitats (Robbins et al. 1987, Hutto 1989, Lynch 1989) and that a diversity of ecological strategies exist among migratory birds (Morton 1980, Greenberg 1984). The alternative explanations for the decline in migrants are related to problems faced on the breeding grounds or on both areas simultaneously (Whitcomb 1977, Hutto 1988). The relative importance of wintering and breeding grounds as limiting habitats may vary with the species under consideration (Baker and Baker 1973, Morse 1980, Holmes et al. 1989). I agree with this assessment and offer the following conservation strategy for Neotropical migratory birds; using the Hooded Warbler as an example:

(1) The precise delineation of a species' geographic range should be the first priority (Hutto 1989). [We have undertaken the investigation of wintering ranges of the migrant North American Parulinae and have begun disseminating the results (Pashley and Martin 1988, Pashley 1988 a, b, c, Pashley and Hamilton ms.)]. Here, I have determined the core wintering and breeding areas for the Hooded Warbler. The Winter range is several times smaller than the breeding range.

(2) The habitat use patterns and relative abundance in major habitat types need to be determined (James et al. 1984). The primary breeding habitat of the Hooded Warbler is the bottomland hardwood forests of the southeastern river valleys, although

forested mountain ravines and streamsides are also important. During the Winter, Hoodeds use their habitat more flexibly. Mature evergreen tropical forest is the primary habitat, although disturbed habitats are also important.

(3) Attempts should be made to determine migratory routes and requirements. Habitat changes along migratory routes may be critical to the survival of some species. The Hooded Warbler apparently uses the Mississippi River Valley as a migration corridor during the Spring (Cooke 1904).

(4) Current availability of potentially usable habitats must be ascertained. A detailed description of how to use remote sensing to evaluate current habitat availability and information on available habitat for the Hooded Warbler in the Yucatan Peninsula has recently been published by Green et al. (1987). Remote sensing can also be used to assess land use changes over time. Attempts should be made to evaluate the extent of past habitat changes so that the present situation can be better understood.

(5) Long-term monitoring plots need to be established within each of the major habitat types occupied throughout the geographic range. These plots should be located on protected sites, such as national wildlife refuges, parks, or biological station grounds. I have established such a plot at the Tensas River National Wildlife Refuge. Other candidate locations appropriate for Hooded Warblers include the Great Smoky Mountains National Park, Los Tuxtlas Biological Station, and the Sian Ka'an Biosphere Reserve, Quintana Roo. As suggested by Wilcove and Terborgh (1984), both marginal and optimal habitats should be included in local monitoring plans.

(6) Management guidelines should be formulated at both the regional and local landscape levels. These guidelines should use information obtained from habitat studies conducted in the region and assimilated into land-use planning efforts whenever possible. For Hooded Warblers I recommend the establishment of natural areas, where the forest can revert to old-growth conditions. Small scale disturbances are a common feature of older forests (Tanner 1986), and should provide optimal habitat for Hooded Warblers. If timber management is a goal, long-term rotation is desirable. The selection cutting system, particularly single-tree selection, is the preferred one due to the resulting resemblance to natural treefall gaps. Land management decisions are based on much different criteria in Mexico and Central America. Gomez-Pompa (1987) suggested a dual system of forest research and development as a solution to deforestation in the tropics. Essentially, his proposal is for an integration of Mayan silviculture and modern forestry practices. This agro-forestry system would provide rural inhabitants with an abundance of forest products for their subsistence, while at the same time preserving biological diversity of the region. The result would be the maintenance of semi-managed natural forests, and areas of forest at varying successional stages (forest regeneration plots), as opposed to the current trend of forest conversion to permanent agriculture and/or regeneration to savanna-like landscapes (i. e., no forest regeneration plan). This seems to be a viable approach, especially in light of the human population expansion in the region (Nations 1987). I believe that it would also be consistent with the needs of the Hooded Warbler and many other migrant warblers.

(7) Studies of survivorship on wintering, migratory, and breeding grounds would be invaluable to those formulating conservation strategies.

In conclusion, I agree with James et al. (1984) that studies of single-species geographical ecology are important in providing information on factors regulating the distribution and abundance of birds. Such studies should be of particular interest to those concerned with the conservation biology of Neotropical migrants.

LITERATURE CITED

Ambuel, B., and S. A. Temple. 1982. Songbird populations in southern Wisconsin forests: 1954 and 1979. J. Field Ornith. 53: 149-158.

