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FIRE REGIMES AND AVIAN RESPONSES IN THE CENTRAL TALLGRASS PRAIRIE

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Abstract. Grasslands make up the largest vegetative province in North America, and one that has been significantly altered over the past two centuries. The tallgrass prairie of the eastern Great Plains and Midwest has declined to a greater extent than any other ecosystem, primarily due to plowing for cereal grain production. Grassland bird populations have declined at a greater rate and over a wider area than any other group of species. Past fire regimes shaped and maintained the tallgrass prairie ecosystem. Fires set by American Indians and caused by lighting were common and probably differed in timing, frequency, and scale from contemporary fire regimes, although historical regimes are not well understood. Fire affects both the composition and the structure of vegetation, and can affect birds in a variety of ways. Direct effects of fire on birds include destruction of nests, while indirect effects may involve changes to vegetation, which favor some bird species over others. Greater-Prairie Chickens (*Tympanuchus cupido*), Henslow's Sparrows (*Ammodramus henslowii*), and Dickcissels (*Spiza americana*) respond negatively to annual fire. Grasshopper Sparrows (*Ammodramus savannarum*) and meadowlarks (*Sturnella* spp.) appear unaffected or respond positively to annual fire. Fire management across the largest remaining portions of tallgrass prairie frequently overemphasizes or de-emphasizes fire over large areas, creating homogenous habitat that does not support the full compliment of tallgrass prairie birds. Availability of adequately sized grasslands in a variety of seral stages is needed to ensure long-term population stability for the suite of bird species inhabiting tallgrass prairie.

Key Words: fire, grassland birds, habitat loss, habitat management, nest success, prairie ecology, tallgrass prairie, vegetation response.

RESPUESTAS DE REGÍMENES DEL FUEGO Y AVES EN LA PRADERA CENTRAL DE ZACATES ALTOS

Resumen. Los pastizales conforman el mayor tipo vegetativo de Norte América, los cuales han sido significativamente alterados en los últimos dos siglos. Los pastizales de zacate alto de las Grandes Planicies del este y del Medio oeste, han decaído mucho más que cualquier otro ecosistema, principalmente debido al arado de la tierra para la producción de granos para cereal. Las poblaciones de aves de pastizales han disminuido en un alto grado y sobre un área mayor, que cualquier otro grupo de especies. Los regimenes anteriores de incendios daban forma y mantenían los ecosistemas de zacates altos en pastizales. Los incendios provocados por los Indios Americanos y por relámpagos eran comunes y probablemente difieren de los contemporáneos en tiempo, frecuencia y escala, sin embargo, los regimenes históricos aún no son del todo comprendidos. El fuego afecta tanto a la composición como a la estructura de la vegetación, y puede afectar a las aves de varias maneras. Los efectos directos del fuego en las aves, incluyen la destrucción de los nidos, mientras que los efectos indirectos quizás involucre cambios en la vegetación, los cuales favorezcan a ciertas especies sobre otras. Los polluelos (*Tympanuchus cupido*), (*Ammodramus henslowii*), y (*Spiza americana*), responden negativamente a los incendios recurrentes. El saltamontes (*Ammodramus savannarum*) y *Sturnella* spp., parece que no son afectados, o responden positivamente a los incendios recurrentes. El manejo del fuego a lo largo de las porciones más grandes que quedan de praderas de zacates altos, frecuentemente sobre enfatiza o minimiza la importancia del fuego sobre grandes áreas, creando habitats homogéneos, los cuales no cumplen completamente con los requerimientos de las aves de las praderas de zacates altos. La disponibilidad del tamaño adecuado de los pastizales con variedad de estados serales es requerido para asegurar la estabilidad a largo plazo de las poblaciones de aves que habitan las praderas de altos pastos.

Grasslands as a whole make up the largest vegetative province in North America, once covering some 17% of the continent (Knopf 1988). Among the varied grasslands of North America, those of the Great Plains are by far the largest. The shortgrass prairie lies west of the mixed grass prairie, and both shortgrass and mixed grass prairies are more arid than the productive tallgrass prairie. I restrict my discussion of fire ecology here to the tallgrass prairie (Fig. 1) where annual precipitation varies from 60–100 cm occurring mostly during the growing season, but late summer droughts are common (Steinauer and Collins 1996, but also see Bock and Bock 1998). Seasonal temperatures range from -35–45 C. Dominant plants include warm-

