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FIRE ECOLOGY AND BIRD POPULATIONS IN EASTERN DECIDUOUS FORESTS

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Abstract. Eastern deciduous forests are located across the central portion of eastern North America and provide habitat for a wide diversity of bird species. The occurrence of fire in the region has been associated with the presence of humans for over 10,000 yr. While pre-European fire regimes are poorly understood, fire is widely thought to have promoted and maintained large expanses of oak forest, woodland, and savanna documented in original land surveys. Forest composition is gradually shifting from fire-tolerant oaks (*Quercus* spp.) to other species (e.g., maples [*Acer* spp.]) and suppression of fire has been implicated as a primary cause. Prescribed fire has been used successfully to restore and maintain oak savannas and has been advocated to improve the sustainability of oak forests. Fire ecology research has addressed short-term effects of prescribed fire on habitat structure, breeding bird populations, and nesting productivity. In the short term, prescribed fire reduces habitat suitability for forest-interior birds that nest on the ground and in low shrubs but provides more favorable conditions for disturbance-dependent birds associated with savannas, woodlands, and early-successional forest. The use of prescribed burning requires tradeoffs in terms of management and conservation because some bird species benefit while others are negatively affected, depending on the degree to which fire changes habitat features. There is a critical need for long-term studies to better understand the effects of different fire regimes on bird populations in the eastern deciduous forest region.

Key Words: eastern deciduous forest, fire history, fire suppression, forest-interior birds, maple, oak, prescribed fire, savanna.

ECOLOGÍA DEL FUEGO Y POBLACIONES DE AVES EN BOSQUES DECIDUOS DEL ESTE

Resumen. Los bosques deciduos del este, se encuentran en la porción central del este de Norte América, y proveen de habitat a un gran número de especies de aves. La ocurrencia de incendios en la región ha sido asociada con la presencia de humanos de hace 10,000 años. Aunque los regimenes del fuego pre-Europeos son pobremente comprendidos, se piensa que el fuego ha promovido y mantenido grandes extensiones de bosque de encino, bosques y sabanas, esto documentado en inspecciones originales de campo. La composición del bosque cambia gradualmente de encinos (*Quercus* spp.) a otras especies (ej. maples [*Acer* spp.]) siendo la supresión del fuego la principal causa. Las quemas prescritas han sido utilizadas exitosamente para restaurar y mantener sabanas de encinos y han sido soportadas, para mejorar las sustentabilidad de los bosques de encino. La investigación en ecología del fuego ha resultado en efectos de corto plazo en quemas prescritas, como en la estructura del habitat., en poblaciones de aves reproductoras y en la productividad de anidamiento. En el corto plazo, las quemas prescritas reducen los requerimientos del habitat apropiados para aves del interior del bosque, las cuales anidan en el suelo y en los arbustos bajos, pero provee condiciones más favorables para las aves dependientes de los disturbios, asociadas con sabanas, bosques, y bosques de sucesión temprana. El uso de quemas preescritas requiere intercambios en términos de manejo y conservación, ya que algunas especies de aves se benefician, mientras que otras son afectadas negativamente, dependiendo el grado en el cual el incendio cambie las características del habitat. Existe una necesidad crítica de estudios de largo plazo, para entender mejor los efectos de diferentes regimenes del fuego en poblaciones de aves en la región de bosques deciduos del este.

Eastern deciduous forests provide habitat for a wide diversity of bird species. Specific habitat requirements for resident, breeding, and migratory bird species in the region include closed-canopy forests, open woodlands, savannas, and early-successional forests (DeGraaf 1991). Bird populations in eastern deciduous forests have been the subject of increasing conservation concern as long-term declines have been detected for many species, particularly forest-interior species (Robbins et al. 1989, Sauer et al. 2001). Declines are also occurring for many bird species associated with disturbance-mediated habitats, such as savannas, woodlands, and early-successional habitats (Askins 2000, Brawn et al. 2001, Hunter et al. 2001, Sauer et al. 2001). Conservation priorities in the region should be balanced to provide a mix of habitat for both forest-interior and disturbance-dependent bird species (Askins 2000, Hunter et al. 2001). Fire was historically an important disturbance factor in some ecosystems, such as oak-dominated forests, savannas, and woodlands, providing habitat for a variety of disturbance-dependent bird species. Fire frequency declined during the period of active fire suppression, but is now increasing through experimental use of prescribed burning. Reintroduction of fire is considered to be necessary to maintain the health and sustainability of ecosystems and to provide habitat for disturbance-dependent bird species. Tradeoffs in the use of prescribed burning may be apparent, however, because some forest-interior bird species may be negatively affected by burning treatments.

Here we review the structure and composition of eastern deciduous forests, the historical and current occurrence of fire, and the effects of fire on bird populations. We focus on ecosystems in which oaks (*Quercus* spp.) are a dominant component because fire was an important process historically and prescribed fire is being advocated and used to restore and maintain these systems (Anderson et al. 1999, Brose et al. 2001, Healy and McShea 2002). Fire is much less frequent in maple-beech-birch and mixed mesophytic forests; fire regimes and effects of fire for these and other ecosystems within the region were reviewed by Wade et al. (2000).

EASTERN DECIDUOUS FORESTS: COMPOSITION AND STRUCTURE

Eastern deciduous forests as defined by Braun (1950) are located across the central portion of eastern North America (Fig. 1), currently covering 155,000,000 ha (Smith et al. 2001). The eastern deciduous forests are bounded to the north and south by coniferous forest and to the west by prairies. The boundaries between vegetation types are based on climatic conditions (Delcourt and Delcourt 2000). The northern boundary where northern hardwood forests blend into boreal forests is defined by average minimum temperatures of -40 C; the southern boundary where oak-pine forests blend into southern pine forests is defined by average minimum temperatures of 0 to -15 C; and the western boundary where oak-hickory forests and savannas make the transition into prairies is defined by annual precipitation of 60–100 cm.

