RELATIONSHIPS BETWEEN BIRD COMMUNITIES
AND FOREST AGE, STRUCTURE, SPECIES COMPOSITION
AND FRAGMENTATION IN THE WEST GULF COASTAL PLAIN

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Abstract.-Bird communities of the West Gulf Coastal Plain are strongly influenced by the stage of forest succession, species composition of understory and overstory vegetation, and forest structure. Alteration of plant communities through forest management and natural disturbances typically does not eliminate birds as a faunal group from the area affected, but will replace some species with others and cause changes in the abundance and species composition of bird communities. Upland, fire disclimax pine savannah communities composed of primarily longleaf pine (Pinus palustris) provide mature pines for Red-cockaded Woodpeckers (Picoides borealis) and Brown-headed Nuthatches (Sitta pusilla) while simultaneously providing grassland ‘ground cover for Bachman’s Sparrows (Aimophila aestivalis) and Henslow’s Sparrows (Aimomimus henslowii). On the mesic mid-slopes where there is an increasing presence of lobolly (Pinus taeda) and shortleaf (Pinus echinata) pine and hardwood species, Northern Cardinals (Cardinalis cardinalis) and White-eyed Vireos (Vireo griseus) find habitat in the understory and midstory vegetation, whereas canopy hardwoods and pines provide habitat for Red-eyed Vireos (Vireo olivaceus) and Summer Tanagers (Piranga rubra). Transition into the wet bottomland hardwood forests increases the abundance of bird species associated with deciduous wetlands such as Prothonotary Warblers (Protonotaria citrea) and Swainson’s Warblers (Limnothlypis swainsonii), whereas species associated with conifers and grassland savannas are lost. Anthropogenic or natural disturbances that set back mature stages of forest succession can dramatically alter the species composition of bird communities. Depending on patch size, forest removal can initiate forest succession and provide habitat for early succession bird species such as Blue Grosbeaks (Guiraca caerulea), Field Sparrows (Spizella pusilla), Prairie Warblers (Dendroica discolor), Painted Buntings (Passerina ciris), Indigo Buntings (Passerina cyanea), and Yellow-breasted Chats (Icteria virens). Although current data are inconclusive, patch size, forest fragmentation, edge effect, and landscape use patterns appear to influence bird communities by affecting area-sensitive species. Of greatest concern are forest-interior bird species that appear to be area sensitive such as the Cerulean Warbler (Dendroica cerulea), Northern Parula (Parula americana), Louisiana Waterthrush (Seiurus motacilla), American Redstart (Setophaga ruticilla), and Worm-eating Warbler (Helmitheros vermivorus).

Forest bird communities of the West Gulf Coastal Plain are influenced primarily by forest age and structure, and tree species composition. Across the forest landscape, anthropogenic effects, that determine the spatial mosaic of forest age-classes and size of forest patches, also influence avian species composition and abundance. Seasonally, bird communities in the West Gulf Coastal Plain are affected by spring influx
and departure of nearctic and neotropical migrants as they arrive from southerly latitudes to establish breeding territories, or stop briefly to feed and then quickly depart for more northerly breeding grounds.

Until the mid 1800s, the landscape of eastern Texas was primarily forest habitat with longleaf pine ecosystems dominating the frequently burned upland sites, bottomland hardwood forests in the lower mesic to wet sites, and loblolly and shortleaf mixed-pine hardwood forests spanning a dynamic zone between the sites of moisture extremes (Maxwell & Baker 1983; Walker 1991). During the late 1800s the rate of timber harvesting in the West Gulf Coastal Plain increased dramatically. A “bonanza era” of timber harvesting occurred from 1880 to 1930 which eliminated the majority of old-growth forests in eastern Texas (Maxwell & Baker 1983; McWilliams & Lord 1988). Upland pine forests and bottomland hardwood forests were both heavily logged. Some of the cut-overforest lands were reforested by artificial planting, some by natural seeding, while other lands were converted to agricultural uses and reservoirs (Truett & Lay 1984; Walker 1991). Thus, the present-day forests that provide habitat for bird communities are second-growth forests, which have again been affected by harvesting during the past several decades (McWilliams & Lord 1988).

This paper presents an abbreviated glimpse of general relationships between birds and their habitats using selected species as illustrations. Our objective is to demonstrate that avian communities are variable, but are also dependent on forest stand age, tree species composition, season, special habitat features such as snags, and the mosaic of age classes across the forest landscape that affect forest fragmentation. Relationships between selected sensitive species, loss of old-growth habitat, and forest fragmentation will also be examined.