Baker, M. C., and A. E. M. Baker. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecol. Monogr. 43: 193-212.

Briggs, S. A., and J. H. Crisswell. 1979. Gradual silencing in Washington. Atlantic Naturalist 32: 19-26.

Cooke, N. W. 1904. Distribution and Migration of North American Warblers. USDA, Biol. Surv. Bull no. 18, Govt. Printing Office, Washington, D. C.

Dickson, J. G. 1988. Bird communities in oak-gum-cypress forests. Pp. 51-62 *in* Bird Conservation no. 3, J. A.. Jackson (ed.). Univ. of Wisconsin Press, Madison.

Flores-Villela, O., and P. G. Fernandez. 1989. Mexico's Living Endowment: an overview of Biological Diversity. Conservation International, Washington, D. C.

Green, K. M., J. F. Lynch, J. Sircar, and L. Z. Greenberg. 1988. Use of Landsat remote sensing to assess habitat for migratory birds in the Yucatan Peninsula. Vida Silvestre Neotropical 1: 27-38.

Greenberg, R. 1984. The Winter Exploitation Systems of Bay-breasted and Chestnut-sided Warblers in Panama. Univ. of Calif. Publ. in Zool., Vol. 116, Univ. Calif. Press, Berkeley.

Holmes, R. T., T. W. Sherry, and L. Reitsma. 1989. Population structure, territoriality and overwinter survival of two migrant species in Jamaica. Condor 91: 545-561.

Hutto, R. L. 1989. The effect of habitat alteration on migratory land birds in a west Mexican tropical deciduous forest: a conservation perspective. Conserv. Biol. 3(2): 138-148.

Hutto, R, L. 1980. Winter habitat distribution of migratory land birds in western Mexico, with special reference to small, foliage-gleaning insectivores. Pp. 181-203 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S. Morton (eds.). Smithsonian Inst. Press, Washington, D. C.

Hutto, R. L. 1988. Is tropical deforestation responsible for the reported declines in Neotropical migrant populations? Amer. Birds 42: 375-379.

James, F. C., R. F. Johnston, N. O. Wamery, G. J. Niemi, and W. J. Boecklen. 1984. The Grinnellian niche of the Wood Thrush. Am. Natur. 124: 17-34.

Karr, J. R. 1976. On the relative abundance of migrants from the north temperate zone in tropical habitats. Wilson Bull. 88: 433-458.

Lynch, J. F. 1989. Distribution of over wintering Nearctic migrants in the Yucatan Peninsula, I: general patterns of occurrence. Condor 91: 515-544.

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

MacDonald, P. O., W. E. Frayand J. K. Clauser. 1979. Documentation Chronology, and Future Projections of Bottomland Hardwood Habitat Loss in the Lower Mississippi Alluvial Plain, 2 fools. U. S. Fish and Wildlife Service, Washington, D. C.

Moreau, R. E. 1972. The Palaearctic-African Bird Migration Systems. Academic Press, New York.

Morton, E. S. 1980. Adaptation to seasonal changes by migrant landbirds in the Panama Canal Zone. Pp. 437-457 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S.. Morton (eds.), Smithsonian Inst. Press, Washington, D. C.

Myers, N. 1980. Conservation of Tropical Moist Forests. National Academy of Science, Washington, D. C.

Pashley, D. N. 1988 b. Warblers of the West Indies II. The Western Caribbean. Carib. J. Sci. 24: 112-126.

Pashley, D. N. 1988 a. Warblers of the West Indies I. The Virgin Islands. Carib. J. Sci. 24: 11-22.

Pashley, D. N. 1988 c. A distributional analysis of the warblers of the West Indies. Ph.D. Dissertation. Louisiana State University, Baton Rouge.

Pashley, D. N., and R. P. Martin. 1988. The contribution of Christmas Bird Counts to knowledge of the Winter distribution of migratory warblers in the Neotropics. Amer. Birds 42: 1164-1176.

Rappole J. H., and E. S. Morton 1985. Effects of habitat alteration on a tropical avian forest community. Pp. 1013-1023 *in* Neotropical Ornithology, P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (eds.). Ornith. Monogr. no. 36, Amer. Ornithol. Union, Washington, D. C.

