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CONSERVATION OF GRASSLAND BIRDS IN NORTH AMERICA: UNDERSTANDING ECOLOGICAL PROCESSES IN DIFFERENT REGIONS

Report of the AOU Committee on Conservation

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Abstract.—Many species of birds that depend on grassland or savanna habitats have shown substantial overall population declines in North America. To understand the causes of these declines, we examined the habitat requirements of birds in six types of grassland in different regions of the continent. Open habitats were originally maintained by ecological drivers (continual and pervasive ecological processes) such as drought, grazing, and fire in tallgrass prairie, mixed-grass prairie, shortgrass prairie, desert grassland, and longleaf pine savanna. By contrast, grasslands were created by occasional disturbances (e.g., fires or beaver [*Castor canadensis*] activity) in much of northeastern North America. The relative importance of particular drivers or disturbances differed among regions. Keystone mammal species—grazers such as prairie-dogs (*Cynomys* spp.) and bison (*Bison bison*) in western prairies, and dam-building beavers in eastern deciduous forests—played a crucial, and frequently unappreciated, role in maintaining many grassland systems. Although fire was important in preventing invasion of woody plants in the tallgrass and moist mixed prairies, grazing played a more important role in maintaining the typical grassland vegetation of shortgrass prairies and desert grasslands. Heavy grazing by prairie-dogs or bison created a low "grazing lawn" that is the preferred habitat for many grassland bird species that are restricted to the shortgrass prairie and desert grasslands.

Ultimately, many species of grassland birds are vulnerable because people destroyed their breeding, migratory, and wintering habitat, either directly by converting it to farmland and building lots, or indirectly by modifying grazing patterns, suppressing fires, or interfering with other ecological processes that originally sustained open grassland. Understanding the ecological processes that originally maintained grassland systems is critically important for efforts to improve, restore, or create habitat for grassland birds and other grassland organisms. Consequently, preservation of large areas of natural or seminatural grassland, where these processes can be studied and core populations of grassland birds can flourish, should be a high priority. However, some grassland birds now primarily depend on artificial habitats that are managed to maximize production of livestock, timber, or other products. With a sound understanding of the habitat requirements of grassland birds and the processes that originally shaped their habitats, it should be possible to manage populations sustainably on "working land" such as cattle ranches, farms, and pine plantations. Proper management of private land will be critical for preserving adequate breeding, migratory, and winter habitat for grassland and savanna species. *Received 12 December 2006, accepted 24 April 2007.*

Resumen.—Muchas especies de aves que dependen de habitats de pastizal o savana han mostrado disminuciones significativas en sus poblaciones en Norte America. Para poder entender las causas de estas disminuciones examinamos los requerimientos de habitat de aves

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en seis regiones del continente. Habitats abiertos originalmente se mantenían por conductores ecológicos (procesos ecológicos continuos y perdurables), como sequía, pastoreo, y/o fuego como en praderas de pastizal alto, mediano, y corto, pastizal desértico y sabana de pino de hoja larga. En contraste, los pastizales se crearon por disturbios ocasionales (fuego o actividad de castores) en el noreste de Norte America. Especies claves de mamíferos (como perrito de las praderas y bisonte en las praderas del oeste y castores en bosque deciduos del este) jugaron un papel crucial, y frecuentemente no apreciado, manteniendo sistemas de pastizales. Mientras el fuego fue importante en prevenir la invasión de especies leñosas en praderas de pastizal alto y mediano, el pastoreo jugo un papel mas importante en mantener la vegetación típica de pastizales cortos y desérticos. Alta presión de pastoreo por perrito de las praderas y bisontes crearon una capa de "césped pastoreado" que es el habitat preferido por algunas especies de aves de pastizal que están restringidas a las Grandes Planicies y pastizales desérticos.

Muchas especies de aves de pastizal estan vulnerables porque la actividad humana ha destruido sus habitats de anidacion, migración e invernacion directamente mediante la conversión a áreas de cultivo o construcción, o indirectamente mediante la modificación de patrones de pastoreo, supresión de fuego, o interfiriendo con otros procesos ecológicos que originalmente mantenían el pastizal abierto. El entendimiento de los procesos ecológicos que mantenían el sistema de pastizal es sumamente importante para esfuerzos de mejoramiento, restauración, o creación de habitats para aves de pastizal y otros organismos. Consecuentemente, de alta prioridad debería de ser la preservación de grandes áreas de pastizal natural o seminatural donde estos procesos se podrían estudiar. Sin embargo, muchas especies de pastizal ahora dependen principalmente de habitats artificiales manejados para maximizar la producción de ganado, madera, u otros productos. Con un claro entendimiento de los requerimientos de habitat de aves de pastizal y los procesos que originalmente moldearon sus habitats seria posible mantener sus poblaciones en terrenos manejados como ranchos ganaderos, granjas, y plantaciones de pino. El manejo apropiado de tierras privadas será critico para la preservación adecuada de areas de habitat de anidacion, migración e invernacion para aves de pastizal y savana.