**The Influence of Forest Stand Age on Avian Communities**

Timber harvesting, and large- and small-scale natural disturbances greatly affect the species composition of bird communities. Typically in the South, species are not eliminated from the forest landscape, but are temporally replaced by others as timber stand age is affected by forest management and natural forest succession (Odum 1950; Conner & Adkisson 1975; Conner et al. 1979; Dickson et al. 1993a; 1993b). Early succession seres created by disturbances such as wind throw, bark beetle infestation, or timber harvesting provide breeding habitat for field
and shrub-nesting species such as Field Sparrows (*Spizella pusilla*) and Blue Grosbeaks (*Guiraca caerulea*). As the shrub vegetation develops, additional species such as Prairie Warblers (*Dendroica discolor*), Painted Buntings (*Passerina ciris*), Indigo Buntings (*P. cyanea*), White-eyed Vireos (*Vireo griseus*) and Yellow-breasted Chats (*Zcteria virens*) become very abundant (Dickson et al. 1993b) (Fig. 1). After 10 to 12 years following a disturbance that removes the overstory, Field Sparrows, Blue Grosbeaks and Prairie Warblers have “bloomed” and virtually disappeared as a result of vegetative changes from forest growth in the West Gulf Coastal Plain (Fig. 1). Indigo Buntings, Yellow-breasted Chats and White-eyed Vireos persist longer as forest regrowth occurs and are present until the regenerating stand reaches about 14 to 16 years old (Fig. 1).

While early succession bird species decline in abundance as a response to vegetation regrowth, bird species associated with older forest age classes begin to use the regenerating forest stand (Dickson et al. 1993b) (Fig. 2). Species such as Red-eyed Vireos (*Vireo olivaceus*), Hooded Warblers (*Wilsonia citrina*), Black-and-white Warblers (*Mniotilta varia*), and Worm-eating Warblers (*Helmitheros vermivorus*) begin to appear in stands that are five to eight years old and gradually
increase in abundance thereafter as the stand continues to age. Kentucky Warblers (*Oporornis formosus*) also begin to appear in stands that are about five years old, increase in abundance until stands reach about 10 years old, but then decline in abundance subsequently as deciduous foliage begins to disappear. Species such as Kentucky Warblers, White-eyed Vireos, Carolina Wrens (*Thryothorus ludovicianus*) and Northern Cardinals (*Cardinalis cardinalis*) are dependent on shrubby patches of deciduous foliage present at understory (0 to 3 m) and midstory (5 to 8 m) layers in all stages of forest succession (Conner & Adkisson 1975; Hamel et al. 1982; Hamel 1992; Dickson et al. 1993a). As the regenerating forest stand grows toward maturity, other species such as Pileated Woodpeckers (*Dryocopus pileatus*) and Summer Tanagers (*Piranga rubra*) reappear in the forest bird community (Odum 1950; Conner & Adkisson 1975; Conner et al. 1979; Hamel et al. 1982; Hamel 1992).

**THE INFLUENCE OF FOREST COVER TYPE ON BIRD COMMUNITIES**

Forest cover type in the West Gulf Coastal Plain was historically determined by the combined effects of soil type (sand vs clay), moisture regime (slope position), and frequency and intensity of fire. Deciduous hardwood tree species were more abundant in the bottomlands whereas pines dominated the uplands (Harcombe et al. 1993; Marks & Harcombe
Historically, mixed pine-hardwood forests existed in a dynamic zone between the bottomlands and uplands with the percentage composition of hardwoods determined by the frequency and severity of fire. Bird communities vary among the major forest cover types depending on tree species composition (Dickson et al. 1993c; 1995). Some bird species are found only in particular forest cover types. Species like Red-cockaded Woodpeckers (*Picoides borealis*) and Brown-headed Nuthatches (*Sitta pusilla*) are primarily associated with the mature, pine-dominated forests of the uplands (Conner & Rudolph 1989; Conner et al. 1983). Conversely, Prothonotary (*Protonotaria citrea*) and Swainson’s warblers (*Limmothlypis swuinsonii*) are primarily associated with deciduous wetlands on the lower slopes and bottoms (Dickson et al. 1980; Hamel 1992).

**Vegetation Structure, Tree Species, Snags and Bird Communities**

The presence and abundance of many nearctic-neotropical migrant and resident species are directly influenced by the amount of deciduous hardwood foliage present in the forest understory and midstory (Dickson & Noble 1978; Conner et al. 1983). The abundance of White-eyed Vireos, Yellow-breasted Chats, Prairie Warblers, Kentucky Warblers, Northern Cardinals and Carolina Wrens is directly correlated with the abundance of deciduous foliage in the understory and midstory. Likewise, presence and abundance of Red-eyed Vireos, Black-and-white Warblers and Tufted Titmice (*Parus bicolor*) are correlated to the amount of deciduous foliage in midstory and canopy (Dickson & Segelquist 1979a; Conner et al. 1983).