Rappole, J. H. 1974. Migrants and space: the wintering ground as a limiting factor for migrant populations. Bull. Texas Ornith. Soc. 7: 2-4.

Remsen, J. V., Jr., and T. A. Parker, III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15: 223-231.

Robbins, C. S., B. A. Dowell, D. K. Dawson, J. Colon, F. Espinosza, J. Rodriguex, R. Sutton, and T. Vargas. 1987. Comparison of Neotropical Winter bird populations in isolated patches versus extensive forest. Acta OEcologica, OEcol. Gener. 8(2): 285-292

Robbins, C. S. 1979. Effects of forest fragmentation on bird populations. Pp. 198-213 in Proceedings of the Workshop on Management of North Central and Northeastern Forests for Nongame Birds, R. M. DeGraaf and K. E. Evans (eds.). USDA, Tech. Rep. NC-51, Washington, D. C.

Sabo, S. R., and R. T. Holmes. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. Condor 85: 121-138.

Steinhart, P. 1984. Trouble in the tropics. National Wildlife 22(1): 16-20.

Terborgh, J. W. 1980. The conservation status of Neotropical migrants: present and future. Pp. 21-30 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation, A. Keast and E. S. Morton (eds.). Smithsonian Inst. Press, Washington, d. c.

U.S. Fish and Wildlife Service. 1984. Blue ribbon panel for bottomland hardwoods. U. S. Dept. of Interior, Fish and Wild. Serv., Vicksburg, Miss.

Whitcomb, R. F. 1977. Island biogeography and "habitat islands" of eastern forests. Am. Birds 31: 3-5.

Wilcove, D. S., and R. F. Whitcomb. 1983. Gone with the trees. Natural History 92: 82-91.

Wilcove, D. S., and J. W. Terborgh. 1984. Patterns of populations declines in birds. Amer. Birds 38: 10-13.

Willis, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5: 187-231.

APPENDIX A

Monthly precipitation (cm) values and seven year mean for January through December 1983 to 1989 in Madison Parish, Louisiana. Data were collected at a People's Water Service weather station 12 km from the bird census area.

Appendix A. Monthly precipation (cm) values and seven year mean for January through December 1983 to 1989 in Madison Parish, Louisiana. Data were collected at a People's Water Service weather station 12 km from the bird census area.

Month	1983	1984	1985	1986	1987	1988	1989	7 yr. x
January	11.2	11.2	6.6	2.5	9.9	5.6	23.9	10.1
February	24.4	15.5	19.3	3.8	24.4	9.7	19.3	16.6
March	21.1	21.1	9.7	6.9	16.0	16.3	17.0	15.4
April	28.4	12.7	4.3	7.9	5.8	7.6	2.3	9.9
May	36.8	11.4	3.6	28.2	17.8	2.5	19.3	17.1
June	15.2	14.0	9.4	7.4	10.2	1.5	18.5	10.9
July	4.3	4.8	8.1	1.8	10.4	4.8	20.8	7.9
August	1.0	17.8	16.3	6.4	7.4	10.4	1.0	8.6
September	5.6	2.3	11.2	10.2	7.6	4.6	2.8	6.3
October	3.0	28.2	20.8	13.7	2.8	15.0	0.3	12.0
November	18.5	12.4	8.4	27.4	37.3	8.1	14.2	18.0
December	17.3	5.8	9.1	9.4	12.2	15.7	8.4	11.1
Total	187.2	157.2	126.9	123.1	161.8	101.8	147.8	143.9

APPENDIX B

Mean daily and seven year mean minimum and maximum temperature (°C) values in Madison Parish, Louisiana. Data were collected at a People's Water Service weather station 12 km from the bird census area.

Appendix B. Mean daily and seven year mean minimum and maximum temperature (oC) values in Madison Parish, Louisiana. Data were collected at a People's Water Service weather station 12 km from the bird census area.