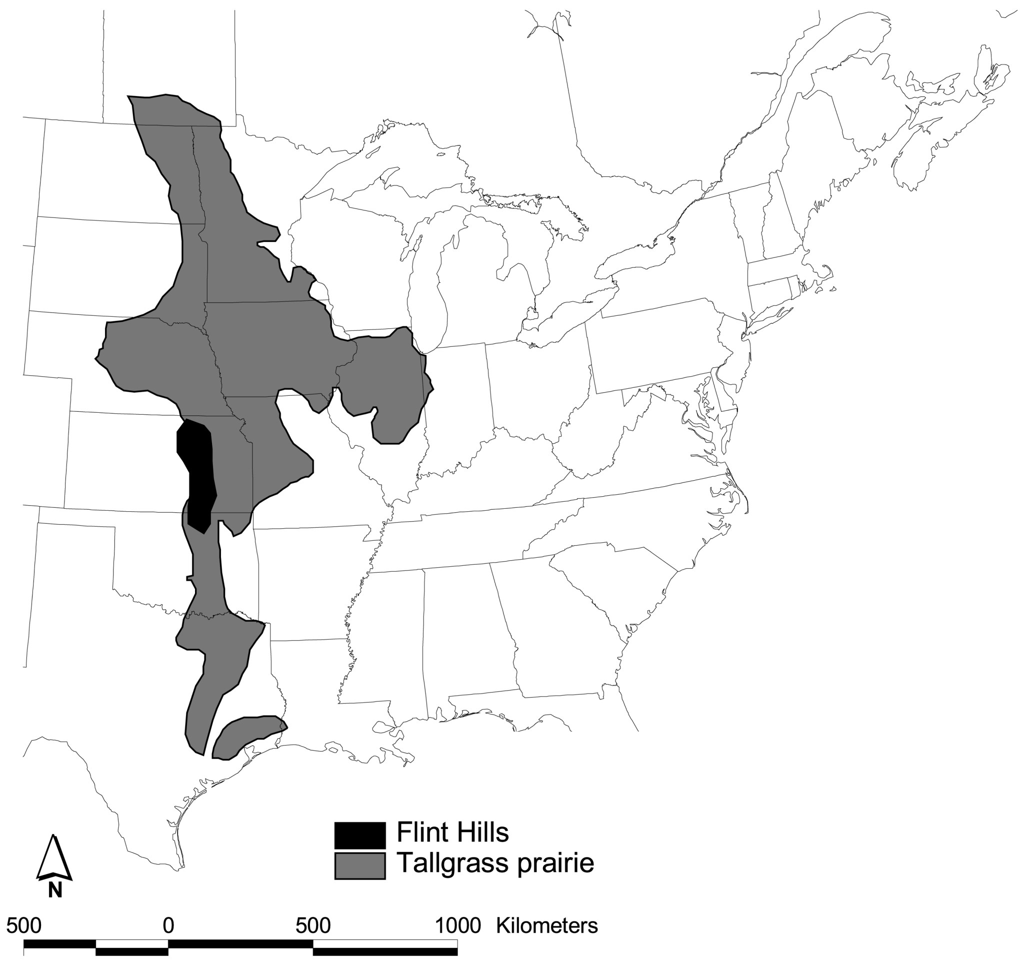

FIGURE 1. Original extent of tallgrass prairie in North America (shaded area), and location of the Flint Hills (darkly shaded area). Adapted from Steinauer and Collins (1996) and Reichman (1987).

season grasses such as big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachrium scoparius*). The tallgrass prairie once covered some 577,500 km^2 in central North America (Knopf 1988), but its level, fertile soils are ideal for cereal grain production and it has been largely plowed and converted to agricultural uses. An estimated 88–99% of the native tallgrass prairie has been lost, a decline greater than any other North American ecosystem has sustained (Vickery et al. 2000; Table 1). These landscape changes are reflected in grassland bird populations, which have shown steeper and more widespread declines than any other guild of North American species (Knopf 1994).

The tallgrass prairie is of relatively recent origin, as evidenced by its shared taxa with adjoining habitats and the scarcity of endemism (Axelrod 1985). For example, no vascular plants are known to be endemic to Kansas (Wells 1970). Despite the once extensive area of grasslands in the North American landscape, only 5% of North American bird species apparently evolved in the Great Plains (Udvardy 1958, Mengel 1970, Knopf 1994). Mengel (1970) lists 12 bird species as endemic to grasslands, most of which are found west of the tallgrass prairie region in mixed or shortgrass plains. Another 25 species are considered secondarily associated with grasslands, but occur within a larger geographic area, including habitats with trees or shrubs at the periphery of the plains (Knopf 1994). Many of these were later defined as obligate grassland species

TABLE 1. ESTIMATED ORIGINAL AND CURRENT AREA AND PERCENT OF ORIGINAL AREA OF TALLGRASS PRAIRIE. ADAPTED FROM SAMSON AND KNOPF (1994) AND STEINAUER AND COLLINS (1996).

State/Province	Historic area (ha)	Current area (ha)	Decline (%)
Manitoba	600,000	300	99.9
Illinois	8,900,000	930	99.9
Indiana	2,800,000	404	99.9
Iowa	12,500,000	12,140	99.9
Kansas	6,900,000	1,200,000	82.6
Minnesota	7,300,000	30,350	99.9
Missouri	5,700,000	30,350	99.9
Nebraska	6,100,000	123,000	98.0
North Dakota	1,200,000	1,200	99.9
Oklahoma	5,200,000	N/A	N/A
South Dakota	3,000,000	449,000	85.0
Texas	7,200,000	720,000	90.0
Wisconsin	971,000	4,000	99.9

(Vickery et al. 1999b). Among this latter group are several species commonly found in tallgrass prairie, including Greater Prairie-Chicken (*Tympanuchus cupido*), Upland Sandpiper (*Bartramia longicauda*), Eastern Meadowlark (*Sturnella magna*), Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*). All but the Upland Sandpiper have shown substantial population declines since Breeding Bird Survey monitoring efforts were initiated in 1966 (Sauer et al. 2001).

Loss and conversion of native grasslands are not the only factors affecting tallgrass prairie birds. Shaped by the forces of drought, grazing, and fire, grasslands are dynamic ecosystems (Axelrod 1985, Gibson and Hulbert 1987, Collins 1990, Coppedge et al. 1998a). These forces have dramatic effects on vegetation composition and structure, as well as on animal life. Axelrod (1985) argued that fire is a key element in the formation and maintenance of the central prairies, and Steuter (1991) emphasized the role of aboriginal peoples in shaping fire regimes. Given that historical fire regimes helped create and maintain the tallgrass prairie, existing tallgrass prairie vegetation and birds are well adapted to conditions in the Great Plains, including periodic fire. Contemporary fire regimes, however, are often very different from these in terms of timing, frequency, and scale (Howe 1994; Engle and Bidwell 2001).

