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EFFECTS OF FIRE REGIME ON BIRDS IN SOUTHEASTERN PINE SAVANNAS AND NATIVE PRAIRIES

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Abstract. Fire, both natural and anthropogenic, has played a critical role in shaping vegetation structure and composition of many of the plant communities of the southeastern United States. Pine savannas, especially longleaf pine (*Pinus palustris*), that were dominant over much of the upland coastal plain, have declined by approximately 97% over the past 100 yr. The inferred natural fire regime of this vegetation type was a fire frequency of 2–8 yr with typically low-severity fires that occurred during the lightning season (June–August). Currently, dormant-season (January through April) fires are used most frequently. Approximately 110–120 species, excluding migrants, comprise the avian community of southeastern pine savannas; and some of these are among the most rapidly declining bird species in the eastern United States. Disruption of the natural fire regime by fire exclusion or lengthened fire interval was detrimental to bird species associated with tree (e.g., Red-cockaded Woodpecker [*Picoides borealis*] and ground cover components (e.g., Bachman's Sparrow [*Aimophila aestivalis*] of the ecosystem. Lightning-season fire has mixed effects on birds (e.g., loss of some nests, but improved brood habitat); therefore, creation of patches of different burn treatments should be carefully considered. The foremost management and conservation challenge is to increase the number of acres of southeastern pine savannas burned frequently through thoughtful application of prescribed burning. Important research challenges include measuring tradeoffs among bird species and other wildlife for different fire regimes, evaluating metapopulation effects of different landscape applications of fire, and considering the nutrient dynamics of different fire regimes on bird populations.

Key Words: birds, fire, longleaf pine, prairie, southeastern United States.

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EFECTOS DE RÉGIMEN DEL FUEGO EN AVES DE SABANAS DE PINO Y PRADERAS NATIVAS DEL SURESTE

Resumen. El fuego ha jugado un importante papel para darle forma a la estructura de la vegetación, así como a la composición de varias comunidades de plantas del sureste de los Estados Unidos. Las sabanas de pino, especialmente de pino (*Pinus palustris*) (las cuales dominaban las tierras altas de la planicie costera), han disminuido aproximadamente en un 97% durante los últimos 100 años. La consecuencia de este régimen natural de este tipo de vegetación era de un frecuencia de incendios de 2–8 años, con incendios típicos de baja severidad, los cuales ocurrieron durante la temporada de relámpagos (junio–agosto). Actualmente, en temporada de inactividad (enero a abril), se utilizan las quemas. Aproximadamente de 110–120 especies (excluyendo a las migratorias), comprenden la comunidad de aves del sureste de sabanas de pino, y algunas de estas se encuentran dentro de las especies de aves con declive mas rápido en el este de los Estados Unidos. La interrupción en el proceso del régimen natural del fuego por la exclusión del fuego o el alargamiento en el intervalo de incendios, fue determinante para las especies de aves asociadas a los árboles (e.g., Pájaro carpintero [*Picoides borealis*], en la composición de la cobertura del suelo del ecosistema (e.g., *Aimophila aestivalis*). Incendios en temporada de relámpagos tienen efectos mezclados en aves (ej. pérdida de algunos de los nidos, pero el mejoramiento del habitat de empollamiento); es por esto, que la creación de parches de distintos tratamientos de los incendios debe ser cuidadosamente considerada. El reto mayor en el manejo y la conservación, es incrementar el número de acres de sabanas de pino del sureste frecuentemente incendiadas, a través de la aplicación de quemas prescritas. Importantes retos para la investigación, incluyen la medición de los intercambios entre las especies de aves y otra fauna para los diferentes regimenes, la evaluación de los efectos de la metapoblación de distintas aplicaciones del fuego en el paisaje, y la consideración de las dinámicas de los nutrientes de los distintos regimenes de incendios en poblaciones de aves.

Many plant communities of the southeastern US have been shaped by fire for thousands of years (Komarek 1974, Myers and Ewel 1990, Boyce and Martin 1993, Frost 1998). Schmidt et al. (2002) identified 23 potential natural vegetation groups that were derived from 43 groups described by Küchler (1964) for the southeastern US (USDA Ecoregion 8: Virginia, North and South Carolina, Kentucky, Tennessee, Alabama, Mississippi, Arkansas, Louisiana, Oklahoma, and Texas). Southeastern vegetation types range along a fire-return-interval continuum from fire-free (e.g., southern floodplain forest and mangrove) to fire every 1–3 yr on average (e.g., longleaf pine [*Pinus* *palustris*] savanna, pocosin, southern cordgrass [*Spartina*] prairie, Florida dry prairie; Abrahamson and Hartnett 1990, Frost 1998). Of course, fire does not behave uniformly within any vegetation type, and each of the broad vegetation classes has other plant communities embedded within it. These communities are variably affected by fire depending on elevation, moisture gradients, and edaphic conditions. We focus this review on the southern mixed forest and wet grassland (groups 56 and 36, respectively; Schmidt et al. 2002) that form the mosaic of pine-dominated woodlands and savannas (Platt 1999) and grass-dominated prairies (Abrahamson and Hartnett 1990) in the southeastern US.

Like all disturbances, fire can be characterized by spatial distribution, frequency, return interval, rotation period, predictability, area or size, magnitude (intensity and severity), synergism, and timing or season (White and Pickett 1985). Fire in contemporary landscapes is further influenced by anthropogenic vegetation communities (e.g., post-agricultural old fields) and prescribed-fire lighting patterns. Many of these aspects of fire are interdependent. In this review we summarize studies of individual bird species and communities within the context of modern day occurrences of fire in pine savannas and native prairies in the southeastern United States.