	1983		1984		1985		1986		1987		1988		1989			
	x °C		x °C		x °C		x °C		x °C		x °C		x °C		7 yr. x °C	
Month	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
January	0.2	11.7	-2.4	10.1	-3.2	9.1	1.1	14.5	0.7	11.1	0.9	10.2	5.2	15.6	0.4	11.8
February	2.2	14.1	4.0	17.2	1.7	11.7	6.0	18.1	4.7	14.3	2.8	14.5	3.1	12.1	3.5	14.6
March	4.6	17.4	8.2	20.1	10.6	21.6	7.3	21.5	6.4	29.9	5.8	19.6	8.3	18.6	7.3	21.2
April	8.2	20.9	11.9	24.0	13.0	25.7	12.5	25.8	8.6	23.5	11.3	24.8	10.8	23.8	10.9	24.1
May	14.0	27.0	15.1	28.5	17.0	29.6	18.2	28.9	17.0	28.0	14.5	29.0	17.2	27.4	16.1	28.3
June	19.4	29.6	18.9	32.1	20.4	33.6	21.5	32.4	17.8	28.1	19.2	32.9	20.7	29.6	19.7	31.2
July	21.5	34.2	19.9	32.4	21.6	33.0	22.9	34.8	19.5	30.3	21.6	32.8	20.9	30.6	21.1	32.6
August	22.0	34.4	20.5	31.6	21.6	33.6	20.9	33.3	22.9	33.2	22.2	32.8	21.2	32.0	21.6	33.0
September	16.7	30.5	16.3	29.7	16.9	30.4	20.2	31.6	17.1	30.3	19.4	29.9	18.5	27.8	17.9	30.0
October	11.1	26.8	14.4	26.4	15.2	26.5	12.9	24.9	7.7	24.2	9.7	22.4	10.9	25.6	11.7	25.3
November	5.2	20.1	4.1	18.4	12.2	21.2	10.0	19.2	6.8	20.1	7.0	19.3	7.2	20.3	7.5	19.8
December	-1.0	8.5	7.4	19.4	0.83	12.1	3.6	11.4	4.6	16.1	1.9	14.4	-2.2	9.4	2.2	13.0

APPENDIX C

Mean number of birds/5 min. recorded along two transects during May-July in the "forest" study site of the Tensas River Basin, 1984-1989.

Appendix C. Mean number of birds/5 min. recorded along two transects during May-July in the "forest" study site of the Tensas River Basin, 1984-1989.

	Forest 1						Forest 2					
	1984	1985	1986	1987	1988	1989	1984	1985	1986	1987	1988	1989
Species	2(18)[1]	1(6)	3(38)	2(34)	5(103)	1(6)	-	3(48)	7(96)	2(24)	1(12)	4(74)
Eastern Wood-Pewee	.167	-	.158	.147	.087	-	-	-	.052	.042	-	.243
Acadian Flycatcher	2.333	2.667	1.316	1.588	1.515	1.167	-	1.396	1.500	1.750	1.750	1.581
Carolina Chickadee	.711	.500	1.158	1.059	.738	1.167	-	.375	.615	.500	2.000	1.027
Tufted Titmouse	1.444	1.500	.868	1.853	1.220	1.833	-	1.125	.677	1.292	2.500	2.514
Carolina Wren	1.944	1.167	1.868	2.029	1.417	1.000	-	1.771	1.604	2.417	2.083	1.865
Blue-gray Gnatcatcher	.667	.167	.026	.441	.087	.500	-	.125	.042	-	.150	.176
White-eyed Vireo	1.444	.667	1.132	.824	1.117	.500	-	1.125	1.656	.792	.833	1.000
Yellow-throated Vireo	.222	-	.127	.147	.087	-	-	-	.198	.083	-	.068
Red-eyed Vireo	1.611	1.333	1.316	1.588	1.204	1.000	-	.458	.646	1.708	.500	.865
Northern Parula	.389	.333	.237	.294	.718	.333	-	1.771	1.469	1.833	1.583	1.554
Yellow-throated Warbler	-	-	-	-	-	-	-	-	-	-	-	-
American Redstart	.167	-	.263	.382	.214	-	-	.063	.688	.208	.500	.135
Prothonotary Warbler	1.333	1.000	.211	.412	.379	-	-	.500	.344	.375	.417	.365
Swainson's Warbler	.556	-	.395	.118	.058	.167	-	.063	.135	.167	-	.270
Kentucky Warbler	.611	.667	.263	.176	.184	.167	-	.188	.333	.125	.167	.459
Hooded Warbler	.778	1.500	.711	.647	.476	.667	-	.500	.740	.958	.667	.446

[1]Number of censuses (number 5 min. counts).

APPENDIX D

Mean number of birds/5 min. recorded along two transects during May-July in the "flat" study site if the Tensas River Basin, 1984-1989.