Within the eastern deciduous forest region, forest types are classified based on location and dominant tree species. Oak-hickory is the dominant forest type within the region, covering 52,000,000 ha (Smith et al. 2001). This forest type, also referred to as the central hardwoods covers expansive areas in the central and southern portions of the region (Fig. 1). Oak-pine forests, forming the transition zone between oak-hickory and southern pine forests, cover 14,000,000 ha. Maple-beech and birch-aspen forests, also referred to as the northern hardwoods cover 29,000,000 ha, and are located in northern portions of the region, between oak-hickory and boreal forests. Elm-ash-cottonwood forests (not shown in Fig. 1), located along northern river and stream bottoms, cover 5,000,000 ha. Oak-gum cypress forests (also not shown in Fig. 1), located along southern river and stream bottoms, cover 12,000,000 ha.

Closed-canopy forests (>70% canopy closure) have been a predominant component of the landscape throughout the region, although the total area of such forests has changed over time due to shifts in land-use practices (Smith et al. 2001). As European settlers replaced American Indians, nearly all forests were harvested for homesteading and agriculture (e.g., crops, livestock, buildings, and firewood) or industrial uses (e.g., lumber, charcoal, and transportation). Most forest clearing was confined to the Atlantic coast prior to 1790 (Delcourt and Delcourt 2000), but a dramatic influx of settlers into the Ohio River valley occurred after 1790, resulting in widespread forest harvesting, which continued into the 20th century (Williams 1989). Since 1940, forest cover has increased in the north following abandonment of agricultural land and remained relatively stable in the south (Smith et al. 2001).

Savannas and woodlands are distinguished from forests by a more open structure, generally 10–70% canopy closure (Anderson et al. 1999). Savannas and woodlands were a significant component of the landscape in the transitional zone between eastern forests and midwestern prairies. Savannas covered some 11–13,000,000 ha at the time of European settlement (Nuzzo 1986). However, following conversion to agricultural use and succession to forest, savannas now occupy less than 1% of their former range (Nuzzo 1986, Anderson and Bowles 1999).

FIRES AND FOREST ECOLOGY

Oak-dominated forests in the region have been maintained, in part, by the recurrence of fire both before and after European settlement. Most species of oaks possess a suite of morphological and physiological traits that promote resistance to fire. These traits include thick bark, effective wound compartmentalization, high root-to-shoot ratios, the ability to sprout repeatedly after being top-killed, and drought tolerance (Crow 1988, Reich et al. 1990, Hengst and Dawson 1994, Huddle and Pallardy 1996, Smith and Sutherland 1999). Fire also creates favorable

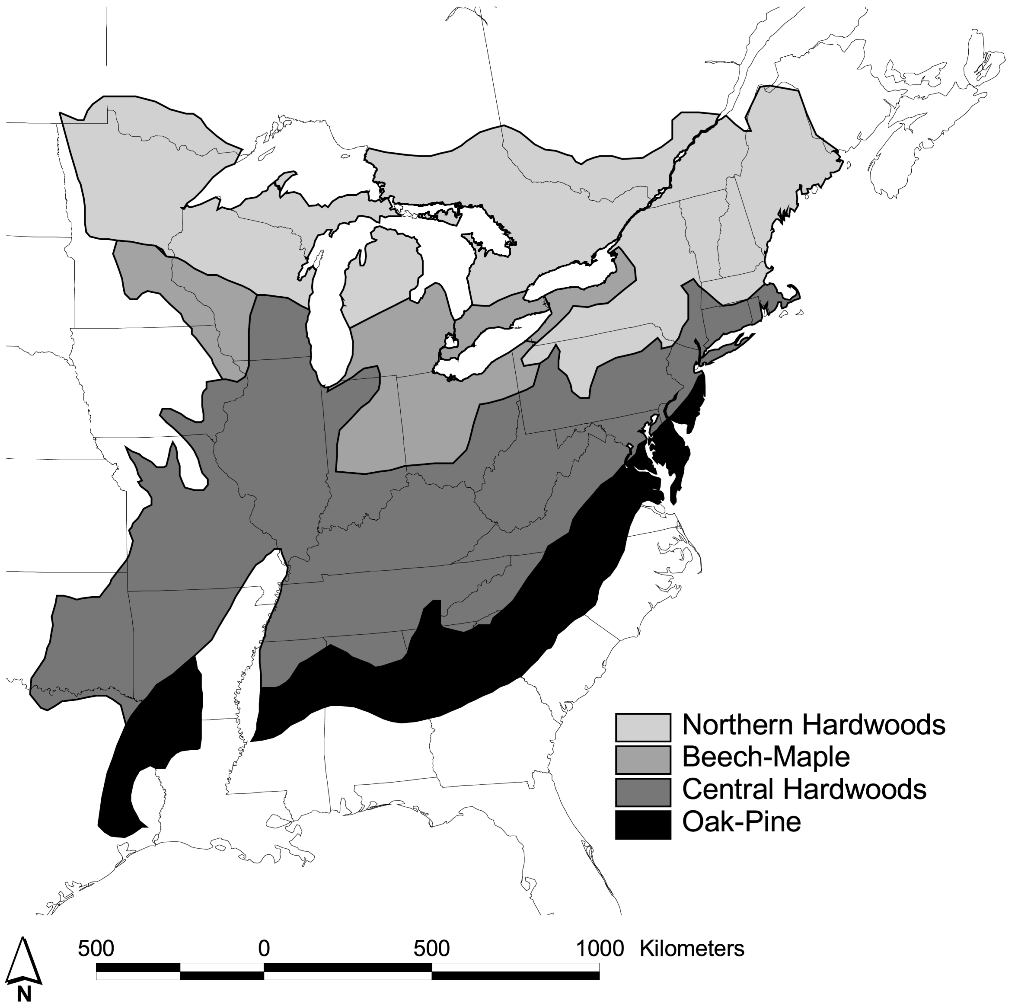

FIGURE 1. Distribution of forest land in the eastern United States by forest type (Smith et al. 2001).

conditions for oak regeneration by creating a suitable seedbed for burial and germination of acorns and reducing competition from fire-intolerant tree species (Lorimer 1985).