FIRE IN SOUTHEASTERN PINE SAVANNAS AND NATIVE PRAIRIES

Spatial Extent and Characteristic Plant Species

Pre-Columbian pine savannas maintained by fire extended from southeastern Virginia to the Florida Keys and westward to Louisiana and Texas (Fig. 1). These savannas can be divided into five general classes: longleaf pine transition savannas (along the northern and western boundaries); longleaf pine-bluestem (*Andropogon* sp.) savannas (in regions of the eastern Coastal Plain and throughout the western Coastal Plain); longleaf pine-wiregrass (*Aristida* spp.) savannas (Atlantic coast and in the eastern Gulf Coastal plain south to central Florida); longleaf-slash (*Pinus elliotii*) pine wiregrass savannas (central Florida); and south Florida slash pine savannas (subtropical Florida south to the keys) (Fig. 2.1 in Platt 1999). Longleaf pine dominated or shared dominance over an estimated 37,000,000 ha of the southeastern Coastal Plain, but this amount has declined by approximately 97%, and much of what remains is in a highly altered condition (Frost 1998). Less than 1% of longleaf pine savannas remain in old-growth condition (Means 1996, Landers and Boyer 1999).

Longleaf pine savannas can be classified into four series (xeric, subxeric, mesic, and seasonally wet) and at least 23 different types based on geographic and edaphic conditions (Peet and Allard 1995). Canopy composition varies from a virtual longleaf monoculture (Schwarz 1907, Wahlenberg 1946) to a mixture of hardwoods (*Quercus, Carya*, etc.) and longleaf pine (Harcombe et al. 1995). Frequently, canopy trees are widely spaced giving an open appearance (30–40% canopy cover) that fosters development of a rich ground flora dominated by perennial plants (Drew et al. 1998). Naturally treeless prairies and pitcher plant (*Sarracenia* spp.) bogs are closely tied to and embedded in southeastern pine savannas creating a mosaic of woodland and prairie with distinct ecotones. The woodland-prairie mosaic is maintained by drainage patterns, soil types, fire, and precipitation (Frost et al. 1986, Abrahamson and Hartnett 1990). Grasslands within the longleaf pine ecosystem are among the most species-rich per unit area (30–50 species per square meter) in the Western Hemisphere (Peet and Allard 1995). In general, however, grasslands in the southeastern United States have received relatively little attention (Vogl 1972, DeSelm and Murdock 1993).

Other southeastern pines occur in stands shaped by fire, but none were as extensive as longleaf. Two pine species are less tolerant of fire than longleaf pine: slash pine is typically found in wetter sites, and loblolly pine (*Pinus taeda*) occurs in hardwood-pine mixtures, ecotones, and is extensively planted for silviculture. On the Ozark Plateau, shortleaf pine (*Pinus echinata*) is a dominant species in fire-maintained savannas, has similar structural characteristics to longleaf savannas, and supports populations of Red-cockaded Woodpecker (*Picoides borealis*) (Sparks et al. 1999). In old fields loblolly and shortleaf pines can replace longleaf pine and form a structural analog to longleaf pine savanna, although the plant community composition can be quite different (Engstrom and Palmer, in press).

Dry prairies occur in flat areas in south-central Florida. Although much of this ecosystem (830,000 ha; Kautz et al. 1993) has been converted to improved pasture, significant preserves of native prairie exist on some public and private lands (e.g., Three Lakes Wildlife Management Area, Kissimmee Prairie State Preserve, National Audubon Society Ordway-Whittell Kissimmee Prairie Sancturary, and Avon Park Bombing Range). These native prairies are treeless, fire-dependent grasslands with scattered shrubs such as saw palmetto (*Serenoa repens*), dwarf oak (*Quercus minima*), fetterbush (*Lyonia lucida*), and gallberry

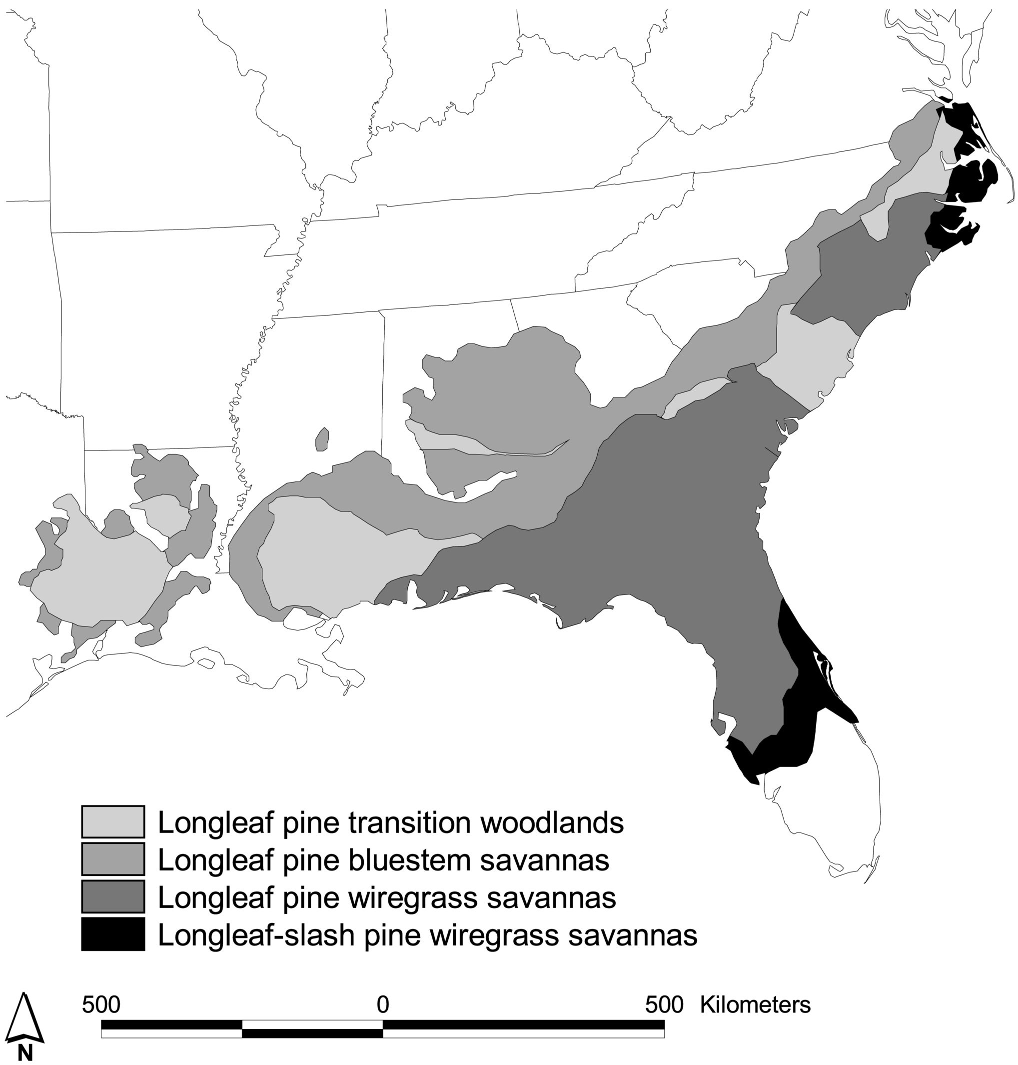

FIGURE 1. Extent of southeastern pine savannas and grasslands (after Platt 1999).