Bird species that depend on grassland and shrubland have declined in many regions in eastern and central North America during the past century, and open-country species frequently outnumber woodland species on state lists of endangered and threatened species (Askins 1993). Grassland birds, in particular, appear to be in trouble; during the past 25 years they have shown "steeper, more consistent, and more geographically widespread declines than any other behavioral or ecological guild" of North American birds (Knopf 1994:251). An analysis of continent-wide population trends on Breeding Bird Survey (BBS) routes between 1966 and 2002 showed that only 3 of 28 species of grassland specialists increased significantly, whereas 17 species decreased significantly (Sauer et al. 2003). Although some species that showed a continent-wide population decline were increasing in particular regions, many species (including Bobolink [*Dolichonyx oryzivorus*] and Eastern Meadowlark [*Sturnella magna*]) declined throughout almost their entire breeding range. Population declines of grassland birds have occurred not only in the northeastern United States (Vickery 1992), where regenerating forest has replaced much of the farmland that dominated the landscape in the 18th and 19th centuries (Norment 2002), but also in the Midwest (Herkert 1995) and the Great Plains (Knopf 1994), the historical centers of abundance and diversity of grassland birds. Population declines have also occurred in grassland birds in South America (Vickery et al. 1999b), Europe (Newton 1998), and other parts of the world (Goriup 1988).

Although declines in particular grassland bird populations can be attributed to a wide variety of factors, such as habitat fragmentation, nest parasitism, pesticides, and invasion by woody vegetation (Peterjohn and Sauer 1999), an overriding cause of regional declines appears to be agricultural intensification. Because most natural grasslands were converted to farmland or are used as ranchland, grassland birds now largely depend on habitats that are managed for agricultural production. Although farmland and pasture may provide good breeding or wintering habitat for some grassland bird species (e.g., Wunder and Knopf 2003), their suitability often declines as agriculture becomes more efficient. Agricultural intensification involves a shift toward monocultures that support fewer natural species (Matson et al. 1997), and the channeling of more primary production toward food or fiber. In a broad sense, intensification would include conversion of rangeland to cropland, and the shift to the use of exotic grasses and forbs in pastures and hay meadows. A suite of factors associated with agricultural intensification tend to degrade grassland bird habitat: these include increased use of pesticides, removal of natural field edges, spring plowing, land drainage, replacement of mixed farms with farms dominated by one crop, harvesting or mowing earlier in the season when birds are still nesting, and higher stocking rates for livestock (Newton 1998). Murphy (2003) showed that population changes in grassland birds in eastern and central North America between 1980 and 1998 were highly correlated with changes in agricultural land use in their breeding areas. The most important factor was loss of rangeland, which was associated with negative population trends for 12 species of grassland birds. Rangeland is used for livestock production, but it generally is not managed as intensively as cropland or pasture and it is dominated by native species of plants, providing habitat for a diverse group of grassland birds (Peterjohn 2003). In the Midwest, population declines in several species of grassland birds are highly correlated with declines in the combined area of pasture and hay meadow (Herkert et al. 1996).

Our goal is to provide recommendations for halting and reversing the decline in grassland birds. In some cases, this may be accomplished by restoring natural grasslands, but in other cases it is more realistic to try to promote farming and ranching methods that make the land both economically productive and biologically diverse. In either case, it is important to understand the ecological processes that sustained grassland habitat before people began to modify the landscape. Here, we explore the main ecological processes that sustained grassland in several distinct regions of temperate North America. Instead of attempting to survey every type of grassland, we focus on some of the most widespread or well-studied systems to illustrate the relative importance of different ecological processes in different regions. The general conclusions derived from this analysis should be applicable to other grassland systems in North America and in other parts of the world where the biodiversity of grassland organisms is declining.

Scope of this Paper

We have decided to define grassland birds broadly, following Vickery et al. (1999b:5): "any species that has become adapted to and reliant on some variety of grassland habitat for part or all of its life cycle." We include species that use the grass stratum of open savanna habitats, such as the longleaf pine savannas of the southeastern United States or oak savannas on the edge of the tallgrass prairie.