Appendix D. Mean number of birds/5 min. recorded along two transects during May-July in the "flat" study site of the Tensas River Basin, 1984-1989.

	Flat 1						Flat 2					
	1984	1985	1986	1987	1988	1989	1984	1985	1986	1987	1988	1989
Species	1(15)[1]	2(23)	2(20)	2(22)	-	1(12)	-	2(20)	10(105)	3(37)	6(85)	9(116)
Eastern Wood-Pewee	.333	.304	.900	.682	-	.583	-	.700	.495	.595	.282	.293
Acadian Flycatcher	.800	1.043	1.100	1.636	-	1.083	-	.400	.6290	.568	.788	.862
Carolina Chickadee	2.200	2.696	1.700	2.318	-	1.583	-	.550	.705	.865	.176	1.422
Tufted Titmouse	2.133	1.826	1.250	2.364	-	1.917	-	.550	.486	1.330	.400	2.009
Carolina Wren	1.133	.913	.050	.136	-	1.167	-	.400	.838	1.162	.5653	1.147
Blue-gray Gnatcatcher	.067	.087	.350	.182	-	.917	-	-	.257	.459	.188	.664
White-eyed Vireo	.600	.391	.550	.045	-	1.000	-	.550	1.514	1.117	.718	1.181
Yellow-throated Vireo	.267	.435	.400	.364	-	.083	-	.050	.190	.087	.165	.328
Red-eyed Vireo	1.067	1.217	.900	1.818	-	.833	-	.350	.419	.541	.212	.259
Northern Parula	.133	.130	.237	.182	-	-	-	.200	.133	.081	.259	.604
Yellow-throated Warbler	-	-	-	-	-	-	-	-	-	-	.035	.250
American Redstart	-	-	-	-	-	-	-	-	.010	-	-	.034
Prothonotary Warbler	1.667	1.609	1.800	1.909	-	1.667	-	1.700	1.171	1.054	.682	1.483
Swainson's Warbler	-	-	-	-	-	-	-	-	-	.058	.024	.060
Kentucky Warbler	.067	.130	-	-	-	-	-	-	.038	.027	-	.198
Hooded Warbler	-	-	-	-	-	-	-	-	-	.054	-	.121

[1]Number of censuses (number 5 min. counts).

APPENDIX E

Mean number of birds/5 min. recorded along two transects during May-July in the "oxbow" study site of the Tensas River Basin, 1984-1989.

Appendix E. Mean number of birds/5 min. recorded along two transects during May-July in the "oxbow" study site of the Tensas River Basin, 1984-1989.

	Oxbow 1						Oxbow 2					
	1984	1985	1986	1987	1988	1989	1984	1985	1986	1987	1988	1989
Species	-	3(29)[1]	2(20)	4(40)	5(123)	3(27)	1(14)	-	4(48)	-	-	1(28)
Eastern Wood-Pewee	-	.345	.300	.250	.130	.444	-	-	.083	-	-	.214
Acadian Flycatcher	-	.724	.500	1.250	1.041	1.111	.857	-	.875	-	-	1.429
Carolina Chickadee	-	1.414	1.150	2.175	.602	.889	.214	-	.250	-	-	1.286
Tufted Titmouse	-	1.345	.750	1.175	.699	1.074	.714	-	.500	-	-	2.107
Carolina Wren	-	.931	.650	1.100	1.073	2.3337	.571	-	1.042	-	-	1.393
Blue-Gray Gnatcatcher	-	-	-	.175	.008	.815	-	-	.021	-	-	.893
White-eyed Vireo	-	1.586	.750	.900	1.496	1.519	1.143	-	1.813	-	-	.857
Yellow-throated Vireo	-	.034	-	-	.057	.074	-	-	.063	-	-	.571
Red-eyed Vireo	-	.172	.150	.315	.276	.704	.786	-	.417	-	-	.321
Northern Parula	-	3.966	3.050	2.650	1.798	1.741	1.571	-	1.688	-	-	1.571
Yellow-throated Warbler	-	1.690	1.300	.950	.439	.481	.286	-	.333	-	-	.643
American Redstart	-	-	-	-	.033	-	-	-	.021	-	-	.143
Prothonotary Warbler	-	2.517	1.500	1.525	.707	.630	.429	-	.521	-	-	1.393
Swainson's Warbler	-	.034	-	-	-	.185	-	-	.188	-	-	.214
Kentucky Warbler	-	.103	.050	.175	.293	.185	.357	-	.229	-	-	.500
Hooded Warbler	-	-	-	.015	.065	.296	-	-	.146	-	-	.286

[1] Number of censuses (number 5 min. counts).