(*Ilex glabra*). Dominant grasses include wiregrass, toothache grass (*Ctenium aromaticum*), bluestem (*Andropogon* spp.), and beakrush (*Rhynchospora* spp.; Perkins et al. 1998).

Fire Regime

Fire is essential to maintenance of the structure and composition of southeastern pine savannas (Christensen 1981). Fire frequency varies according to ground cover characteristics and landscape context, but typically low fires burn only the understory vegetation and rarely burn into the canopy or kill canopy trees (Greene 1931, Harper 1962, Christensen 1981). Lightning-started fires during the peak of the thunderstorm season (May–July) probably were the most common type of fires in Florida longleaf savannas (Komarek 1968, Robbins and Myers 1992) before human settlement. American Indians in the Southeast likely used fire on the landscape for purposes such as hunting, game management, and warfare (Swanton 1946, Robbins and Myers 1992, Williams 2002), but his is not extensively documented. Fires that start in upland longleaf pine woodland can burn into adjacent habitat types depending on moisture and weather conditions, which creates a gradient of plant occurrence based on tolerance to fire and water.

The natural fire frequency in the region prior to settlement by European colonists is poorly documented, but has been estimated at every 3–4 yr (Chapman 1932) and 2–8 yr (Christensen 1981). These estimates are based on the observations that (1) lightning frequency in the Southeast is among the highest in the world with annual rates of 1–10 cloud-to-ground lightning flashes per square kilometer; (2) fuel from pyrogenic grasses and shrubs accumulates rapidly in the absence of fire; and (3) the dominant plants of southeastern pine savannas thrive in the presence of frequent fire and are commonly replaced by less fire tolerant plants over longer fire-return intervals (Chapman1932, Wahlenberg 1946, Christensen 1981, Waldrop et al. 1992, Platt 1999). The fact that open pine savannas were commonly reported by some of the earliest written accounts of vegetation conditions in southeastern coastal plain uplands strongly suggests that lightning-started fire and fires used by American Indians occurred typically more than once every 10 yr (Robbins and Myers 1992, Platt 1999). Fire intervals within pine savannas undoubtedly varied according to vegetation associated within a range of edaphic and hydrological conditions and drought cycles (Brenner 1991, Robbins and Myers 1992, Peet and Allard 1995).

Little is known about the natural fire regime of dry prairies, but the vegetation association clearly has a great tolerance of fire and many species persist because of its occurrence (Abrahamson and Hartnett 1990). Frequent (1–3 yr) fires prevent succession from graminoid to woody vegetation domination.

Modifications to the Fire Regime

Compared to the presettlement fire regime, fire interval in contemporary southeastern pine savannas commonly has been greatly lengthened or fire has been altogether excluded. (For photographic documentation of the effects of long-term fire exclusion on vegetation structure, see Myers [1990], Engstrom et al. [1984], and Woolfenden and Fitzpatrick [1984]). Fire in southeastern pine savannas has the general effect of favoring pines and grasses and suppressing hardwoods (Waldrop et al. 1992, Glitzenstein et al. 1995). Kush et al. (1999) described the effects of 45 yr of fire removal on an old-growth longleaf pine stand in the Flomaton Natural Area in Alabama. In the absence of fire, a substantial midstory dominated by water oak (*Quercus nigra*), laurel oak (*Quercus laurifolia*), southern red oak (*Quercus falcata*), and black cherry (*Prunus serotina*) developed. This hardwood midstory shaded the understory to the point that only 5% of all regenerating saplings were longleaf. This description closely follows the effects of fire exclusion on an old field pineland in north Florida (Engstrom et al. 1984) that will be described in further detail.

The modern landscape fragmented by roads, urban areas, and agricultural fields has broken up what were extensive pine savannas. Some of the earliest (16th and 17th century) explorers in the region described vast pinelands dissected by creeks and rivers (see Robbins and Myers 1992). Major roads and urban areas typically require fire-free buffers and careful smoke management that are challenges within a fire-dependent ecosystem.

Prescribed Fire

The southeastern US has a long tradition of application of fire by humans for land management purposes from prehistoric use by American Indians to the present (Komarek 1981, Johnson and Hale 2002). Few details are known about fire techniques used by American Indians in the Southeast compared to other native cultures, such as Australian aborigines (Lewis 1989), but documents indicate it was used extensively (Robbins and Myers 1992). Early Europeans, particularly English and Scottish settlers, readily adopted the use of fire for range management (Pyne 1982). Traditional uses of fire in the Southeast persisted despite a strong campaign against its use in the early twentieth century, and fire practitioners in the Southeast can be considered some of the leaders in recognizing the ecological role of fire (Johnson and Hale 2002).

Fire in the Southeast is used by a wide variety of practitioners, and the region is unique because fire is used on many private and public (especially federal) lands. Historically, fire has been used for a variety of agricultural and wildlife management purposes, and two bird species, Northern Bobwhite (*Colinus virginianus*) and Red-cockaded Woodpecker, have played especially important roles. (See discussion of these species below.) Where fire has been applied frequently in pine savannas over a long period of time (e.g., private hunting estates in Georgia, Florida, and South Carolina), prescribed fire is often applied by workers on foot using drip torches typically shortly after the end of the bobwhite hunting season. Applications on public land are more variable. Use of helicopters to apply fire is common and the season of fire is broader. Currently, prescribed burning is widely acknowledged as being essential for the long-term ecological health of the longleaf pine ecosystem (Platt 1999), but the long-term use of burning is dependent on societal acknowledgment and permission (Wade 1993).