The vertical structure of foliage layers in the forest as well as forest cover type influence the presence and abundance of bird species within bird communities (MacArthur 1964). Bird species richness, species diversity, and abundance within forests are related to density of foliage and number of vertical foliage layers within forests as they mature or progress through forest succession (MacArthur & MacArthur 1961; Kricher 1972). In general, increasing foliage density and the addition of more vertical layers of foliage as canopy height increases, permit additional species to be added to bird communities (James & Warner 1982). James & Warner (1982) concluded that the highest densities of birds in forests are found where tree species richness and canopy height are high and trees are spaced at moderate densities. Highest bird species richness is associated with intermediate values of tree species richness,
canopy height and tree density. Low bird species richness and abundance are associated with forests that have low tree species richness and low canopy heights, but a high density of small trees (James & Warner 1982). Typically, the density of breeding bird territories in second-growth deciduous habitat is lower than in old-growth deciduous habitat, but higher than that of similarly-aged coniferous habitat.

Spatial heterogeneity of vegetation, patchiness as viewed horizontally across the forest landscape, also influences bird communities. Roth (1976) observed that bird species diversity significantly increased as horizontal spatial heterogeneity increased in shrub stages of forest habitats. However, as forests mature, bird species diversity is increasingly influenced by the addition of foliage layers and vertical patchiness.

The presence of snags and older trees containing decayed branches are important for cavity-using birds in timber stands of all ages and tree species composition (Conner 1978). Dickson et al. (1983) observed that breeding season bird diversity, species richness, and abundance were significantly higher in eastern Texas clearcuts where snags had been retained than in similar cuts where they had been removed. Woodpeckers and other cavity-nesting birds used the snags for nesting, whereas other ground and shrub-nesting species used them as song perches. The presence of snags also increased bird diversity, species richness, and abundance during winter in the same stands (Dickson & Conner 1982), and were valuable as hunting perches for raptors (Conner et al. 1981).

**THE INFLUENCE OF SEASON AND MIGRANTS ON BIRD COMMUNITIES**

Bird communities in the West Gulf Coastal Plain are strongly influenced by seasonal influx of spring migrants from the neotropics. Although many species arrive in spring to establish breeding territories, an equally large number are transients, most notable of which are many warbler species that pass through to more northerly breeding grounds in hardwood and boreal coniferous forests. The migrants that breed in eastern Texas add to the existing community of residents, such as Bachman’s Sparrows (*Aimophila aestivalis*) and Northern Cardinals, that winter and breed in the coastal plain forests. A number of species, such as Red-breasted Nuthatches (*Sitta canadensis*), Brown Creepers (*Certhia americana*), Winter Wrens (*Troglodytes troglodytes*), and Henslow’s Sparrows (*Ammodramus henslowii*), are nearctic migrants that winter on the South’s coastal plain, but leave prior to spring to breed in the
northern United States and Canada (Dickson & Segelquist 1979b; Root 1988). Grasses present in the ground cover of longleaf pine savannas are important winter habitat for the little-studied Henslow’s Sparrow (Hamel 1992; Smith 1992). Bottomland hardwood forests in the West Gulf Coastal Plain are extremely important as winter habitat for a diverse winter bird community (Dickson 1978). Bird abundance in bottomland hardwood forests is greatest during winter with Red-headed Woodpeckers (*Melanerpes erythrocephalus*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*), Brown Thrashers (*Toxostoma rufum*), American Robins (*Turdus migratorius*), Hermit Thrushes (*Catharus guttata*), and Ruby-crowned Kinglets (*Regulus calendula*) present in very high densities (Dickson 1978). The continued loss of mature bottomland hardwood forest, a relatively rare forest type, poses a potential threat to the wintering habitat of many of these species, particularly those that depend on acorns for food during winter such as Red-headed Woodpeckers (Kilham 1958; Moskovits 1978).