HISTORICAL AND CONTEMPORARY FIRE REGIMES IN THE TALLGRASS PRAIRIE

At the outset, it must be said that our understanding of historical (i.e., pre-European settlement) fire regimes in the central grasslands is incomplete. Few interpretable biological data exist from which to elucidate historical fire regimes. The largely treeless plains offer few scarred tree rings for examination, nor extensive, long-lived woody vegetation (trees) from which to evaluate age structures of vegetation over wide areas (Higgins 1986). The mean fire interval in gallery forests in tallgrass prairie of northeastern Kansas, as determined from fire scars on trees, was estimated to be about 11–20 yr during the period 1858–1983. Because of a limited sample size, Abrams (1985) believed the actual interval to be smaller. In one innovative study, Umbanhowar (1996) tested core samples from four lakes in the northern Great Plains for charcoal concentrations which indicate fire activity, including one in South Dakota at the western edge of the tallgrass prairie. He concluded that charcoal deposition was much lower in the years following European settlement than in the years prior to it, suggesting a decrease in fire activity post-settlement.

Beyond the scanty physical evidence, our understanding of fire regimes is largely based on accounts of early explorers. This written historical record is geographically spotty, biased toward frequently traveled routes, and relies more on anecdotal comments than on observations systematic in terms of geography, timing, or observer. After considering these problems and reviewing a large number of historical accounts, Higgins (1986) concluded that for the northern Great Plains, Fires started by American Indians were mentioned much more often than lightning-caused fires in historical accounts. Indian-set fires occurred in every month except January, with peak frequency of occurrence in the months of April and October. Lightning-caused fires sharply peaked in July and August, with lesser numbers from April through June and in September. Indians used fire as a means of directing movements of bison (*Bos bison*) herds, setting relatively frequent but smaller fires for this purpose. Accidental fires were also common near Indian campgrounds. Most of the really large fires were probably lightning-caused, occurred less frequently, and may have caused hardships for tribes.

Reichman (1987, p. 106) indicates a likely fire interval of 3–4 yr, with a maximum interval of 10 yr, noting that Kansas tallgrass prairie vegetation is most productive in terms of biomass with a fire interval of 2–4 yr. Moore (1972) suggests that the highest frequency of fires in the southern plains region occurred in late summer and fall, coinciding with the peak lightning season.

The effects of fire on tallgrass prairie vegetation have been summarized by Reichman (1987, pp. 107–111). The most obvious and direct effect of fire is to remove standing dead vegetation and litter, reducing the aboveground biomass and exposing the soil to the sun. This allows the soil to warm dramatically faster in the spring, encouraging seed germination. New leaves are able to undergo photosynthesis and push upward much more easily. Fires also recycle small amounts of nutrients, such as nitrogen, which are retained in dead vegetation. Removal of the dead vegetation also allows more rainfall to reach the soil instead of being trapped above ground on vegetation where it can be lost to evaporation. Lightning changes some of the plentiful atmospheric nitrogen to a form that can be used by plants, which falls in rain. Significant amounts of the available nitrogen in tallgrass prairie result from this process, and a host of nitrogen-consuming microbes exist on dead vegetation and in litter, so their removal by fire allows more nitrogen to reach the soil where plants can use it, although frequent fires actually reduce available nitrogen. Fire also kills plants such as forbs and woody vegetation, whose growing tissues are at the top rather that at the base of the plant as in the fire-adapted grasses. All of these factors together favor biomass increases in grasses in the years immediately following a burn.

Public opinion and resulting management of tallgrass prairie has changed over time. Early ecological studies in the drought years of the 1930s resulted in the belief that fire was harmful and should be suppressed (Collins 1990). Over the subsequent decades, research began to show some of the now well-understood positive effects of burning. One study in Kansas tallgrass prairie showed a 34% increase in tree and shrub cover from 1937–1969 on unburned sites, while burned sites showed a mere 1% increase (Bragg and Hulbert 1976). Similarly, Briggs and Gibson (1992) documented a 60% increase in the number of trees in a northeastern Kansas prairie over a 5-yr period without fire, while the number of trees decreased in an annually burned area. This gives a strong indication of the importance of fire in maintaining tallgrass prairie, because woody vegetation encroached rather rapidly without fire. The rate of woody invasion in the absence of fire varies depending on topography and soil type, but such invasion seems characteristic of tallgrass prairie, which does contain trees in moist riparian areas and steep valleys. This change in relative dominance between grasses versus forbs and woody vegetation makes tallgrass prairie an example of a non-equilibrium ecological system (Knapp and Seastedt 1998). It is also important to note that the effects of disturbances such as fire and grazing on tallgrass prairie vegetation may be interactive. Collins (1987) showed that burning significantly reduced plant species diversity on ungrazed plots, while grazing significantly increased diversity on burned plots.

The vast majority of original, native tallgrass prairie has been converted to row-crop agriculture (Table 1) and no longer functions ecologically as a grassland. Virtually all of the prairie peninsula extension of the tallgrass prairie through Iowa and Illinois has yielded to the plow. What little remains of the northern and eastern portions of the original tallgrass prairie exists mostly in small areas of South Dakota, Minnesota, Missouri, and Nebraska, with additional areas in Texas (Knopf 1994, Steinauer and Collins 1996; Table 1). The decline of the tallgrass prairie has one notable exception within a relatively large landscape of eastern Kansas and northeastern Oklahoma. This region, known as the Flint Hills, consists of from 1.6–2,000,000 ha of native tallgrass prairie, and is the largest remaining such area in North America. Its existence today is a result of the region's topography and geology, with hills and shallow, rocky soils making cultivation impractical. Grazing of livestock is instead the major economic use of this area.