Fires have also been important in maintaining oak savannas and woodlands in the transitional region between eastern deciduous forests and central prairies. Frequent low-intensity surface fires control invading woody species and maintain the open structure of savannas and woodlands (White 1983, Faber-Langendoen and Davis 1995, Peterson and Reich 2001). Without recurring fire, savannas rapidly convert to closed-canopy forests, with eastern red cedar (*Juniperus virginiana*) being one of the most aggressive woody invaders (Wade et al. 2000).

Fires have been relatively unimportant in the ecology of the northern hardwood forests (Wade et al. 2000). Forests in these areas, dominated by a mix of maples (*Acer* spp.), beech (*Fagus grandifolia*), and birch (*Betula* spp.), have been called asbestos forests because fires are so uncommon (Bormann and Likens 1979). The lack of fires has been attributed to a rapid turnover of litter from high decomposition rates and minimal amounts of dead wood on the forest floor, thus limiting fuel loads (Bormann and Likens 1979). Fires in these areas occur occasionally as catastrophic, stand-replacing burns, following major windfalls such as hurricanes or tornadoes (Stearns 1949, Bormann and Likens 1979, Wade et al. 2000).

HISTORY OF FIRE

Pre- and Post-European Settlement

The history of fire in the region has been dictated by a combination of human activity, climatic conditions, and vegetation types (Wade et al. 2000). Fire regimes varied from low-intensity surface fires in the central hardwoods to high-severity stand-replacement fires in the northern hardwoods and savannas (Wade et al. 2000). Humans have been and continue to be the primary source of ignition (Leete 1938, Wade et al. 2000), although lightning-caused fires occur rarely, particularly during drought years (Ruffner and Abrams 1988). Humans have been present in the region throughout its postglacial development, and American Indian populations were large prior to European contact (Denevan 1992). Although precise fire regimes are unknown, evidence from several sources suggests that fire has been a recurring disturbance in parts of the region prior to and after European settlement, and that fire played an important role in shaping the structure and composition of vegetation.

Written accounts of the landscape by early European explorers provide evidence that Americans Indians used fire to manage the landscape for hunting, gathering, agriculture, and travel (Day 1953, Pyne 1982, Williams 1989, Whitney 1994, Bonnickson 2000). Direct observations of fire and burned-over landscapes were numerous, and indirect evidence of fire was provided by descriptions of open park-like forests. While most reviews conclude that human use of fire was frequent and widespread, Russell (1983) argued that fire was only frequent around settlements, at least in New England. However, Denevan (1992) argued that much of the landscape had recovered from intensive American Indian land use practices by the time of early European exploration and description. Bonnickson (2000) summarized early accounts of presettlement forests as consisting of "a mosaic of young, middle-aged and old pioneer forests, and dense old transitional forests and self-replacing forests." Variation in topography and human disturbance thus interacted to maintain "a dynamic and diverse landscape of people and forests" (Bonnickson 2000).

Analyses of fire scars on tree rings and fossil pollen and charcoal in peat deposits have shown that fire frequency and extent have been highly variable throughout the region (Table 1). Most variation in fire frequency has been attributed to changes in human activity, population levels, and cultural values. Fire regimes have also been affected by local topography, with the spread of fire inhibited by rugged terrain and barriers such as steep bluffs, streams, lakes, and rock outcrops (Dey and Guyette 2000, Guyette et al. 2002, Guyette et al. 2003). Weather patterns have been unimportant in influencing local fire regimes with no correspondence between fire and drought (Cutter and Guyette 1994, Sutherland 1997, Guyette et al. 2003), possibly because insufficient fuel was available to sustain fires during drought years (Cutter and Guyette 1994).

Before European settlement, fire frequency was directly correlated with population levels of American Indians. Fire frequency increased during periods of American Indian occupation and declined when American Indians moved away from specific geographic areas (Guyette and Cutter 1991, Clark and Royall 1995, Dey and Guyette 2000, Guyette et al. 2003). In southern Ontario, for example, the highest charcoal accumulation rates in sediments occurred during Iroquois occupation, from 1350–1650 (Clark and Royall 1995). Low fire frequencies at sites in Missouri, Indiana, and southcentral Ontario were attributed to movement of American Indians away from the sites (Guyette and Cutter 1991, Dey and Guyette 2000, Guyette et al. 2003).

Frequent fires associated with American Indians contributed to major changes in forest composition. Clark and Royall (1995) reported that a change in forest composition occurred 600 yr ago in southern Ontario, with oaks replacing beech and maple. The timing of this transition was substantiated by the co-occurrence of charcoal deposits, changes in abundance of oak, maple, and beech pollen, and archaeological evidence of Indian occupation. After Indian occupation ended, oaks were replaced by the more typical northern hardwood forest (Clark and Royall 1995). Similarly, Delcourt and Delcourt (1998) observed the co-occurrence of charcoal deposits and abundant oak pollen in pond and bog sediments from Kentucky, Tennessee, and North Carolina. The timing of increases in charcoal deposits and oak pollen at these sites also coincided with evidence of Indian settlement (Delcourt and Delcourt 1998).

Fires continued to occur after European settlement but the frequency varied spatially and temporally based on factors such as fuel loads, land use changes, and cultural values. Guyette et al. (2002) identified distinct stages in the history of fire regimes after European settlement, based on tree-ring analyses in Missouri: (1) from 1850–1890, greater numbers of ignitions caused frequent fires but limited the accumulation of fuels; (2) from 1890–1940, land use changes such as agricultural and rural development caused fragmentation of fuels, limiting the spread,

TABLE 1. SUMMARY OF LITERATURE ON THE FREQUENCY OF FIRE IN EASTERN DECIDUOUS FORESTS OF NORTH AMERICA.