Characteristic Bird Species of Savannas and Prairies

The avian community of this once-extensive ecosystem is composed of approximately 110–120 species, excluding species that occur only as migrants (Jackson 1988, Engstrom 1993, Hunter et al. 2001). Depending on location in woodland subtypes, approximately 40% of this avifauna is resident, 34% is found during the breeding season only, and 26% is found during the winter only (Engstrom 1993). Indicative of the importance of ground cover in this ecosystem, about one third of the species that characterize the ecosystem forage on or close to the ground or in shrubs in mature, fire-maintained woodlands. Of all southeastern pinewoods bird species, the Red-cockaded Woodpecker, Brown-headed Nuthatch (*Sitta pusilla*), and Bachman's Sparrow (*Aimophila aestivalis*) use longleaf habitats extensively and are largely sympatric with southeastern pine savannas. An endangered subspecies, Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) that is restricted to dry prairies, Northern Bobwhite (*Colinus virginianus*), because of its economic importance and historic role in use of fire, and a wintering species, Henslow's Sparrow (*Ammodramus henslowii*), are also characteristic of the region and are covered in more detail below.

Effects of Changes to Fire Regime

Fire Frequency Including Fire Exclusion

More than any other component of fire regime, fire frequency has profound effects on vegetation and associated bird life in southeastern pine savannas and prairies. After long-term fire removal, shifts from herbaceous-dominated, open pine savannas (25–60% crown closure) to hardwood pine woodland (>60% canopy cover) have contributed to dramatic declines in pine savanna bird species. Askins (1993) drew attention to widespread declines in grassland and shrubland birds and attributed the declines to loss of early successional habitat. Fire is the primary ecological factor that shaped southeastern pine savannas and native prairies, and prescribed fire is the management tool that will enable pine savanna ecosystems to persist.

Most studies of the effects of alteration of fire frequency on birds in southeastern pine savannas can be separated into two types: fire exclusion and fire reintroduction. We compared the results of two studies of the effects of fire exclusion on bird species (Engstrom et al. 1984, White et al. 1999).

Engstrom et al. (1984) reported the results of annual spot-mapping of the breeding-season avian community of an 8.9-ha study plot (named NB66). The site was an old-field pine woodland that had been burned annually until 1967, at which point fire was excluded. The woodland had developed on abandoned agricultural fields, and although it was dominated by loblolly and shortleaf pines, it was a structural analog to longleaf pine woodland. Frequent (annual or biannual) application of prescribed fire can maintain the structure of longleaf pine woodlands for decades, although recent evidence suggests that the community in old-field pine woodlands, composed of less pyrogenic plants, is not so stable (Engstrom et al. 1999). The size-class distribution of pines in the 1966 data indicated a shortage of pine recruits. Without intensive management, including soil disturbance, loblolly and shortleaf pines were not regenerating in the frequent fire regime.

During the 15 yr from 1967 through 1981, the breeding bird community lost species richness at an average rate of 0.5 species per year. Of 44 species encountered, 17 showed no clear changes following fire exclusion, 19 declined, and eight responded positively to fire exclusion (Table 1). Many of the bird species that rapidly declined on NB66 were pine woods specialists that occurred in all years on a nearby old-growth longleaf pine site and were never recorded at a nearby American beech (*Fagus grandifolia*)-southern magnolia (*Magnolia grandiflora*) forest (Engstrom et al. 1984). These same species are also declining throughout the southeastern United States (Hunter et al. 2001). Although NB66 was not replicated, had no control, and no pretreatment data were collected, the patterns of bird species loss are consistent with large-scale bird population trends. This is a strong indication of fire's role in determining vegetation composition and structure that is critical for selected bird species. The plant succession and changes in the avian community observed by Engstrom et al. (1984) may be typical of widespread habitat alteration throughout the Southeast as application of prescribed fire has declined. For example, the avian community of an old-growth longleaf pine woodland in central Florida that had obvious signs of decades of fire suppression (i.e., large diameter water oaks) lacked several of the longleaf pine specialists, such as Brown-headed Nuthatch, Red-cockaded Woodpecker, and Bachman's Sparrow (Hirth et al. 1991).

White et al. (1999) compared point-count results on 18 postfire sites (eight 1-yr postfire, six 2-yr postfire, and four 3-yr postfire) and six sites that were not burned for >20 yr during 1993–1995. Results of the 18 postfire sites were pooled because no differences

TABLE 1. RESPONSE OF INDIVIDUAL BIRD SPECIES TO FIRE EXCLUSION, FIRE REINTRODUCTION, AND FIRE SEASON. STUDY SEASON: B = BREEDING, W = WINTER. RESPONSE TO FIRE EXCLUSION WOULD BE EXPECTED TO BE THE OPPOSITE OF RESPONSE TO FIRE REINTRODUCTION. THE TWO SYMBOLS IN THE FIRE REINTRODUCTION COLUMN REFER TO RESPONSES OBSERVED IN CONTROL AND BURNED PLOTS, RESPECTIVELY.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Black Vulture	breeding			0	1
(*Coragyps atratus*)					
Turkey Vulture	dormant			0	1
(*Cathartes aura*)					
Wood Duck	breeding	–			2
(*Aix sponsa*)					
Red-shouldered Hawk	dormant			0	1
(*Buteo lineatus*)					
American Kestrel	breeding		0/0		3
(*Falco sparverius*)	dormant			0	1
Wild Turkey	breeding	0			4
(*Meleagris gallopavo*)	dormant			0	1
Northern Bobwhite	breeding	–			2
(*Colinus virginianus*)	breeding	0			4
	breeding		+/+		3
	breeding			–	6
Common Snipe	dormant			0	1
(*Gallinago gallinago*)					
Mourning Dove	breeding	0			2
(*Zenaida macroura*)	breeding	+			4
	dormant			0	1
	breeding			0	5
Yellow-billed Cuckoo	breeding	+			2
(*Coccyzus americanus*)	breeding	+			4
Common Nighthawk	breeding		0/0		3
(*Chordeiles minor*)	breeding			0	5
Red-headed Woodpecker	breeding	–			2
(*Melanerpes erythrocephalus*)	breeding	0			4
	dormant			0	1
	breeding			0	5
Red-bellied Woodpecker	breeding	0			2
(*Melanerpes carolinus*)	breeding	+			4
	dormant		0/0		6
	breeding		+/0		3
	dormant			0	1
	breeding			0	5
Yellow-bellied Sapsucker	dormant		0/0		6
(*Sphyrapicus varius*)	dormant			0	1
Downy Woodpecker	breeding	0			2
(*Picoides pubescens*)	dormant		0/0		6
	breeding	0			4
	dormant			0	1
Hairy Woodpecker	breeding	0			2
(*Picoides villosus*)	breeding	0			4
	dormant		0/0		6
	dormant			0	1
Red-cockaded Woodpecker	breeding	–			2
(*Picoides borealis*)	breeding	–			4
	dormant		+/0		6
	breeding		+/+		3
	dormant			0	1
	breeding			0	5