During recent decades, the burning of tallgrass prairie has been increasingly used as a management tool for promoting productivity of vegetation utilized by grazers, as well as for management of ungrazed areas. The percentage of cover of warm season grasses declines with time since last burning, while forbs and woody plants increase (Gibson and Hulbert 1987). The total herbage production increases with regular fire treatment, with early spring burns producing the greatest effect (Towne and Owensby 1984), provided that adequate moisture is available after the burn. In the Flint Hills, this understanding of the relationship between burning and herbage production has led to the development of a grazing system known as intensive early stocking, (hereafter IES) (Launchbaugh and Owensby 1978, Smith and Owensby 1978, Vermeire and Bidwell 1998). Under this system, prairie is burned annually or biennially in the spring, which promotes growth of warm season grasses such as big bluestem and Indiangrass. The lush re-growth of palatable, nutritious grass resulting from the burn enables managers to graze twice as many cattle (*Bos*) per unit area as would be done under a year-round, continuous grazing system. Yearling steers are allowed to graze for about 100 d before being removed in July. This allows the grass to recover from grazing pressure, rebuild fuel loads, and go to seed before winter. This system is profitable for ranchers, but results in a high percentage of land in this region receiving fire treatment nearly every year, an interval shorter than that believed to be the historical fire interval of 3–4 yr (Robbins and Ortega-Huerta 2002). The spring timing of these burns also differs from the historical timing of lightning-set fires, which were usually ignited in late summer.

Gibson (1988) evaluated the effects of a 4-yr burning interval (burning in early April) on tallgrass prairie vegetation. Total live biomass of vegetation was lowest after the fire in the year of the burn (called year 0), while biomass was significantly higher in years one, two, and three. Grass biomass, however, was highest in year 0 and 1 and declined thereafter. Biomass of forbs was lowest in year 0, and increased during the following 3 yr. A recent review of vegetation responses to fire in tallgrass prairie indicates that the conventional belief that all fires except those taking place late spring act to decrease desirable forage grasses and increase weedy forbs may not be accurate (Engle and Bidwell 2001). Burning date is just one of many factors influencing vegetation response to fire; other factors include fire frequency, grazing history, and topographic and edaphic factors. Several studies indicate some positive (from a grazing manager's perspective) responses of vegetation to early dormant-season burns (Hulbert 1988; Mitchell et al. 1996, Coppedge et al. 1998b.). Furthermore, Engle and Bidwell's review (2001) also suggests that the assumed or perceived increase in weedy forbs following an early dormant-season fire is often nonexistent or much less than believed.

Engle and Bidwell also point out the irony in the scarcity of studies evaluating the effects of late growing season fires on tallgrass vegetation, given that a high proportion of pre-settlement fires in this habitat occurred at this season. Ewing and Engle (1988) found that the effects of late summer fire on tallgrass vegetation in Oklahoma were influenced by the intensity of the fire, something that is partially dependent on fuel loads at the time of the burn. Intense late summer fires in areas with high fuel loads changed community composition by reducing warm season grasses and increasing non-matrix ruderals, though total biomass production remained consistent and matrix grasses recovered by the end of the following growing season. Engle et al. (1993, 1998) further addressed the issue of late summer fire and concluded that its effects on vegetation were variable, especially with regard to little bluestem, forbs, and cool-season, annual grasses. Such burns did not severely reduce herbage production nor drastically alter community composition for more than 1 yr. Tallgrasses tolerated growing-season fire, a result valuable to document but not too surprising, given the evolutionary history of repetitive fires in this habitat and the resulting dominance of warm-season tallgrasses.

While contemporary range management in large portions of the Flint Hills overemphasizes fire within an historical context, fire suppression in other portions of the Flint Hills and wider tallgrass prairie ecosystem has induced biologically important changes as well. As discussed above, fire acts to reduce woody vegetation and encourages dominance of warm season grasses. Fire suppression therefore allows encroachment of woody vegetation into tallgrass prairie. Among the most significant examples of this process is the invasion of eastern red cedar (*Juniperus virginiana*) and ashe juniper (*Juniperus ashei*) into western rangelands. By 1950 these two species had invaded 607,000 ha in Oklahoma; by 1985 the total was nearly 1,500,000 ha, and by 1994 almost 2,500,000 ha were occupied by these species (Engle et al. 1996). The extent of this problem goes beyond tallgrass prairie into more western grasslands, but significant portions of tallgrass prairie in Oklahoma and other states have been affected. Briggs et al. (2002) demonstrated that Kansas tallgrass prairie can be converted to closed-canopy, red cedar forest in as little as 40 yr. Junipers are well suited to colonization of prairie given their rapid growth rate, high reproductive output, and dispersal ability (Holthuizjen and Sharik 1985, Briggs et al. 2002). Housing developments in tallgrass prairie regions result in fire suppression, and residential planting of junipers for landscaping purposes exacerbates the spread of these species (Briggs et al. 2002). The effectiveness of burning as a control measure for red cedar is primarily a function of tree height (Engle and Kulbeth 1992). Red cedar trees in

Oklahoma tallgrass prairie grow faster than those located farther west in the state in more arid grasslands, and therefore fire frequency must be greater in tallgrass prairie to constrain cedar expansion (Engle and Kulbeth 1992). Juniper invasion reduces available herbaceous forage in tallgrass prairie, and therefore reduces the sustainable stocking rates for livestock (Engle et al. 1987, 1996). Annual grazing of livestock can reduce the above-ground fuel load to a point where even annual fires are not effective in controlling red cedars because the fires are of insufficient intensity to cause tree mortality (Briggs et al. 2002). This relationship between grazing, fire, and red cedar control warrants further study, and managers need to be vigilant for indications that this process may be occurring on their lands. The prompt reintroduction of fire (and/or mechanical methods of tree removal) into areas that have been burned too infrequently is needed if the widespread and rapid succession of tallgrass prairie to red cedar forest is to be halted or reversed (Engle et al. 1996).