Reference	Time	Location, habitat	Number of samples	Mean fire-return interval
Tree-ring analyses				
Guyette and Cutter 1991	1656–1989	southern Missouri, oak savanna	43	pre-1810—4.3 yr post-1810—6.4 yr
Cutter and Guyette 1994	1734–1991	Missouri, oak-hickory forest	24	pre-1850—2.8 yr post-1850—24 yr
Sutherland 1997	1856–1995	southern Ohio, mixed-oak forest	14	5.4 yr for all fires; 11.3 yr for major fires
Dey and Guyette 2000	1636–1994	southcentral Ontario, oak forest	7	Range—6–29 yr
Shumway et al. 2001	1615–1958	western Maryland, oak forest	20	7.6 yr; no fires after 1959
Guyette et al. 2002	1680–1990	southeastern Missouri, oak-pine forests	257	pre-1850—10 yr (range 2.3–45 yr) 1851–1890—3.5 yr (range 1.5–6.8 yr) 1891–1940—5.8 yr (range 1.7–19 yr) post-1940—>20 yr (range 6.8–50 yr)
Guyette et al. 2003	1650–1999	southern Indiana, barren-forest mosaic	27	Overall—8.4 yr (range 1–129 yr) pre-1820—23.0 yr (range 4–129 yr) post-1820—5.3 yr (range 1–40 yr)
Fossil pollen and charcoal analysis				
Clark and Royall 1995	pre-1360 to present	Crawford Lake, Ontario		pre-1350—low accumulation 1350–1650—accumulation with two major fires 1650–1900— low accumulation post-1900—high accumulation with no major fires

frequency, and size of fires; and (3) from 1940–1996, active fire suppression, motivated in part by increased economic value of timber, resulted in significant reductions in fire frequency. Not all evidence supports these general characterizations, however. Fire frequency was higher before than after European settlement at two sites in Missouri (Guyette and Cutter 1991, Cutter and Guyette 1994). In contrast fires occurred more frequently after European settlement at a site in southern Indiana, with burning occurring on almost an annual basis from 1896–1908 (Guyette et al. 2003). Overall, a significant heterogeneity in fire regimes occurred at the landscape scale throughout the history of the region.

Fire-suppression legislation was passed in the early 20th century in response to destructive fires that hampered reforestation efforts. The Weeks Act of 1911 provided federal funds to state forestry bureaus for fire protection on state and private lands. Funding increased in 1924 with the Clarke-McNary Act which, over time, produced an effective fire detection and suppression infrastructure (Pyne 1982). Analyses of fire scars showed that fire frequency was much lower after 1930 at sites in southern Ohio (Sutherland 1997) and western Maryland (Shumway et al. 2001). Wildfire statistics for southern Ohio (1912–2001) provide an example of the dramatic decline in the annual area burned since organized fire suppression began (Fig. 2).

As forest succession and fire suppression have proceeded in many areas, early-successional habitats have been reduced and oak-dominated forests are gradually being replaced by forests dominated by a mix of maples and beech (Griffith et al. 1993, Abrams 1998, Askins 2000, Hunter et al. 2001). In an old-growth forest in western Maryland, the overstory is currently dominated by oaks, but the recruitment layer has shifted from oaks to maple and birch, with the timing of this shift corresponding with a lack of major fires since 1930 (Shumway et al. 2001).

Current Use of Prescribed Fire

In the last 10 yr, concern has increased regarding the long-term sustainability of oak-dominated forests as has interest in the history and ecological effects of fire in the region. Prescribed fire, alone or in combination with silvicultural treatments, has been widely advocated to restore the historic fire regime, particularly in savannas and oak-dominated forests (Lorimer 1993, Van Lear and Watt 1993, Brose et al. 2001, Healy and McShea 2002). The actual use of prescribed fire, however, has been limited. Prescribed burning has been used in national

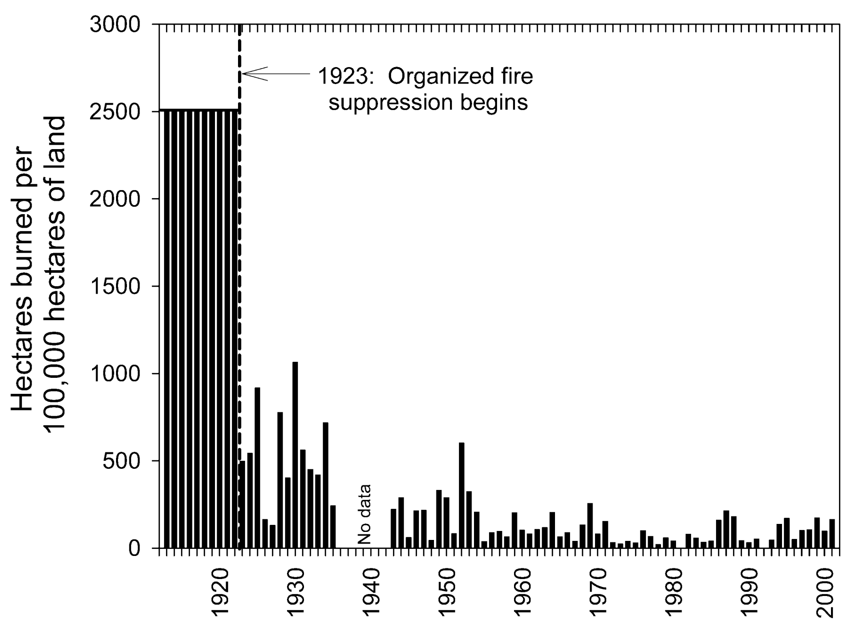

FIGURE 2. Annual area burned per 40,000 ha of land for 10 counties in southern Ohio, 1912–2001. The 1913–1922 annual value is based on an estimate that 133,418 ha (of 520,000 total forest ha) were burned within the previous 10 yr, from a 1931 Ohio Division of Forestry report titled "Forest fire control plan for Ohio." Data from 1923–1935 are from Leete (1938). Other data (1943–2001) are from Ohio Division of Forestry records.