**Forest Fragmentation and Effects of Forest Edge**

Fragmentation of forest landscapes through loss of forest habitat to alternative land uses and timber harvesting within second-growth forests is a concern to biologists and land managers because of its potential influence on biological diversity (Harris 1984). Concepts and preliminary data from island biogeography theory have indicated that species will be lost as “size of the island” (forest fragment) decreases and also lost as the distance between islands of forest habitat and large blocks of continuous forest increases (MacArthur & Wilson 1963; 1967; MacArthur et al. 1973). More recently, empirical and theoretical investigations have explored the mathematics of metapopulation dynamics, where species cycle through extirpation and recolonization of smaller blocks of habitat based on the spatial proximity to conspecific populations in other neighboring blocks of habitat (Gilpin & Hanski 1991; Simberloff 1994). However, most forest landscapes are not a simple system of forest islands; they often cover a variety of landscape conditions ranging from large tracts of uncut forest, forests with patches of mature timber removed, to woodlot-like islands of forest surrounded by agricultural or urban areas (Fig. 3). Wiens (1994) suggests that forest habitat exists in a complex landscape mosaic, and dynamics within a forest patch change as external factors affect the landscape mosaic.

Annand & Thompson (1997) evaluated effects of forest patch size on
Figure 3. Progression of forest removal eventually leading to forest fragmentation and the existence of forest islands in a non forested landscape.

bird communities during a study examining the effects of a variety of even-aged and uneven-aged silvicultural techniques on breeding birds in southeastern Missouri. They observed that Prairie Warblers, White-eyed Vireos, and Yellow-breasted Chats were significantly more abundant in clearcuts than any other silvicultural treatment. Brown-headed Cowbirds (*Molothrus ater*), a parasitic nester, also reached their greatest abundance in clearcuts. Indigo Buntings and Field Sparrows were more abundant in clearcuts and shelterwood cuts than other treatments, whereas Hooded Warblers and Northern Parulas (*Panda americana*) were significantly more abundant in selection harvesting treatments. Ovenbirds (*Seiurus aurocapillus*) and Wood Thrushes (*Hylocichla mustelina*) were significantly more abundant in mature forest habitat that lacked open patches, whereas Acadian Flycatchers (*Empidonax virescens*) and Red-eyed Vireos were significantly more abundant in the patchy forest habitats created by both single-tree and group selection harvesting. Annand & Thompson (1997) concluded that the habitat
requirements of birds in managed forests was best met by using a variety of even-aged and uneven-aged techniques to create a range of disturbance patch sizes.

Although more mobile than most mammals and reptiles because of their ability to fly, birds are still influenced by forest fragmentation (Robbins et al. 1989; McIntyre 1995). Some forest interior species are of particular concern because their occurrence and abundance appear to be area sensitive (Galli et al. 1976; Blake and Karr 1987; Robbins et al. 1989; Villard et al. 1993; Hoover et al. 1995). In the Georgia Piedmont, McIntyre (1995) observed that breeding Summer Tanagers, Yellow-throated Warblers (*Dendroica dominica*), Louisiana Waterthrushes, Northern Parulas, Black-and-white Warblers, and Red-eyed Vireos decreased in abundance or were extirpated as habitat changed from continuous forest landscapes, through large isolated patches to small isolated patches. Wintering species such as Yellow-bellied Sapsuckers, Brown Creepers, Hermit Thrushes, and Golden-crowned Kinglets (*Regulus satrapa*) also decreased in abundance or were extirpated as forest area decreased (McIntyre 1995). Year-round residents that either decreased or were extirpated included Sharp-shinned Hawks (*Accipiter striatus*), Downy Woodpeckers (*Picoides pubescens*), Pileated Woodpeckers, Red-bellied Woodpeckers (*Melanerpes carolinus*), Carolina Chickadees (*Parus carolinensis*), Tufted Titmice, Brown-headed Nuthatches, and Pine Warblers (*Dendroica pinus*). All of these species occur in the West Gulf Coastal Plain. The possibility that the smaller forest fragments serve as population sinks for birds produced on the dwindling numbers of larger forest blocks is a major recent concern (Donovan et al. 1995a; 1995b).

Some of the bird species vulnerable to forest fragmentation in eastern Texas are Northern Parulas, Summer Tanagers, Louisiana Waterthrushes, and Worm-eating Warblers (Robbins et al. 1989), because in many areas they only begin to become moderately abundant when unbroken forest tracts approach or exceed 1,000 ha (Fig. 4). Cerulean Warblers (*Dendroica cerulea*), which breed only in the northeastern portion of the West Gulf Coastal Plain, are perhaps the most area-sensitive bird in this region and are likely the most vulnerable species to the forest fragmentation in this region. Populations of many of these species are very low in abundance, or have declined like the Cerulean Warbler over the past decades (Fig. 5) (Sauer et al. 1996). Two additional species of concern in the West Gulf Coastal Plain are the Swallow-tailed Kite (*Elanoides*
Cerulean Warbler — Worm-Eating Warbler — Louisiana Waterthrush — Northern Parula

Figure 4. Probability of occurrence of selected forest breeding birds relative to forest area (combined and redrawn from Robbins et al. 1989). The Cerulean Warbler is the most sensitive of the four species to forest fragmentation in the West Gulf Coastal Plain.