EFFECTS OF FIRE REGIMES ON BIRDS

Too Much Fire or Not Enough?

Fire is required for the maintenance of tallgrass prairie and its associated birds. As defined by Vickery et al. (1999b), obligate grassland birds are "species that are exclusively adapted to and entirely dependent on grassland habitats and make little or no use of other habitat types... Obligate grassland birds would almost certainly become extinct without the appropriate grassland habitat." The nonequilibrium tallgrass prairie ecosystem shifts to a state of dominance by woody vegetation in the absence of fire, at the expense of the appropriate grassland habitat needed by grassland birds. As an example, the ongoing rapid invasion of tallgrass prairie by junipers, occurring largely as a result of fire suppression, has consequences for a range of tallgrass prairie species. Given known habitat preferences of Greater Prairie-Chickens (Schroeder and Robb 1993), Grasshopper Sparrows (Vickery 1996), Henslow's Sparrows (Herkert et al. 2002), and Dickcissels (Temple 2002), just to name a few, it is clear that expanding areas of red cedar forest are unlikely to support most tallgrass prairie bird species. Increased use of fire as a habitat maintenance tool is required in portions of the tallgrass prairie.

How then are birds affected by fire in the tallgrass prairie? As illustrated by the preceding section, the effects of fire on tallgrass prairie vegetation are highly variable and are dependent upon a host of factors. The effects of fire on tallgrass prairie birds are varied as well, ranging from direct effects such as nest mortality to less direct but still obvious effects on vegetation structure and subsequent habitat suitability. In some cases, fire effects on one bird species may be opposite those on another species, so management objectives must be clear to understand the relative value or harm of a tallgrass prairie fire. Several examples may help illustrate the variable nature of avian responses to tallgrass prairie fire.

Because most bird species are highly mobile, fires generally create little in the way of direct adult mortality (Reichman 1987). However, a fire occurring during a vulnerable time in the life cycle of a bird, such as the nesting season, may result in mortality of nests or recently fledged young. Early nesting species such as Greater Prairie-Chickens may be harmed by frequent spring burning of tallgrass prairie for IES grazing operations (Zimmerman 1997, Robbins and Ortega-Huerta 2002). In contrast, the use of late summer fires after the nesting season which at one time were the most frequent seasonal fires, would minimize effects on most bird species. While it is true that many species (including prairie-chickens) will re-nest after the loss of a first nest, presumably some species that may have had the opportunity to rear more than one brood in a season may be unable to do so as a result of losing a first brood.

Short-term effects of fire depend upon several factors, such as precipitation in the months following a fire. As indicated earlier, vegetative productivity of tallgrass prairie often increases following a fire, but in years of below-average rainfall, productivity in burned prairie is lower than that of unburned prairie (Hulbert 1988; Briggs et al. 1989). Zimmerman (1992) found reduced bird abundances in burned Kansas prairie during drought years for a large group of species as a whole, with striking differences for a number of individual species including Northern Bobwhite (*Colinus virginianus*), Brown Thrasher (*Toxostoma rufum*), Bell's Vireo (*Vireo belli*), Common Yellowthroat (*Geothlypis trichas*), Field Sparrow (*Spizella pusilla*), and Henslow's Sparrow.

Grassland birds are known to respond to habitat structure (Wiens 1973, Rotenberry and Wiens 1980, Bock and Webb 1984, Patterson and Best 1996, Zimmerman 1997). Frequent fires in tallgrass prairie have been shown to reduce avian diversity in part by removing woody vegetation required by many bird species (Zimmerman 1992, 1997). Frequently burned grasslands are structurally simpler than unburned grasslands, and as a result support fewer species. From studies in Kansas, Zimmerman (1992) stated "Fire has a direct structural impact on the community and eliminates certain species by affecting critical dimensions of their niches, not as a result of competitive resource partitioning, but rather by obliterating species-appropriate resource space." Henslow's Sparrows (*Ammodramus henslowii*) and Common Yellowthroats were particularly affected this way by burning in Zimmerman's study. This reduction in structural complexity of vegetation through the use of frequent fires, and the resulting reduction in avian diversity, is biologically significant given current widespread use of IES as a grazing regime. Significant portions of the Flint Hills landscape are burned annually or near-annually, creating structurally homogenous grasslands rather than the naturally occurring patchy mosaic of varying structure that once existed.