Because we surveyed such a wide range of grassland habitats, we attempted to use ecological terms precisely and consistently to improve clarity. In regions where the dominant vegetation is forest, grassland ecologists emphasize the "disturbances" that remove woody plants to create and sustain grassland. They emphasize the importance of understanding the frequency, seasonality, and intensity of disturbances, and the size of disturbance patches. In prairie regions, where the dominant vegetation was originally grass, this terminology does not work well. The grassland was sustained by frequent or even continual processes such as drought, fire, and grazing, and prairie ecologists emphasize that the real "disturbance" was removing or modifying these processes (Evans et al. 1989). These more continual and pervasive ecological processes are called "ecological drivers" by prairie ecologists. We use the term "driver" for ecological processes that are continual and pervasive and the term "disturbance" for ecological events that are infrequent and episodic. We recognize that there is a gradient from continual to highly infrequent processes, so this distinction is not always clear-cut.

For each region, we describe the history and status of grassland birds and their habitats. This is not intended as a comprehensive review of the ecology of grassland birds in each region, however. Instead, we focus on the dominant ecological disturbances or drivers that sustained the most widespread types of grassland and savanna before European settlement, including a consideration of the extent to which these processes have been suppressed and replaced with artificial processes that sustain grassland. Our goal is to show how understanding the original ecological processes in a region can aid efforts to maintain or restore grassland habitat for birds.

Northeastern Grasslands

History of grasslands.—Before European settlement, grasslands in temperate northeastern North America (defined as Pennsylvania, Ohio, New York, New Jersey, New England, eastern Ontario, and the Canadian Maritimes) were the result of natural disturbances such as fire, wind, disease, beaver (*Castor canadensis*) activity, flooding, and insect damage. These habitats are now more commonly a product of human disturbances, including farming and management of conservation areas to provide habitat for rare species (Askins 1999, 2000).

Fire has been an important disturbance mechanism in northeastern North America, especially in coastal areas that have sandy soils and support fire-adapted trees and vegetation such as pitch pine (*Pinus rigida*) and little bluestem (*Schizachyrium scoparium*). However, the historical frequency, intensity, and source of these ignitions are less clear (Patterson and Sassaman 1988, Parshall and Foster 2002). The presence of large sandplain grasslands along the coastal lowlands from New York to Maine before European settlement provides strong evidence that fires were frequent enough to maintain open habitats suitable for grassland birds (Vickery and Dunwiddie 1997, Askins 1999). The Hempstead Plains, a 24,000-ha grassland on Long Island, New York, that once supported a full complement of grassland birds, including the extinct Heath Hen (*Tympanuchus cupido cupido*; Askins 1997), was one of the most striking examples of these large grasslands.

Most of the pre-Columbian Northeast was heavily forested (Norment 2002): large openings that depended on fire were widely scattered, and many may have been created by periodic burning by Native Americans. Other forms of disturbance provided habitat for grassland birds, however. Until their widespread extirpation in the Northeast in the 18th century, beavers created large "beaver meadows," especially in flat floodplains. Before most rivers were dammed, frequent seasonal flooding also resulted in wet meadows in floodplains. These habitats would have been suitable for species of grassland birds, such as Bobolinks and Savannah Sparrows (*Passerculus sandwichensis*), that can nest in relatively small areas of grassland (Askins 1999). Presumably windthrows from hurricanes and other storms, tree diseases, and damage from infestations of insects such as spruce budworm (*Choristoneura fumiferana*) also helped create conditions that were favorable for extensive and intense fires that would have resulted in temporary grasslands (Runkle 1990).

The extent of grassland habitat in northeastern North America has changed drastically over the past 400 years, in conjunction with changing land-use practices. Population declines in grassland birds in the 20th century are the result of habitat loss resulting from forest succession, human development (Vickery and Dunwiddie 1997), and fire suppression (Patterson and Sassaman 1988, Vickery et al. 2005). In addition, more intensive agricultural practices, such as converting hay fields to alfalfa (*Medicago sativa*), have substantially reduced grassland bird habitat. Finally, earlier and more frequent mowing of remaining hay fields has made them less suitable for grassland birds because of destruction of nests (Bollinger and Gavin 1989, Jones and Vickery 1997).

Grassland bird assemblage.—Fifteen species of obligate grassland birds (*sensu* Vickery et al. 1999b) breed in northeastern North America. Horned Larks (*Eremophila alpestris*) and Vesper Sparrows (*Pooecetes gramineus*) prefer sparse vegetation with large amounts of bare ground. Grasshopper Sparrows (*Ammodramus savannarum*) typically select somewhat denser grassland vegetation, often with native bunchgrasses, such as little bluestem or poverty grass (*Danthonia spicata*; Bollinger 1995). Savannah Sparrows, Bobolinks, and Eastern Meadowlarks breed in a wider range of grasslands, including dense rhizomatous hay fields with exotic grasses such as timothy (*Phleum pratense*) (Wiens 1969, Vickery et al. 1999a, Shriver et al. 2005). Upland Sandpipers (*Bartramia longicauda*) tolerate a range of grassland conditions but appear to select sites with substantial heterogeneity (Vickery et al. 1994). Henslow's Sparrows (*A. henslowii*) and Short-eared Owls (*Asio flammeus*) generally prefer thicker, often moist grasslands (Holt and Leasure 1993, Herkert et al. 2002).