APPENDIX F

Characteristics of microhabitat use by 14 bird species (n>10) and availability in the "forest" study site of the Tensas River Basin.

Appendix F. Characteristics of microhabitat use by 14 bird species (n>10) and availability in the "forest" study site of the Tensas River Basin.

Species	Percent cover						Foliage density (%)								Sample size
	water		ground litter		fallen debris		ground		shrub		subcanopy		canopy		
	x	sd	x	sd	x	sd	x	sd	x	sd	x	sd	x	sd	
Acadian Flycatcher	18.92	35.79	75.27	33.61	6.93	10.76	34.80	35.64	33.90	30.58	28.79	27.91	74.73	19.26	92
Carolina Chickadee	9.03	24.02	93.44	9.01	8.68	19.82	47.86	37.91	38.63	31.72	31.91	28.68	57.89	29.90	45
Tufted Titmouse	10.00	29.54	86.09	25.99	10.33	18.61	39.19	38.54	37.34	41.95	25.31	26.67	59.86	30.88	36
Carolina Wren	0.41	1.82	88.38	26.69	15.00	21.47	38.51	34.52	50.54	34.66	46.89	35.13	70.68	26.07	37
Blue-gray Gnatcatcher	10.00	27.07	85.17	20.32	8.04	10.92	45.83	37.46	40.44	35.41	32.41	30.80	37.36	26.61	30
White-eyed Vireo	2.64	14.30	84.25	22.94	10.70	16.17	51.64	34.71	55.58	30.53	48.30	31.10	62.04	41.87	71
Yellow-throated Vireo	8.20	25.61	90.20	22.05	7.73	12.41	33.00	35.88	26.14	27.12	11.09	14.30	41.44	27.41	25
Red-eyed Vireo	15.30	32.64	77.58	34.03	5.42	9.08	36.06	36.33	37.19	30.95	21.54	23.61	68.55	22.39	38
Northern Parula	0.63	3.31	93.09	16.29	10.18	19.72	61.27	31.39	35.03	31.14	27.73	29.34	60.87	29.38	92
Yellow-rumped Warbler	6.14	21.38	92.86	7.34	2.62	6.25	27.14	24.63	33.86	23.04	15.00	15.97	42.59	26.03	27
American Redstart	0.26	1.60	90.38	15.32	7.42	17.41	55.38	33.35	42.09	28.85	37.50	28.40	67.04	20.71	49
Prothonotary Warbler	47.14	46.18	50.52	44.77	9.81	21.24	13.21	26.92	22.52	34.80	38.00	25.52	56.47	29.04	34
Swainson's Warbler	1.56	5.07	98.44	3.97	18.18	19.40	27.50	25.69	62.94	35.53	50.00	37.37	91.56	7.00	16
Kentucky Warbler	0.00	0.00	96.97	4.32	15.00	27.16	47.88	31.02	52.88	30.26	59.69	37.44	64.75	41.78	40
Hooded Warbler	0.43	3.59	93.36	13.75	11.35	20.78	45.64	35.69	52.29	31.69	57.42	31.51	68.53	28.41	85
Availability	3.58	16.90	81.60	29.45	12.58	18.83	29.89	30.05	30.33	30.44	22.69	26.93	67.71	26.44	225

APPENDIX G

Characteristics of microhabitat use by 10 bird species (n>10) and availability in the "flat" study site of the Tensas River Basin.

Appendix G. Characteristics of microhabitat use by 10 bird species (n>10) and availability in the "flat" study site of the Tensas River Basin.