Herkert et al. (1999) monitored Northern Harrier (*Circus cyaneus*) and Short-eared Owl (*Asio flammeus*) nests in Illinois grasslands. Areas that had been mowed, burned, hayed, or grazed (all of which reduce the height or density of vegetation) during the preceding 12 mo were managed grasslands, while those that had not received any management treatment were unmanaged grasslands. Northern Harriers showed strong selection for unmanaged grasslands for nesting, while Short-eared Owls nested only in managed grasslands. These divergent habitat preferences are related to the height of vegetation in the different treatments, and possibly to the amount of standing dead vegetation as well. Harriers in the Great Plains generally nest in areas with vegetation >55 cm tall and where dead vegetation makes up at least 12% of total cover (Duebbert and Lokemoen 1977, Kantrud and Higgins 1992). In contrast, Short-eared Owls usually nest in grasslands with vegetation <50 cm tall (Duebbert and Lokemoen 1977, Kantrud and Higgins 1992).

Such contrasting responses to changes in vegetation structure are apparent in passerines as well. At The Nature Conservancy's Tallgrass Prairie Preserve in northeastern Oklahoma, study plots were monitored for nesting birds and habitat changes in response to land management from 1992–1996. Avian relative abundance data and vegetation structure data were collected on plots with differing fire and grazing histories. Relative abundance of Grasshopper Sparrows following a burn was highest and essentially stable in year 0 and one, but declined with each passing year in the absence of fire through year six, the longest interval measured (G. M. Sutton Avian Research Center, unpubl. data). No Henslow's Sparrows were detected in areas which were 0 and 1 yr after burning, while areas 2, 3, and >3 yr after burning all contained similar numbers of birds (Reinking et al. 2000). Vegetation height and structure are dramatically different in areas recently burned versus areas that have not been burned for several years. Results from this and other studies indicate that Grasshopper Sparrows prefer areas with sparser vegetation (at least in tallgrass prairie), while Henslow's Sparrows require areas with tall, dense, vegetation (also see Dechant et al. 2001, Herkert 2001; Table 2). Annual burning therefore seems either to benefit or at least pose little threat to Grasshopper Sparrows in tallgrass prairie, while effectively eliminating suitable habitat for Henslow's Sparrows (Table 2).

Avian abundance in response to habitat manipulation is usually apparent and relatively easy to measure by point counts or other survey methods. Other potential effects of fire on birds, such as nest success, may be more subtle or harder to measure, or may interact with other factors such as grazing, complicating our interpretation of observed responses to fire. Nest success is a critical demographic parameter for managing bird populations and may not be correlated with relative abundance, which is easier to measure (Van Horne 1983, Maurer 1986, Vickery et al. 1992). Fire may affect nest success through changes in vegetation height and density, potentially providing nest predators with either easier or harder access to nests. Johnson and Temple (1990) found several grassland birds in Minnesota to have higher nest success in areas that had been recently burned. They attributed this response to the tall, dense re-growth following a fire providing better nest concealment, along with increased seed and insect production, allowing more time to be spent in nest defense and less time in foraging.

Fires have varied effects on insect diversity and abundance (Swengel 2001), with grasshoppers and predaceous ground beetles becoming much more abundant in the months following a fire. Zimmerman (1997) found no increase in either nest success or in fledging weights of young from successful nests for a number of species including Dickcissels, Eastern Meadowlarks, Red-winged Blackbirds (*Agelaius phoeniceus*), or Mourning Doves (*Zenaida macroura*) in burned versus unburned Kansas prairie and concluded that food was not a limiting resource, even in unburned prairie.

In the largest remaining area of tallgrass prairie, the Flint Hills, it is often difficult to separate the effects of fire from those of grazing, given the near-ubiquitous and closely associated burning and grazing of grasslands in this region. Both Zimmerman (1997) and Rohrbaugh et al. (1999) found reduced

TABLE 2. SHORT-TERM RESPONSES TO PRESCRIBED FIRE IN TALLGRASS PRAIRIE FOR SELECTED SPECIES. ALL STUDIES TOOK PLACE DURING THE BREEDING SEASON. YEAR 0 REPRESENTS THE NESTING SEASON FOLLOWING A SPRING FIRE. N/A MEANS NOT APPLICABLE OR NOT REPORTED.

Species	State	Year after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Northern Harrier	Kansas	0–1	variable	several	m	1	Nested in unburned; foraged in burned.
(*Circus cyaneus*)	Illinois	0–1	8–120	17	–	2	Mowing used more than burning.
Greater Prairie-Chicken	Kansas	0	N/A	N/A	–	3	Spring fires cause direct mortality of early nesters.
(*Tympanuchus cupido*)	Kansas	0	variable	many	–	4	No population declines where rangeland is not burned annually.
Upland Sandpiper	Wisconsin	0–1?	N/A	several	–	5	No nesting in year with burning.
(*Bartramia longicauda*)	Kansas	N/A	N/A	N/A	0	6	
	Kansas	0	varied	several	m	1	No nesting in burned areas during year of fire; foraged in burned areas.
Short-eared Owl (*Asio flammeus*)	Illinois	0–1	8–120	17	+	2	Mowing used more than burning.
Grasshopper Sparrow (*Ammodramus savannarum*)	Minnesota	0–3	16–486	8	+	7	Nest success declined with ≥4 yr since burning in larger fragments.
	Kansas	0	varied	2 burned; 7 unburned	0	1, 3, 8	Relative abundance similar in burned and unburned areas.
	Illinois	1–3	0.4–650	11	+	9	More abundant in recently burned areas.
	Missouri	varied	6–571	42	+	10	Declined with increasing time since last disturbance.
	Kansas	0	9.3–13.8	10	+	11	More abundant in burned tallgrass than in burned CRP fields.
	Kansas	0–4	9.7–16.8	12	0	12	Abundance non-significantly greater in burned areas.
	Missouri	0–2	31–1084	13	0	13	Abundance not affected by burning.
	Oklahoma	0–3+	>16	6	0	14	Nest success, clutch size and number fledged per successful nest did not differ in burned vs. unburned. Nesting densities declined with time since last burn.
Henslow's Sparrow	Kansas	0	varied	4	–	3, 15	
(*Ammodramus henslowii*)	Oklahoma	0	varied	20	–	16	Nests only in areas not recently burned.
	Kansas	0	9.8–39.1	14	–	17	Absent in spring burns.
	Illinois	0–2	0.5–650	24	–	9, 18	Absent in year 0, present in year 1, more abundant in year 2 after fire.
	Missouri	0–3	6–571	42	–	10	More abundant in yr 1–3 after a fire than in year 0.
	Missouri	0–2	31–1084	13	–	13	Reduced abundance in year 0 of fire; numbers increased by yr 1 and 2 after fire.
	Illinois	0–4	125–300	3	–	19	Nearly absent in year 0 after a burn; present in similar numbers in yr 1, 2, 3, and 4 after fire.