forests to improve sustainability of oak-dominated forests, improve wildlife habitat, restore savannas, and reduce fuel loads, but the spatial extent of burning has been relatively small on most forests. Nearly 70% of forest land in the region is owned by nonindustrial private landowners (Smith et al. 2001) where prescribed fire is seldom used. Several states (Ohio, Virginia, and North Carolina) have initiated programs to certify public land managers and private citizens in the use of prescribed burns. Prescribed burning thus may be used more frequently on private lands in the future.

Most prescribed fires in the region are low- to moderate-intensity surface fires, occurring during early spring prior to the greening of vegetation or in autumn following senescence. Fewer fires occur during summer, when the canopy is closed, understory vegetation is lush, and humidity levels are high. The primary fuel is unconsolidated leaf litter. Single low-severity fires cause little mortality to overstory trees (Barnes and Van Lear 1998, Brose and Van Lear 1999, Elliott et al. 1999), but repeated fires can result in reduced tree survival (Huddle and Pallardy 1996). In contrast to the overstory, single and repeated fires result in high mortality of small trees and saplings (Barnes and Van Lear 1998, Blake and Schuette 2000). On the forest floor, the cover and richness of herbaceous plants increases and shrub cover decreases following fire (Hutchinson and Sutherland 2000). A single fire may consume 30–80% of the leaf litter and repeated fires expose mineral soil as the duff layer is also reduced (Barnes and Van Lear 1998, Boerner et al. 2000).

Although prescribed fire has been widely advocated to improve oak regeneration, short-term studies have shown mixed results. Use of prescribed fire alone (or understory removal to simulate fire) has been shown to either improve the competitive status of oaks (Lorimer et al. 1994, Barnes and Van Lear 1998) or have a neutral effect (McGee et al. 1995, Elliott et al. 1999, Kuddes-Fisher and Arthur 2002). Use of prescribed fire in combination with overstory thinning has shown positive and negative effects on the competitive status of oaks (Wendel and Smith 1986, Kruger and Reich 1997, Brose and Van Lear 1998). In part, there must be a long enough fire-free interval for oak seedlings to attain a sufficient degree of fire resistance (Johnson 1993). For example, no oak recruitment occurred from 1750–1810 in Missouri when the mean fire-return interval was only 4.3 yr (Guyette and Cutter 1991). Variation in fire frequency, with some long fire-free intervals, thus appears to be critical to oak regeneration.

BIRDS AND FIRE ECOLOGY

Prescribed Fire in Closed-canopy Forests

Little information has been published on bird responses to fire in eastern deciduous forests (Table 2). Research was conducted to assess short-term effects of prescribed fire on bird populations in closed-canopy forests in southern Ohio (Artman et al. 2001, Artman and Downhower 2003) and southern Indiana (Aquilani et al. 2000). In southern Ohio, prescribed burns were applied as a repeated series of low-intensity, surface fires with treatments occurring over a 4-yr period. Frequent sites were burned 4 yr in a row and infrequent sites were burned twice during a 4-yr period (Artman et al. 2001, Sutherland et al. 2003). All fires occurred during early spring, before leaf-out and before arrival of most migratory bird species. Bird populations were monitored 1 yr before burning, during each of the 4 yr after burning, and at control (unburned) sites for comparison. The size of burned and unburned sites ranged from 20–30 ha, and the experimental design included four replicates for each treatment. In southern Indiana, prescribed burns were applied twice during a 3-yr period (Aquilani et al. 2000). These fires also occurred during early spring. Bird populations were monitored in the burned site for 2 yr after the fires and at an adjacent unburned site for comparison. The size of each site was approximately 140 ha.

The low-intensity surface fires in both Ohio and Indiana resulted in significant reductions in population levels of several species of ground- and low-shrub-nesting bird species. Among the affected bird species were the Ovenbird (*Seiurus aurocapillus*) Worm-eating Warbler (*Helmitheros vermivorus*), Hooded Warbler (*Wilsonia citrina*), Northern Cardinal (*Cardinalis cardinalis*), and Black-and-white Warbler (*Mniotilta varia*) (Aquilani et al. 2000, Artman et al. 2001). Four years of repeated fires in southern Ohio resulted in incremental population declines, with no recovery within one year after the fires, as shown for the Hooded Warbler and Ovenbird in Fig. 3a and 3b (Artman et al. 2001). Populations of ground- and low-shrub nesting bird species continued to occur at low population levels even after the four successive years of fires (Artman et al. 2001). However, nesting success rates for ground- and low-shrub-nesting bird species were lower in burned than unburned areas in both Ohio and Indiana, possibly because nests were more exposed to predators in burned areas (Aquilani et al. 2000, Artman, unpubl. data). If prescribed fire is applied on a frequent basis or across large spatial scales in closed-canopy forests,

TABLE 2. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSE OF BIRD SPECIES (CHANGE IN ABUNDANCE) TO PRESCRIBED FIRE IN EASTERN DECIDUOUS FORESTS OF NORTH AMERICA.