TABLE 1. CONTINUED.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Northern Flicker	dormant	0			2
(*Colaptes auratus*)	breeding	–			4
	breeding		+/+		3
	dormant			0	1
	breeding			0	5
Pileated Woodpecker	breeding	0			2
(*Dryocopus pileatus*)	breeding	0			4
	breeding			0	5
Eastern Wood-Pewee	breeding	–			2
(*Contopus virens*)	breeding	–			4
	dormant			0	1
Eastern Phoebe	dormant		0/0		6
(*Sayornis phoebe*)	dormant			0	1
Acadian Flycatcher (*Empidonax virescens*)	breeding	–			4
Great Crested Flycatcher	breeding	0			2
(*Myiarchus crinitus*)	breeding	+			4
	breeding			0	5
Eastern Kingbird	breeding	–			2
(*Tyrannus tyrannus*)	breeding			0	5
Loggerhead Shrike (*Lanius ludovicianus*)	breeding	–			2
White-eyed Vireo	breeding	+			2
(*Vireo griseus*)	breeding	0			4
Yellow-throated Vireo	breeding	0			2
(*Vireo flavifrons*)	breeding	–			4
Blue-headed Vireo	dormant		0/0		6
(*Vireo solitarius*)	breeding	–			4
	dormant			0	1
Red-eyed Vireo	breeding	+			2
(*Vireo olivaceus*)	breeding	–			4
Blue Jay	breeding	0			2
(*Cyanocitta cristata*)	breeding	+			4
	dormant			0	1
American Crow	breeding	0			4
(*Corvus brachyrhynchos*)	dormant			0	1
Carolina Chickadee	breeding	0			2
(*Poecile carolinensis*)	breeding	0			4
	dormant		0/0		6
	dormant			0	1
	breeding			0	5
Tufted Titmouse	breeding	0			2
(*Baeolophus bicolor*)	breeding	0			4
	dormant		0/0		6
	breeding		–/–		3
	dormant			0	1
Red-breasted Nuthatch (*Sitta canadensis*)	dormant			0	1
White-breasted Nuthatch	breeding	–			2
(*Sitta carolinensis*)	dormant			0	1
Brown-headed Nutchatch	breeding	0			2
(*Sitta pusilla*)	breeding	–			4
	dormant		0/0		6
	dormant			0	1
	breeding			0	5

TABLE 1. CONTINUED.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Carolina Wren	breeding	0			2
(*Thryothorus ludovicianus*)	breeding	–			4
	dormant			0	1
House Wren	dormant		0/0		6
(*Troglodytes aedon*)					
Golden-crowned Kinglet	dormant		x/0		6
(*Regulus satrapa*)	dormant			0	1
Ruby-crowned Kinglet	dormant		0/0		6
(*Regulus regulus*)	dormant			0	1
Blue-gray Gnatcatcher	breeding	0			2
(*Polioptila caerulea*)	breeding	–			4
	dormant		0/0		6
	breeding			0	5
Eastern Bluebird	breeding	–			2
(*Sialia sialis*)	dormant		0/+		6
	dormant			0	1
	breeding			0	5
Hermit Thrush	dormant		0/0		6
(*Catharus guttatus*)	dormant			0	1
Wood Thrush	breeding	+			2
(*Hylocichla mustelina*)	breeding	0			4
American Robin	breeding	0			4
(*Turdus migratorius*)	dormant			0	1
Gray Catbird	dormant			0	1
(*Dumetella carolinensis*)					
Brown Thrasher	breeding	0			2
(*Toxostoma rufum*)	breeding	0			4
	breeding		–/0		3
Cedar Waxwing	dormant			0	1
(*Bombycilla cedrorum*)					
Northern Parula	breeding	+			2
(*Parula americana*)	breeding	–			4
Yellow-rumped Warbler	dormant		0/0		6
(*Dendroica coronata*)	dormant			0	1
Yellow-throated Warbler	breeding	+			2
(*Dendroica dominica*)	breeding	–			4
Pine Warbler	breeding	+			2
(*Dendroica pinus*)	breeding	–			4
	dormant		0/0		6
	dormant			0	1
	breeding			0	5
Prairie Warbler	breeding	–			2
(*Dendroica discolor*)	breeding	–			4
	dormant			0	1
Palm Warbler	dormant		0/0		6
(*Dendroica palmarum*)	dormant			0	1
Black-and-White Warbler	breeding	+			4
(*Mniotilta varis*)					
Kentucky Warbler	breeding	0			4
(*Oporornis formosus*)					
Common Yellowthroat	breeding	–			2
(*Geothlypis trichas*)	breeding	–			4
	dormant			0	1
	breeding			0	5