TABLE 2. CONTINUED.

Species	State	Year after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Henslow's Sparrow (*continued*)	Kansas	0–2	N/A	N/A	–	20	Mostly absent in yr 0 and 1 following a burn; present in yr 2 and 3 after fire.
	Oklahoma	0–3+	varied	5	–	21	Absent in yr 0 and 1 after burn; similar numbers in yr 2, 3 and >3 after fire.
Dickcissel (*Spiza americana*)	Illinois	0–5+	1.5–48.2	139	–	22	Peak nest density in year 2 after burn.
	Kansas	0	varied	2 burned, 7 unburned	0	1, 8	Abundance unaffected by burning.
	Missouri	0–3	6–571	42	0	10	Abundance unaffected by burning.
	Kansas	0	varied	2 burned, 7 unburned	–	3	When combined with grazing, burning reduced abundance and nest success.
	Kansas	0–4	9.7–16.8	12	–	12	Abundance and nest success lower in year 0 after a burn.
	Missouri	0–2	31–1084	13	0	13	
	Oklahoma	0–3+	>16	6	–	14	Nest success lower in burned and grazed areas; nest numbers, clutch size, and number fledged per successful nest did not differ.
Eastern Meadowlark (*Sturnella magna*)	Illinois	0–5+	1.5–48.2	139	0	22	Nest density similar in burned and unburned areas.
	Kansas	0	varied	2 burned, 7 unburned	0	1, 3, 8	
	Illinois	0–2	0.5–650	24	0	9	
	Missouri	0–2	31–1084	13	0	13	Abundance slightly lower in year 0 after burn than in later yr.
	Oklahoma	0–3+	>16	6	0	14	Nest success, clutch size, and number fledged per successful nest did not differ in burned and grazed areas vs. unburned/ungrazed areas; nest numbers declined in unburned areas over time.
(*Sturnella* spp.)	Kansas	0–4	9.7–16.8	12	+	12	Abundance increased in year 0 after burn.

[a] All reported fires were prescribed.
[b] + = positive; – = negative; 0 = no effect or study inconclusive; m = mixed response.
[c] References: 1 = Zimmerman (1993); 2 = Herkert et al. (1999); 3 = Zimmerman (1997); 4 = Robbins and Ortega-Huerta (2002); 5 = Buss and Hawkins (1939); 6 = Bowen (1976); 7 = Johnson and Temple (1990); 8 = Zimmerman (1992); 9 = Herkert 1994a; 10 = Swengel (1996); 11 = Klute et al. (1997); 12 = Robel et al. (1998); 13 = Winter (1998); 14 = Rohrbaugh et al. 1999; 15 = Zimmerman (1988); 16 = Reinking and Hendricks (1993); 17 = Schulenberg et al. (1994); 18 = Herkert (1994b); 19 = Herkert and Glass (1999); 20 = Cully and Michaels (2000); 21 = Reinking et al. (2000); 22 = Westemeier and Buhnerkampe 1983.

nest success rates for Dickcissels in burned and grazed tallgrass prairie of Kansas and Oklahoma, respectively. Zimmerman's study did not indicate reduced nest survival in grazed but unburned prairie, nor in burned but ungrazed prairie. These studies provide examples about bird responses to factors that interact with fire, which are potentially different from conditions produced by fire alone. Rohrbaugh et al. (1999) found no difference in clutch size or in the number of young fledged per successful nest for Dickcissel, Grasshopper Sparrow, or Eastern Meadowlark between burned/grazed plots versus unburned/ ungrazed plots. Zimmerman (1997) also noted no differences in fledging weights of birds in burned versus unburned areas.

Mechanisms behind observed nest success differences in burned/grazed versus unburned/ungrazed prairie are not well understood. The close association between burning and subsequent grazing in this region makes separation of the effects of fire from those of grazing difficult to interpret, but both disturbances act to reduce vegetation density. Fretwell (1977) argued that density of Dickcissels was significantly related to nest predation rates. Zimmerman (1984), however, demonstrated that there was no density-dependent effect on nest predation rates in this species. Askins (2000) suggested that the succulence and nutrition of new vegetation growth resulting from a fire provides increased foraging opportunities for grazers (such as insects), and consequently such areas also offer better foraging for insect predators, including birds and other vertebrates. By inference, this suggests that potential nest predators could also benefit from increased prey biomass in recently burned areas.

Relatively little research has been conducted on the winter ecology of tallgrass prairie birds. Zimmerman (1993) reported a mean species richness of 7.7 and 1.2 during winter in unburned prairie and annually burned prairie, respectively. American Tree Sparrows (*Spizella arborea*) and Northern Harriers were the only species regularly found in annually burned areas and both were more abundant in unburned areas.