Species by nest site position	State	Years after fire	Size of fire (ha)	No. replicate sites [a]	Response [b]	Reference[c]
Ground						
Black-and-white Warbler	IN	2–3	140	1 b, 1 u	–	1
(*Mniotilta varia*)	OH	1–2	20–30	8 b, 4 u	0	2
Carolina Wren	OH	1–2	20–30	8 b, 4 u	0	2
(*Thryothorus ludovicianus*)						
Field Sparrow	MN	1	8–18	5 b, 2 u	+	3
(*Spizella pusilla*)						
Kentucky Warbler	IN	2–3	140	1 b, 1 u	0	1
(*Oporornis formosus*)	OH	1–2	20–30	8 b, 4 u	0	2
Lark Sparrow	MN	1	8–18	5 b, 2 u	+	3
(*Chondestes grammacus*)						
Louisiana Waterthrush	OH	1–2	20–30	8 b, 4 u	0	2
(*Seiurus motacilla*)						
Ovenbird	IN	2–3	140	1 b, 1 u	–	1
(*Seiurus aurocapillus*)	OH	1–2	20–30	8 b, 4 u	–	2
	MN	1	8–18	5 b, 2 u	–	3
Ruffed Grouse	WV	1–2	3	10 b	+	4
(*Bonasa umbellus*)						
Vesper Sparrow	MN	1	8–18	5 b, 2 u	+	3
(*Pooecetes gramineus*)						
Wild Turkey	MS	1–5	400	26 b	+	5
(*Meleagris gallopavo*)						
Worm-eating Warbler	IN	2–3	140	5 b, 2 u	0	1
(*Helmitheros vermivorus*)	OH	1–2	20–30	8 b, 4 u	–	2
Low shrub						
Gray Catbird	MN	1	8–18	5 b, 2 u	–	3
(*Dumetella carolinensis*)						
Chestnut-sided Warbler	MN	1	8–18	5 b, 2 u	–	3
(*Dendroica pensylvanica*)						
Indigo Bunting	OH	1–2	20–30	8 b, 4 u	0	2
(*Passerina cyanea*)						
Hooded Warbler	IN	2–3	140	1 b, 1 u	0	1
(*Wilsonia citrina*)	OH	1–2	20–30	8 b, 4 u	–	2
Brown Thrasher	MN	1	8–18	5 b, 2 u	+	3
(*Toxostoma rufum*)						
Mid-story						
Acadian Flycatcher	OH	1–2	20–30	8 b, 4 u	0	2
(*Empidonax virescens*)						
American Goldfinch	MN	1	8–18	5 b, 2 u	+	3
(*Carduelis tristis*)						
American Redstart	OH	1–2	20–30	8 b, 4 u	0	2
(*Setophaga ruticilla*)						
American Robin	OH	1–2	20–30	8 b, 4 u	+	2
(*Turdus migratorius*)	MN	1	8–18	5 b, 2 u	+	3
Baltimore Oriole	MN	1	8–18	5 b, 2 u	+	3
(*Icterus galbula*)						
Cedar Waxwing	MN	1	8–18	5 b, 2 u	+	3
(*Bombycilla cedrorum*)						
Northern Cardinal	OH	1–2	20–30	8 b, 4 u	–	2
(*Cardinalis cardinalis*)						
Red-eyed Vireo	OH	1–2	20–30	8 b, 4 u	0	2
(*Vireo olivaceus*)	MN	1	8–18	5 b, 2 u	–	3
Wood Thrush	OH	1–2	20–30	8 b, 4 u	0	2
(*Hylocichla mustelina*)						

TABLE 2. CONTINUED.

Species by nest site position	State	Years after fire	Size of fire (ha)	No. replicate sites [a]	Response [b]	Reference[c]
Yellow-billed Cuckoo (*Coccyzus americanus*)	OH	1–2	20–30	8 b, 4 u	0	2
Canopy						
Blue-gray Gnatcatcher (*Polioptila caerulea*)	OH	1–2	20–30	8 b, 4 u	0	2
Blue Jay (*Cyanocitta cristata*)	OH	1–2	20–30	8 b, 4 u	0	2
Cerulean Warbler (*Dendroica cerulea*)	OH	1–2	20–30	8 b, 4 u	0	2
Eastern Kingbird (*Tyrannus tyrannus*)	MN	1	8–18	5 b, 2 u	+	3
Eastern Wood-Pewee (*Contopus virens*)	OH	1–2	20–30	8 b, 4 u	+	2
Least Flycatcher (*Empidonax minimus*)	MN	1	8–18	5 b, 2 u	–	3
Scarlet Tanager (*Piranga olivacea*)	OH	1–2	20–30	8 b, 4 u	0	2
Summer Tanager (*Piranga rubra*)	OH	1–2	20–30	8 b, 4 u	0	2
Yellow-throated Vireo (*Vireo flavifrons*)	OH	1–2	20–30	8 b, 4 u	0	2
Cavity						
Carolina Chickadee (*Poecile carolinensis*)	OH	1–2	20–30	8 b, 4 u	0	2
Downy Woodpecker (*Picoides pubescens*)	OH	1–2	20–30	8 b, 4 u	0	2
Eastern Bluebird (*Sialia sialis*)	MN	1	8–18	5 b, 2 u	+	3
Great Crested Flycatcher	OH	1–2	20–30	8 b, 4 u	0	2
(*Myiarchus crinitus*)	MN	1	8–18	5 b, 2 u	–	3
Hairy Woodpecker (*Picoides villosus*)	OH	1–2	20–30	8 b, 4 u	0	2
Northern Flicker (*Colaptes auratus*)	OH	1–2	20–30	8 b, 4 u	0	2
Pileated Woodpecker (*Dryocopus pileatus*)	OH	1–2	20–30	8 b, 4 u	0	2
Red-bellied Woodpecker (*Melanerpes carolinus*)	OH	1–2	20–30	8 b, 4 u	0	2
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	MN	1	8–18	5 b, 2 u	+	3
Tufted Titmouse (*Baeolophus bicolor*)	OH	1–2	20–30	8 b, 4 u	0	2
White-breasted Nuthatch (*Sitta carolinensis*)	OH	1–2	20–30	8 b, 4 u	0	2
Other						
Brown-headed Cowbird	IN	2–3	140	1 b, 1 u	0	1
(*Molothrus ater*)	MN	1	8–18	5 b, 2 u	+	3
Eastern Phoebe (*Sayornis phoebe*)	OH	1–2	20–30	8 b, 4 u	0	2

[a] All studies prescribed fire; b = number of burned sites; u = number of unburned sites.
[b] + = increase; – = decrease; 0 = no effect or study inconclusive.
[c] References: 1 = Aquilani et al. 2000; 2 = Artman et al. 2001; 3 = Davis et al. 2000; 4 = Rogers and Samuel 1984; 5 = Palmer et al. 1996.