TABLE 1. CONTINUED.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Hooded Warbler	breeding	+			2
(*Wilsonia citrina*)	breeding	0			4
Yellow-breasted Chat	breeding	–			2
(*Icteria virens*)	breeding	–			4
Summer Tanager	breeding	–			2
(*Piranga rubra*)	breeding	0			4
	breeding			0	5
Eastern Towhee	breeding	–			2
(*Pipilo erythrophthalmus*)	breeding		0/+		3
	breeding	–			4
	dormant			0	1
	breeding			0	5
Bachman's Sparrow	breeding	–			2
(*Aimophila aestivalis*)	breeding				7
	breeding	–			4
	dormant			0	1
Chipping Sparrow	dormant		0/0		6
(*Spizella passerina*)	breeding	–			4
	dormant			0	1
Field Sparrow					
(*Spizella pusilla*)	breeding	–			2
	breeding	–			4
Fox Sparrow	dormant			0	1
(*Passerella iliaca*)					
Song Sparrow	dormant			0	1
(*Melospiza melodia*)					
White-throated Sparrow	dormant			0	1
(*Zonotrichia albicollis*)					
Dark-eyed Junco	dormant		0/0		6
(*Junco hyemalis*)	dormant			0	1
Northern Cardinal	breeding	0			2
(*Cardinalis cardinalis*)	breeding	–			4
	dormant			0	1
Blue Grosbeak	breeding	–			2
(*Guiraca caerulea*)	breeding		+/+		3
Indigo Bunting	breeding	–			2
(*Passerina cyanea*)	breeding	–			4
Eastern Meadowlark	breeding			0	5
(*Sturnella magna*)					
Common Grackle	dormant			0	1
(*Quiscalus quiscula*)					
Brown-headed Cowbird	breeding	0			2
(*Molothrus ater*)	breeding	–			4
Orchard Oriole	breeding	–			2
(*Icterus spurius*)					
American Goldfinch	breeding	–			4
(*Carduelis tristis*)	dormant			0	1

[a] References: 1 = King et al. (1998); 2 = Engstrom et al. (1984); 3 = Provencher et al. (2002b); 4 = White et al. (1999); 5 = Engstrom et al. (1996); 6 = Provencher et al. (2002a); 7 = Shriver and Vickery (2001).

were detected. A comparison of the burned sites versus the fire-excluded sites indicated that of a total of 46 species, 16 showed no differences between burned and fire-excluded sites, 24 species declined, and six increased after fire was excluded (Table 1).

Thirty-seven of 53 total species were encountered in both studies (Engstrom et al. 1984, White et al. 1999). Of these 37 species six had no response to fire exclusion, the Yellow-billed Cuckoo (*Coccyzus americanus*) had a consistently positive response in both studies, nine species consistently declined, 18 species had no response in one of the studies despite showing a response in the other, and three species had contrary responses (Table 1).

Hardwood removal using herbicides or mechanical means and reintroduction of fire is being employed widely to improve Red-cockaded Woodpecker habitat on many federal lands. Breeding birds such as Northern Bobwhite and Bachman's Sparrow, that are associated with open grass- and pine-dominated savannas (Hunter et al. 2001), responded positively to hardwood removal (Burger et al. 1998, Brennan et al. 1995, Masters et al. 2002).

Experimental habitat restoration of fire-excluded longleaf pine savannas was recently conducted in northern Florida, and the effects of restoration were measured for winter (Provencher et al. 2002a) and breeding birds (Provencher et al. 2002b). Six plots (81 ha each) were randomly chosen for each of three experimental treatments and a control (no treatment) for a total of 24 plots. Habitat restoration treatments (primarily oak reduction) were: herbicides, chainsaw felling and girdling, and growing-season burns. Plots were burned in 1995 and birds were sampled in 1998 and 1999. The symbols in Table 1 (e.g., 0/0) reported for these two studies reflect the contrast of the control vs. burned plots for each of the 2 yr (1998 and 1999). For example, the '+/+' for Northern Bobwhite (Table 1) means that statistically significant increases in detections of bobwhite were made in both 1998 and 1999. A total of 29 species were counted during the 2 studies combined, but, somewhat surprisingly, only three, Red-bellied Woodpecker (*Melanerpes carolinus*), Red-cockaded Woodpecker, and Tufted Titmouse (*Baeolophus bicolor*), were found in both the winter (Provencher et al. 2002a) and breeding season (Provencher et al. 2002b). Of these three species, the Red-cockaded Woodpecker came close to increases in both years in both seasons; the Red-bellied Woodpecker showed no change in response to reintroduction of fire in all contrasts except for an increase in breeding-season detections in 1999; and the Tufted Titmouse declined in response to fire when measured in the breeding season, but showed no effect in the winter (Table 1). During the breeding-season study only, three additional species responded positively to fire (Northern Bobwhite, Northern Flicker (*Colaptes auratus*), and Blue Grosbeak (*Passerina caerulea*); Provencher et al. 2002b). During the winter study, species richness was not significantly different among the control and three treatments over the 2-yr study period, but flock size on the treated plots was larger than control plots. This increase was primarily influenced by the abundance of Chipping Sparrows (*Spizella passerina*; Provencher et al. 2002a).

Season

Debate in the Southeast about the proper season of fire developed from the observation that lightning-started fires predominantly occur between June and August, whereas most land managers century have applied fire during the dormant season (December–March) (Robbins and Myers 1992, Brennan et al. 2000; Fig. 1). The strongly seasonal natural fire regime over thousands of years must have exerted selection pressure on organisms that inhabited pine savannas (Komarek 1965). Concern about wiregrass, a pyrogenic species that has a physiological trigger to flower in the fall following fire (or other disturbance) during the late spring—early summer (Clewell 1989), further pushed the debate, because it is functionally important within portions of the southeastern pine-woodland complex (Noss 1989). Use of prescribed fire during the lightning season to better mimic the season of natural fire has increased on some land ownerships such as national forests (Ferguson 1998).

Application of prescribed fire during the lightning season is more effective at killing hardwoods and shrubs than winter or dormant-season prescribed burning (Waldrop et al. 1992). This results in maintenance of herbaceous vegetation typical of grassland communities. The possibility of more effective control of hardwoods makes lightning-season fire an attractive management technique. Counterbalancing interest in use of lightning-season, prescribed fires for vegetation management is concern that such fires will have strongly negative effects on nesting birds, particularly ground-nesting game birds (Stoddard 1931) and insects such as rare butterflies (Swengel 2001).