	Percent cover						Foliage density (%)								
	water		ground litter		fallen debris		ground		shrub		subcanopy		canopy		Sample
Species	x	sd	x	sd	x	sd	x	sd	x	sd	x	sd	x	sd	size
Eastern Wood-Pewee	43.52	46.45	44.26	41.57	9.81	22.55	38.89	42.52	13.49	22.28	23.65	29.58	13.49	15.18	29
Acadian Flycatcher	18.33	33.26	74.17	41.28	32.00	27.00	13.33	18.38	16.92	27.20	25.45	28.06	76.84	17.89	19
Carolina Chickadee	48.83	47.59	74.20	37.07	19.26	27.59	14.07	30.48	9.69	21.70	24.71	28.32	42.67	33.83	43
Tufted Titmouse	45.38	47.16	68.46	40.66	26.25	30.15	6.73	19.69	5.63	12.10	24.35	19.38	44.83	31.21	29
Blue-gray Gnatcatcher	50.38	46.86	48.46	42.77	5.00	13.07	36.35	41.46	21.41	35.81	40.80	41.41	34.70	29.37	33
Yellow-throated Vireo	38.00	43.36	61.50	38.94	17.63	22.38	15.50	27.29	5.53	19.50	25.00	29.39	39.75	31.05	20
Red-eyed Vireo	20.59	34.90	73.09	38.08	21.41	26.56	15.88	31.94	3.38	7.25	28.45	22.12	53.42	26.64	38
Tennessee Warbler	66.56	37.18	65.00	44.57	5.56	4.64	1.25	3.42	23.61	27.32	15.00	11.18	40.83	29.22	24
Northern Parula	53.08	46.48	71.88	29.51	28.89	35.16	33.13	40.26	23.64	37.22	42.50	35.46	25.53	27.73	19
Prothonotary Warbler	53.40	47.10	46.22	47.32	21.90	25.76	5.56	15.23	7.23	20.10	29.12	26.10	37.49	35.45	53
Availability	10.80	30.27	81.79	33.01	18.58	24.50	9.53	19.18	3.91	12.98	21.72	26.52	55.97	28.57	201

APPENDIX H

Characteristics of microhabitat use by 6 bird species (n>10) and availability in the "oxbow" study site of the Tensas River Basin.

Appendix H. Charateristics of microhabitat use by 6 bird species (n>10) and availability in the "oxbow" study site of the Tensas River Basin.

	Percent cover						Foliage density (%)								
	water		ground litter		fallen debris		ground		shrub		subcanopy		canopy		Sample
Species	x	sd	x	sd	x	sd	x	sd	x	sd	x	sd	x	sd	size
Eastern Wood-Pewee	44.60	44.11	37.60	37.53	10.60	19.17	32.40	36.00	36.40	35.84	37.20	33.91	27.41	27.21	26
Acadian Flycatcher	14.72	31.55	60.83	37.86	17.00	24.06	62.78	39.53	27.50	33.15	38.18	29.60	54.74	28.60	19
Carolina Chickadee	62.38	43.81	22.50	36.43	9.21	15.48	18.42	33.08	43.25	35.55	42.81	28.98	35.23	26.88	22
Northern Parula	39.74	40.04	40.35	38.73	10.00	15.92	39.21	39.72	42.73	32.31	32.05	26.07	50.48	28.37	104
Yellow-throated Warbler	42.59	44.13	37.70	33.16	3.30	10.64	8.58	18.87	36.46	29.56	39.87	22.55	33.84	22.70	138
Prothonotary Warbler	74.36	37.59	19.09	32.75	10.69	24.31	9.81	26.04	39.06	38.67	33.33	32.98	44.46	32.69	56
Availability	49.79	46.85	17.44	29.11	8.77	15.56	4.67	12.07	313.14	21.87	28.39	28.99	40.23	28.29	199

VITA

Wylie Clark Barrow, Jr. was born on 7 July 1955 in Baton Rouge, Louisiana. He graduated from University High School in May, 1973. In 1978 he graduated from Louisiana State University with a B.S. in Forestry. He graduated from West Virginia University with a M.S. in Wildlife Ecology in 1982. He worked for the U.S. Fish and Wildlife Service as a cooperative education employee during parts of 1986 and 1987. He worked for The Nature Conservancy from November 1987 to May 1989.

He married Barbara Christine Benson in November 1988, and he adopted Lindsey Christine Benson in January 1989. A son, Wylie Clark Barrow, III, was born to them in April 1989.

Wylie began his Ph.D. work in the School of Forestry, Wildlife, and Fisheries at Louisiana State University, Baton Rouge, in August 1983 and is presently a candidate for that degree.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Wylie C. Barrow, Jr.

Major Field: Wildlife and Fisheries Science

Title of Dissertation: Ecology of Small Insectivorous Birds in a Bottomland Hardwood Forest

Approved:

Robert B. Hamilton
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

William R. Wolters

Date of Examination:

July 20, 1990