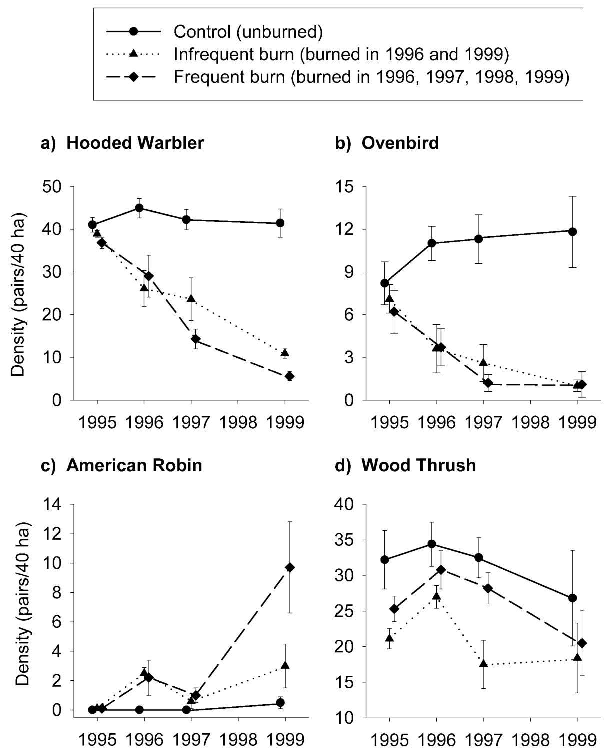

FIGURE 3. Mean (standard error) densities of bird species in relation to prescribed burning treatments in mixed-oak forests, southern Ohio; 1995 represents pre-burn conditions (Artman et al. 2001).

shifts in the composition of the breeding bird community may result from declines of ground- and low-shrub-nesting bird species (Artman et al. 2001).

Population levels of two bird species, the Eastern Wood-Pewee (*Contopus virens*) and American Robin (*Turdus migratorius*), increased in response to the fires in southern Ohio (Artman et al. 2001). Eastern Wood-Pewees were common in both burned and unburned areas, but burning may have improved their foraging habitat by creating more open and park-like conditions in the understory. American Robins did not occur in unburned areas but population levels gradually increased in response to repeated burning (Fig. 3c). Burning may increase food accessibility for ground-foraging birds such as robins by removing leaf litter, brush, and dense vegetation, exposing both seeds and insects. Ground-foraging bird species, including robins, Ovenbirds, Brown-headed Cowbirds (*Molothrus ater*), and Wood Thrushes (*Hylocichla mustelina*) were frequently observed feeding in recently burned areas in southern Ohio (Artman et al. 2001). Indeed, prescribed fire is recognized as an appropriate management strategy to improve habitat for ground-foraging gamebirds such as the Wild Turkey (*Meleagris gallopavo*) and Ruffed Grouse (*Bonasa umbellus*) (Rogers and Samuel 1984, Palmer et al. 1996).

Other bird species may be unaffected by prescribed fire, as long as low-intensity, surface fires maintain the closed-canopy forest structure. The objective of prescribed burning in southern Ohio was to maintain the existing oak-dominated forest, not to restore a different habitat type. Population levels of canopy-nesting bird species, including the Cerulean Warbler (*Dendroica cerulea*), were unaffected by the low-intensity fires in southern Ohio because the fires did not affect the density of over-story trees (Artman et al. 2001). Flexibility in habitat selection minimized effects of prescribed fire on other forest bird species. Population levels of the mid-story-nesting Wood Thrush did not differ between burned and unburned areas in southern Ohio (Fig. 3d), despite mortality of shrubs and saplings. Instead Wood Thrushes continued to inhabit recently burned areas, selecting nest patches where fire intensity was lower and placing their nests higher above the ground and in larger trees in burned than unburned areas (Artman and Downhower 2003). Nesting success of Wood

Thrushes did not differ between burned and unburned areas, suggesting that their shifts in nest site selection had no adverse consequences in terms of breeding productivity (Artman and Downhower 2003).

Prescribed Burning and Shelterwood/Thinning

Prescribed fire alone may be insufficient to maintain oak-dominated forests. Instead, a combination of prescribed fire with thinning of the canopy may be necessary to provide more light to the understory, thus promoting growth of oak recruitment. Research is currently being conducted to assess the combined effects of prescribed fire and thinning on forest bird populations in southern Ohio (D. Miles, Ohio University, pers. commun.). A combination of burning and thinning may provide habitat for a diverse community of birds, including a mix of both forest-interior species and disturbance-dependent species (Lanham et al. 2002). Shelter-wood harvesting in Missouri, for example, supported a greater diversity of birds than uncut forests, although abundance of some forest-interior species, such as the Acadian Flycatcher (*Empidonax virens*), Wood Thrush, Red-eyed Vireo (*Vireo olivaceus*), and Ovenbird, was lower in shelter-wood stands than uncut stands (Annand and Thompson 1997).