In field experiments over 2 yr on four replicate pairs of 12-ha plots (one dormant-season and one growing-season plot per pair), the effects of biennial dormant- and growing-season prescribed fire on bird populations in longleaf pine savannas in northern Florida were measured (Engstrom et al. 1996). Spot-mapping and nest data were collected before and after dormant- (January-February), and growing-season (May–July) prescribed fires during the treatment year (1995) and during the breeding season in the non-treatment year (1994). Breeding bird densities ranged from 11–15 pairs per plot, and 250 nests of mostly cavity-nesting and canopy species were located. No statistically significant differences in species richness or the number of territories were found between growing-season and dormant-season paired plots, nor were statistically significant differences found between pre-fire and postfire bird species richness or number of individuals in the dormant-season plots during years in which fire was applied. Growing-season prescribed fires have limited short-term effects on bird communities in longleaf pine woodland (Table 1; Engstrom et al. 1996). King et al. (1998) in a study of the effects of growing-season versus dormant-season fire in Georgia pinelands detected no significant differences in abundance in 47 species counted (Table 1).

Severity

As in many ecosystems, fire severity in southeastern pine savannas can be inversely related to fire frequency. In general, the frequent fires in well-managed longleaf pine savannas are low severity and cause little mortality in the dominant plant species. When the fire regime is disrupted and fire is excluded for extended periods, reintroduction of fire can kill even the most fire-tolerant species, such as mature longleaf pines. In a study of restoration of an old-growth longleaf pine woodland in Flomaton, Alabama, in which many large hardwoods had grown over years of fire exclusion, a low intensity-fire killed some of the oldest longleaf pine trees by severely pruning overstory feeder roots that had grown into the duff layer (Wade et al. 1998). The challenge of reintroducing fire into longleaf pine savannas after long periods of fire exclusion is being faced at several locations throughout the Southeast (e.g., Eglin Air Force Base, Florida; Moody Tract, Georgia; Chinsegut Preserve, Florida). Little documentation has been made of the avian response to severe fires that cause extensive areas of overstory mortality in southeastern pine savannas.

FIRE EFFECTS ON CHARACTERISTIC BIRD SPECIES OF SAVANNAS AND PRAIRIES

Northern Bobwhite

Research on population ecology of the Northern Bobwhite played a pivotal role in development of fire ecology in the southeastern US (Johnson and Hale 2002). Herbert Stoddard's work on the Northern Bobwhite stands as a classic monograph on wildlife management of a bird species and is additionally influential because it recognized the utility of fire as a management technique and provided an ecological basis for the role of fire in southeastern upland ecosystems (Stoddard 1931). Stoddard established the critical role of fire in maintaining ecosystem health, but he was highly concerned about negative effects (primarily loss of nests and young) of lightning-season fire on bobwhites and ground-nesting birds in general (Stoddard 1931, 1963). Seasonal application of prescribed fire in the area of north Florida to south Georgia where Stoddard lived and worked tended to occur during a narrow window immediately after the bobwhite hunting season and before bobwhites initiated nesting. As previously noted, this is not when natural, lightning-caused fires happen. Stoddard's opposition cast a long shadow on use of prescribed fire during the lightning-season when maintaining populations of bobwhites was the primary management objective. In a recent study, application of prescribed fire during May and June resulted in slight increases in arthropod biomass and slightly increased hunting success on sites burned in the lightning season versus those burned during the dormant season (Brennan et al. 2000). The authors recommended that small-scale application of lightning-season fire could be used to control hardwoods without short-term negative effects on bobwhites.

Red-cockaded Woodpecker

Since the 1970s, concern for populations of the endangered Red-cockaded Woodpecker has played a significant role in re-evaluation of the role of fire in management of southeastern pine savannas, particularly on federal lands (Ferguson 1998, Provencher et al. 2002a, 2002b). The woodpecker typically forages on living pine trees and excavates its roosting and nesting cavities in old living pine trees (Conner et al. 2001). Lengthened fire interval is one of the key agents in declines in habitat quality and population size of the Red-cockaded Woodpecker (Conner et al. 2001, Saenz et al. 2001), because this facilitates an increase in hardwoods and eventual elimination of pine regeneration that results in a slow transition from a pine-dominated to a hardwood-dominated forest. The exact mechanism that causes the Red-cockaded Woodpecker to abandon hardwood-encroached pine habitats is not fully understood, but the species avoids hardwood dominated forests and pinelands in which a hardwood midstory is thickly developed (Conner et al. 2001).

Fire also has more subtle effects on the life history of the Red-cockaded Woodpecker than setting the successional stage. The species' distinctive habit of creating wounds on the tree bole that exude resin around the cavity creates a highly flammable zone. Cavities that have copious and extensive resin flow or are low on the tree may be particularly vulnerable. Effects of burning this resin may be as minor as a temporary loss of predator or competitor inhibition, but it can cause tree death and abandonment by the woodpecker of the cavity tree. This may be most devastating if burning the resin barrier results in loss of a nesting effort, but any loss of cavity trees is important, because of the high investment by the woodpeckers to excavate the cavities. Minimizing loss of cavity trees to fire may be particularly critical in the younger pinelands following extensive harvest in the early twentieth century to the point that fuels are often reduced manually on public lands on which woodpecker population recovery is a high priority.

Use of growing season prescribed fire has been identified as a critical component of habitat management to enhance Red-cockaded Woodpecker population recovery (USDI Fish and Wildlife 2000, Conner et al. 2001). In a woodland in which fire increased nesting productivity in the first year after a fire, James et al. (1997) also found that some of the variation in group size (an important indicator of population health) could be explained by variation in composition of the ground cover. They hypothesized that nutrient cycling and variation in the arboreal arthropod community, particularly ants, are influenced by the fire regime and could play important roles in regulation of woodpecker populations.

Brown-headed Nuthatch

This species occurs almost exclusively in southeastern pine forests (Withgott and Smith 1998) where it forages on living pines and often nests in well-decayed snags and stumps. Brown-headed Nuthatch median nest height of 1.5 m throughout its range (McNair 1984) is among the lowest of North American cavity nesters (Withgott and Smith 1998). The mean egg date is 9 April ± 19 days, and 90% of the clutches are complete by 5 May (McNair 1984). The combination of low nest height and early nesting could make some nests of this species vulnerable to late dormant-season fires, although the effects of fire on nuthatch nests has not been studied to date. Fire exclusion resulted in slow decline in numbers of this species in north Florida (Table 1; Engstrom et al. 1984), and no change in abundance resulted from application of different seasons of prescribed fire (Table1).