Causes of fragmentation's negative effects.—The causes for declines of forest interior bird species as forest fragment size decreases are variable and not completely understood. Bird species richness, diversity, and abundance are known to increase along forest-edge habitat in the West Gulf Coastal Plain (Strelke & Dickson 1980). However, many studies of artificial nests suggest that nest depredation rates may reduce productivity of birds nesting close to forest-edge habitat created by clearcutting or agricultural land uses (Yahner & Scott 1988; Rudnicky & Hunter 1993; Leimgruber et al. 1994; Yahner & Mahan 1996). Hoover et al. (1995) observed severe reproductive dysfunction in Wood Thrushes as a result of high nest predation rates in small forest fragments, whereas reproduction remained high in large contiguous forests. Porneluzi et al. (1993) suspected that predation was the prominent factor decreasing reproductive performance of Ovenbirds in small forest fragments. Hagan et al. (1996) suggested that initial lower reproductive attainment of Ovenbirds in forest fragments may also result from behavioral dysfunction associated with higher breeding densities caused by concentration of Ovenbirds following forest removal. Nest parasitism by Brown-headed Cowbirds is perhaps the major cause of
lower nest productivity for some interior forest birds that use forest fragments (Brittingham & Temple 1983; Coker & Capen 1995).

Robinson (1992) observed that approximately 76% of neotropical migrant nests were parasitized by Brown-headed Cowbirds in central Illinois, and further suggested that the small forest fragments he studied appeared to be population sinks for some interior forest bird species. Robinson et al. (1995) examined source-sink habitat models relative to the negative effects of forest fragmentation. Their correlation analyses clearly demonstrated that nest predation and cowbird nest parasitism rates significantly decreased as the percentage of forest cover increased from 6 to 95% for a large number of avian species in the midwestern United States. They observed that reproductive rates for some bird species in the most fragmented landscapes were sufficiently low to suggest that these areas were population sinks that only existed because of immigration from other source populations in less fragmented forest landscapes. Robinson et al. (1995) concluded that forest managers should consider “preservation, and restoration of large, unfragmented ‘core’ areas in each region.”

Figure 5. Breeding bird survey trends of selected bird species in the southeastern United States (Sauer et al. 1996). Plots for the Louisiana Waterthrush and the Worm-eating Warbler are virtually identical and overlay each other showing slightly increasing population trends. Cerulean Warbler and American Redstart populations have been declining over the past 29 years.
Past Losses of Bird Species and Potential Candidates for Future Losses

Within the past century, the bird communities of the West Gulf Coastal Plain have lost four bird species. The extinctions of the Passenger Pigeon (*Ectopistes migratorius*) and Carolina Parakeet (*Conuropsis carolinensis*) was most likely caused by excessive human hunting pressure (Greenway 1967). Prior to the turn of the last century, both of these species bred in the West Gulf Coastal Plain. Passenger Pigeons numbered in the billions south wide. Oberholser (1974) noted two Passenger Pigeon breeding records from Texas during the late 1800s in Cooke and Henderson Counties. Possible breeding records for the Carolina Parakeet from northeastern Texas in Red River County exist prior to 1880. Both of these species became extinct in 1914.

The more recent likely extinctions of Ivory-billed Woodpeckers (*Campephilus principalis*) and Bachman’s Warblers (*Vermivora bachmanii*) appear to be closely linked to the harvest and loss of old-growth bottomland hardwood forests (Tanner 1966; Hooper & Hamel 1977; Hamel 1995). Loss and fragmentation of forest habitat, particularly bottomland hardwood forest and upland longleaf pine forest habitats, continue to be the greatest threat for bird species in the West Gulf Coastal Plain. The recent intensified management and population increases of Red-cockaded Woodpeckers (Conner et al. 1995) are good signs that many of the problems of this species have been solved. However, forest-interior bird species of hardwood forests, as noted above, appear to be the potential problem areas of the future because they are sensitive to both the loss and fragmentation of large blocks of contiguous forest. They are likely the most vulnerable avian species to future population declines and possible extirpation. Provision of large blocks of unbroken mature forest appears to be essential to assure that species such as Cerulean Warblers, Northern Parulas, American Redstarts, Louisiana Waterthrushes, and Swallow-tailed Kites continue as viable components of the West Gulf Coastal Plain’s avifauna.

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