Savanna Restoration

In the transitional zone between eastern deciduous forests and midwestern prairies, prescribed fire is being used in combination with mechanical removal of vegetation to convert closed-canopy forests into a mix of forest and open grasslands to restore savannas. These treatments result in more substantial changes in bird communities, with forest-interior bird species being replaced by disturbance-dependent bird species. Research has been conducted to assess effects of savanna restoration on bird populations in Minnesota (Davis et al. 2000). Prescribed fires were applied over a 32-yr period, from 1964–1995. Fires were applied over a range of frequencies, from nearly every year to complete fire exclusion. The size of the burned areas ranged from 8–18 ha. Bird populations were monitored during 2 yr after burning (in 1995 and 1996). Restored savannas supported increased numbers of open-country and disturbance-dependent bird species, including the Red-headed Woodpecker (*Melanerpes erythrocephalus*), Eastern Bluebird (*Sialia sialis*), Baltimore Oriole (*Icterus galbula*), Indigo Bunting (*Passerina cyanea*), and Brown Thrasher (*Toxostoma rufum*). Abundance of some forest-interior bird species, including the Ovenbird, Red-eyed Vireo, and Scarlet Tanager (*Piranga olivacea*), were lower in savannas than unburned forests (Davis et al. 2000).

Studies of the local abundances of passage migrants in the Chicago area, an important migratory stopover site in the Midwest, have suggested that restoration sites offer better foraging opportunities than closed-canopy forests (Brawn and Stotz 2000). Open woodlands and early-successional habitats tend to exhibit earlier budbreak and flowering, and, presumably, arthropod abundances in these habitats are higher during the migration period (late April-May) than in closed-canopy forests that are weeks later phenologically (Brawn and Stotz 2000).

CONSERVATION IMPLICATIONS

The use of fire in eastern deciduous forests requires tradeoffs in terms of management and conservation because some bird species benefit from fire while others are negatively affected, depending on the degree to which fire changes habitat features. Frequent burning creates less favorable conditions for forest birds that nest on the ground and in low shrubs, but provides more favorable conditions for disturbance-dependent birds associated with savannas and woodlands.

Is reintroduction of fire to eastern deciduous forests restoring bird communities to what they were when fire was more prevalent in the region? It is impossible to speculate because effects of pre-European fire regimes on regional bird populations are unknown. Bird populations undoubtedly have undergone massive retractions and expansions in response to land use changes within the region. Widespread clearing of forest during the 19th century may have contributed to the extinction of the Passenger Pigeon (*Ectopistes migratorius*) and Carolina Parakeet (*Conuropsis carolinensis*) (Whitney 1994, Askins 2000). Open-country and disturbance-dependent bird species (e.g., American Crow [*Corvus brachyrhynchos*] and Red-tailed Hawk [*Buteo jamaicensis*]) replaced closely related forest species (e.g., Common Raven [*Corvus corax*] and Red-shouldered Hawk [*Buteo lineatus*]) (Whitney 1994). Restoration of forest habitat began during the early 20th century, with forest regeneration occurring on abandoned farmlands and initiation of fire suppression activities. Given extensive forest regeneration and fire suppression, population levels of some forest bird species may be at their highest level since European settlement. Widespread declines of disturbance-dependent bird species have been occurring in the region, but declines have also been observed for some forest-interior bird species (Askins 2000, Brawn et al. 2001, Sauer et al. 2001). One of the key strategies for conservation and management within the region is to maintain a balance between restoring disturbance regimes and minimizing forest fragmentation.

In general, prescribed burning is unlikely to be applied on a widespread or frequent basis in the region, given specific management objectives, economic costs, and other constraints such as land ownership. Restoration of disturbance regimes such as fire may be appropriate in more fragmented landscapes, thus minimizing effects on forest-interior bird species. The consideration of tradeoffs is necessary, however, as forest managers and conservation ecologists balance the need to maintain viable populations of bird species dependent on the entire range of successional habitats. The effectiveness of conservation strategies for birds in eastern deciduous forests requires maintaining a mosaic of habitats covering the entire successional range within and across landscapes.

FUTURE RESEARCH NEEDS

Appropriate questions for future research are:

1. What are the long-term effects of prescribed burning of varying frequencies on bird population levels, nesting success, and population sustainability?
2. What are the effects of prescribed burning on life-history characteristics such as territory size, mating success, survival, and food availability of different bird species, including forest-interior and disturbance-dependent bird species?
3. Does prescribed fire or do shifts in forest composition affect habitat suitability for forest bird species of concern, such as the Cerulean Warbler?
4. How do microsite conditions, patchiness within burns, and seasonality of fires affect bird populations?
5. What are the long-term effects of excluding and suppressing fire on bird populations and other community and ecosystem components in the region?
6. What are the appropriate criteria for deciding where and when to use prescribed fire in the context of ecosystem management?
7. Should prescribed fire be used on a more widespread or frequent basis in the region, given the historical context, specific management objectives, economic costs, and ownership constraints?
8. What is the appropriate balance of multiple resources and habitats (early-successional, savanna, late-successional, burned, unburned) given conservation concerns?

One of the most critical needs for research is to address the effects of fire frequency on forest bird populations. Previous research has focused on the immediate and short-term response of forest bird communities to prescribed fires but long-term effects and the amount of time necessary for potential recovery of reduced populations are unknown. It is essential to monitor the response of forest bird populations to a burning regime that replicates the fire-return interval of 5–7 yr that occurred before and after European settlement. Other changes may also occur on a long-term basis that are not detectable during short-term monitoring.

The importance of forest composition to bird communities in the region also remains to be determined. If current successional trends continue, oaks and hickories may be replaced by other tree species such as maple. The consequences of this shift in forest composition depend on the specific habitat requirements of particular wildlife species. Oak-dominated forests are often identified as important habitat because acorns provide a valuable and energy-rich food resource for many wildlife species (Martin et al. 1961, Kirkpatrick and Pekins 2002). Many resident bird species consume acorns but other forest species, including most Neotropical migrants, are not directly dependent on acorns or other resources provided specifically by oaks.