Florida Grasshopper Sparrow

Prescribed burning is the primary management option to maintain habitat in Florida dry prairies, a formerly extensive vegetation association embedded within longleaf/south Florida slash pine savannas (Kautz et al. 1993). Fire affects vegetation by reducing litter, exposing bare ground, and reducing shrub encroachment. In a 3-yr spot-mapping study, densities and indices of reproductive success of the Florida Grasshopper Sparrow, an endangered grassland specialist, were greater in units that had been dormant-season burned within the past 6 mo compared to units that were 1.5 or 2.5 yr postfire (Shriver and Vickery 2001). To optimize dry prairie habitat for Florida Grasshopper Sparrows, burns should be conducted every 2–3 yr. This burn regime will optimize habitat for Grasshopper Sparrows without adversely affecting Bachman's Sparrows (Shriver and Vickery 2001). In a point-count study of Florida Grasshopper Sparrow response to growing-season fire (June), Shriver et al. (1999) noted that male sparrows established territories on sites within a week of the fires and initiated a second bout of breeding activity that extended into mid-August and early September. This contrasted with a steady decline in sparrow breeding activity on control plots that had been burned 3 yr earlier.

Bachman's Sparrow

Fire creates and maintains the open structure within southeastern pine savannas that are the primary habitat of this species, although it also occurs in utility right-of-ways, clearcuts, and abandoned agricultural fields. In the southern part of its range, egg dates are from late April to late August (85% in May–July) in cupped or domed ground nests (Dunning 1993). Bachman's Sparrows abandoned a site after 3 yr of fire exclusion in north Florida (Engstrom et al. 1984), but no difference in Bachman's Sparrow density was noted in a 3-yr spot-mapping study of three burn classes (0.5-yr, 1.5-yr, and 2.5-yr postfire) in dry prairie (Shriver and Vickery 2001). Counts of singing males did not differ between growing season and dormant season burned plots in north Florida (Engstrom et al. 1996); however, Seaman and Krementz (2000) found that 18 marked Bachman's Sparrows abandoned two stands burned in the growing season and did not return. They suggested that displacement of all of the marked sparrows from the growing-season burned areas could have had a negative effect on reproduction and cautioned managers against burning too much suitable breeding habitat within the same year. Seaman and Krementz (2000) did not discuss use of sites burned in the growing-season as post-breeding habitat.

Henslow's Sparrow

Henslow's Sparrow has shown one of the most extreme population declines of any landbird in eastern North America (Wells and Rosenberg 1999). This decline is caused in part by loss or degradation of grassland habitats on both the winter and breeding ranges (Peterjohn et al. 1994, Pruitt 1996, Wells and Rosenberg 1999). The winter range of Henslow's Sparrow is largely congruent with the lower coastal plain of the southeastern United States, where longleaf pine woodland was once the dominant ecosystem. Winter populations of Henslow's Sparrows have become fragmented even in the center of the winter range on the north Gulf Coastal Plain (Pruitt 1996). Some of the largest known remaining populations are located in Mississippi (Chandler and Woodrey 1995), Louisiana (Carrie et al., unpubl. data), Alabama (Plentovich et al. 1999), and northwest Florida (McNair, unpubl. data). Henslow's Sparrows in winter are often found in wet prairies and bogs that have been recently burned (<6 yr postfire); maximum abundance of sparrows occurred on sites that were burned or disturbed one growing season previously in Alabama (Plentovich et al. 1999) and on sites that had been burned within 1 yr in Louisiana (Bechtoldt and Schaefer, unpubl. report). The role of fire in management of its breeding habitat in the midwestern United States indicates that sparrow populations decline the first growing season after fire (Herkert 1994, Swengel 1996), but increase in subsequent years. Reduced populations of Henslow's Sparrows in the first year postfire appear to be related to the species' preference for dense vegetation with a well-developed litter layer and a high density of standing dead vegetation (Zimmerman 1988).

CONCLUSIONS

Some general conclusions about use of fire for conservation and management of birds in southeastern pine savannas seem clear:

1. More burning is needed in pine woodlands, savannas, and associated grasslands to retard hardwood intrusion. The continuing reduction in the number of acres burned annually in southeastern pine savannas has the effect of lengthening the fire interval. This will increase the fuel load and could increase fire severity. Planning for prescribed fire to minimize severity (i.e., overstory mortality) when a heavy fuel load is present will inevitably narrow the weather and fuel moisture conditions that are acceptable to meet management objectives. This means that fewer days may be available for burning and the risk of wildfire will increase. Use of herbicides to maintain a desired vegetation structure as an alternative to burning has been proposed (Wigley et al. 2002), but this is more expensive and its long-term effects on vegetation are unknown. At least for some rare plants (e.g., *Schwabea*), herbicides are unlikely to be an effective substitute for fire (Kirkman et al. 1998). In no way do we endorse a call for more burning at any cost. Prescribed fire must be applied thoughtfully to reduce fire severity, especially in chronically fire suppressed situations.
2. Efforts to determine natural fire regime may be overdrawn. Mimicking nature may be impossible when the relative influences of anthropogenic and natural fires are impossible to separate (e.g., natural and Native American fire regimes). We agree with Whelan (1995) and Agee (1993) that a more practical approach would be to measure the response of organisms, populations, and communities to experimentally imposed fire regimes and to set goals based on those results. Efforts to understand natural fire regimes are useful within the context of establishing a starting point for adaptive management (Engstrom et al. 1999), not as an end in itself.
3. One of our most important research challenges is to assess the tradeoffs among different species of different seasonal and landscape patterns of prescribed fire. Any management action, including use or exclusion of fire, affects bird populations. For example, use of prescribed fire improved gross habitat structure for the Red-cockaded Woodpecker, Northern Bobwhite, and other grassland birds (Brennan et al.1995, Masters et al. 2002), but negatively affected bird species associated with hardwoods. Dormant-season fire, particularly midwinter, removes cover and foraging substrate of species that are active close to the ground. Growing-season fire can eliminate the reproductive effort of some individuals (loss of eggs and young), although it may enhance the reproductive effort of others through improved

brood habitat, which sets up a compensatory dynamic within a population of a single species. Better understanding of these relations can only be derived from further scientific study, but until then, it seems practical to adopt a strategy of application of fire that is diverse in time (season and frequency) and space.

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