PERSPECTIVES IN MANAGING AND UNDERSTANDING THE CENTRAL TALLGRASS PRAIRIE

Tallgrass prairie habitat continues to be lost (Warner 1994), making effective management of remaining prairie critical to sustaining grassland bird populations. In portions of remaining tallgrass prairie, fire is under utilized (Engle et al. 1996, Briggs et al. 2002), a trend that if not halted and reversed will have increasingly severe consequences for grassland birds. Understanding the consequences of different fire-return intervals is necessary for maintaining the long-term floristic and faunal diversity of the tallgrass prairie. When fire is applied at a shorter return interval than is considered natural for this ecosystem (Robbins and Ortega-Huerta 2002), the objective is usually to promote dominance of a few livestock forage species (Fuhlendorf and Engle 2001). This leads to reduced structural diversity in vegetation, which then results in reduced bird species diversity owing to exclusion of some species, and may reduce nest success in others (Table 2).

Patch burning involves burning roughly one-third of a given area in each year (Fuhlendorf and Engle 2001). This creates focal points of intense herbivory, results in a fire-return interval of 3 yr, leads to increased structural heterogeneity, and, at least initially, appears to be productive in terms of herbivore response. This management regime is probably closer to the natural patterns and processes of tallgrass prairie (Howe 1994). Burning annually (IES) or taking no action to reduce encroachment of red cedar both create large areas of homogenous habitat that do not support the full complement of grassland bird species. Results of several studies have demonstrated area sensitivity in a number of grassland bird species (Johnson and Temple 1986; Herkert 1994a, 1994c; Vickery et al. 1994; Winter 1998). Species-specific area requirements reported by Herkert (1994c) for Illinois include 5 ha for Eastern Meadowlark, 30 ha for Grasshopper Sparrow, and 55 ha for Henslow's Sparrow. In Missouri, Upland Sandpipers occurred only in grasslands larger than 75 ha, and while Dickcissel density was not correlated with fragment size, nest success in this species was positively correlated with fragment size (Winter 1998). This underscores the importance of collecting and using demographic population measures in addition to population density when evaluating the effects of fragment size. Samson (1980) indicated that >100 ha were needed for Greater Prairie-Chickens, though a total of 4,000–8,000 ha has recently been suggested as a necessary land area for sustaining a healthy population of this species (Bidwell 2003).

Historical evidence suggests that pre-settlement tallgrass prairie fires took place at irregular intervals of perhaps 3–10 yr in any given area. Fires were ignited by both American Indians and by lightning at various times of the year but especially in late summer. Contemporary use of fire in tallgrass prairie is a necessary and powerful management tool that can yield dramatic results in terms of the response of both vegetation and birds. Fire and grazing today rarely operate at the same frequency or with the same seasonality as they did historically, and certainly not at the same scale. Contemporary fire regimes have been altered for a variety of reasons, including agriculture, development to accommodate expanding human populations, profitability of ranching, and changes in our understanding of the importance and consequences of fire in the tallgrass prairie ecosystem. In Oklahoma, areas of low human population density favor Neotropical migrants, ground and shrub-nesting species, and three obligate grassland species (Greater Prairie-Chicken, Grasshopper Sparrow and Dickcissel), whereas areas of high human population density favored habitat generalist species (e.g., European Starling [*Sturnus vulgaris*], Common Grackle [*Quiscalus quiscula*], and House Sparrow [*Passer domesticus*]; Boren et al.1999). As human populations and land development increase, effective management of remaining tallgrass prairie becomes increasingly important.

Long-term research on the interactions of fire, vegetation, and bison grazing has been conducted at both the 3,500-ha Konza Prairie near Manhattan, Kansas, and at the Tallgrass Prairie Preserve, a 15,700-ha property managed by The Nature Conservancy in northeastern Oklahoma (Vinton et al. 1993, Hamilton 1996, Hartnett et al. 1996, Coppedge et al. 1998a; Knapp and Seastedt 1998). Monitoring is ongoing to understand avian responses to the developing mosaic of habitats created by dynamic applications of fire and grazing (i.e., patch burning). Studies examining the relationships among vegetative, invertebrate, and vertebrate responses to varying applications of fire and grazing will help our understanding of land management activities to sustain tallgrass prairie systems. Additional research into the mechanisms behind nest success differences among disturbance regimes will help managers in sustaining bird populations. Perhaps most useful would be intensive nest monitoring using cameras or other technology to determine the identity of the significant nest predators, together with measures of predator abundance in areas subjected to differing fire applications. The reported reduction in nest success for several bird species in burned and grazed prairie suggests that this relationship between disturbances and nest predation rates is important for prairie management. Predator species and key factors (vegetation structure, food availability, or others alone or in combination) influencing the abundance of these birds remain unclear. More evaluation on the economics (from a ranching perspective) of patch burning in tallgrass prairie will help in deciding the extent to which such management techniques can be implemented. Finally, further investigation of the winter ecology of tallgrass prairie birds is also needed to determine the effects of prairie burning on birds during this understudied but critical period of the avian life cycle.

Current widespread use of annual or near-annual burning in the spring, together with widespread lack of burning in other areas, promotes a single type of grassland habitat available to birds. Such uniformity of management does not provide adequate habitat for the suite of tallgrass prairie bird species. A shift to more varied fire regimes, which still maintain the profitability of ranching, would allow for greater avian species diversity and potentially higher nest success as well.

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