Between 1997 and 2000, a regional survey of breeding grassland birds in New England and New York estimated the occurrence and relative abundance of seven obligate grassland bird species at 1,140 sites (Shriver et al. 2005). Sites included hay fields, fallow fields, pastures, airports, and military bases. Of the seven species surveyed, Savannah Sparrows and Bobolinks were most common, occurring on 72% and 69% of all sites, respectively. Eastern Meadowlarks were detected on 37% of the sites. Upland Sandpipers, Vesper Sparrows, Grasshopper Sparrows, and Henslow's Sparrows were generally uncommon and occurred on <20% of the sites.

Current habitat for grassland birds.—Privately owned agricultural land clearly represents the largest proportion of graminoid-dominated open land in northeastern North America. In 1997, there were 1,760,000 ha of open farmland in New England, of which ~720,000 ha were hay fields, pastures, and idle cropland (data from National Agricultural Statistics Service; see Acknowledgments). These habitats are most likely to provide suitable nesting habitat for grassland birds. Commercial lowbush blueberry (*Vaccinium angustifolium*) barrens, located primarily on sandy glacio-marine deltas in northeastern North America, constitute a unique type of agricultural landscape that is very important to grassland birds, especially Upland Sandpipers and Vesper Sparrows (Weik 1998, Shriver et al. 2005). The vegetation of the barrens comprises native grasses, shrubs, and trees that are adapted to frequent fires. Fire has been a regular component on some of these barrens for >1,700 years, and palynological evidence suggests that the habitat in these xeric areas was some form of grassland pine–shrub barren (Winne 1997). Presently managed for lowbush blueberry production by regular mowing and burning, these barrens occupy >50,000 ha, with 26,000 ha in Maine (D. Yarborough pers. comm.) and 26,700 ha in the Canadian Maritimes (K. McAloney pers. comm.).

Federal, state, and municipal grasslands account for a small fraction of the total grassland habitat in northeastern North America. Despite the small proportion of public grassland habitat, some of these sites support large numbers of regionally threatened grassland birds. Because of their size, many airports in the Northeast are important for grassland birds, especially species such as Upland Sandpipers and Grasshopper Sparrows that require large areas of continuous grassland (Melvin 1994, Jones and Vickery 1997; Fig. 1).

Although of recent origin, reclaimed surface mines in eastern North America provide extensive grassland habitat (Whitmore and Hall 1978). For example, in Pennsylvania, there are ~35,000 ha of reclaimed surface mines that support high densities of grassland birds, including Grasshopper Sparrows and Henslow's Sparrows (Mattice et al. 2005). Reclaimed grasslands are also found in West Virginia, Virginia, Ohio, and Indiana (Bajema et al. 2001, DeVault et al. 2002). Nest success of grassland birds in a relatively small reclaimed surface mine in West Virginia was apparently too low to sustain their populations (Wray et al. 1982), but preliminary results of research in larger reclaimed surface-mine grasslands in Indiana indicate that grassland birds were reproducing successfully (DeVault et al. 2002). Also, Henslow's Sparrows had similar nest-success rates on reclaimed mine sites and nonmined sites in Kentucky (Monroe and Ritchison 2005). Additional studies are needed in the Northeast to determine whether reclaimed surface mines can provide good breeding habitat for grassland birds.

Managing habitat for grassland birds.—Presently, grassland habitat in northeastern North America is created and maintained primarily as a result of three types of habitat management: mowing, livestock grazing, and prescribed burning. In New England, hay fields and pastures compose the largest proportion of open land, and traditionally these fields have been mowed or grazed. The ~355,000 ha of hay fields in New England are cut one or more times annually. Although hay fields make up >50% of the grassland habitat in the Northeast, early and frequent mowing schedules are likely to make many of these hay fields substantial population sinks (Bollinger and Gavin 1992).

Livestock grazing is an important form of habitat management that affects grassland birds. In New York, Smith (1997) found that moderate grazing with stocking rates of 0.12–0.24 head of cattle per hectare provided adequate habitat for Henslow's and Grasshopper sparrows in the Finger Lakes National Forest.

Modifications in habitat management practices at military and municipal airports have clearly benefited grassland birds. These practices include deferred mowing schedules and reduced vehicular traffic in grassland areas. For example, at Westover Air Reserve Base, Chicopee, Massachusetts, populations of Upland Sandpipers and Grasshopper Sparrows

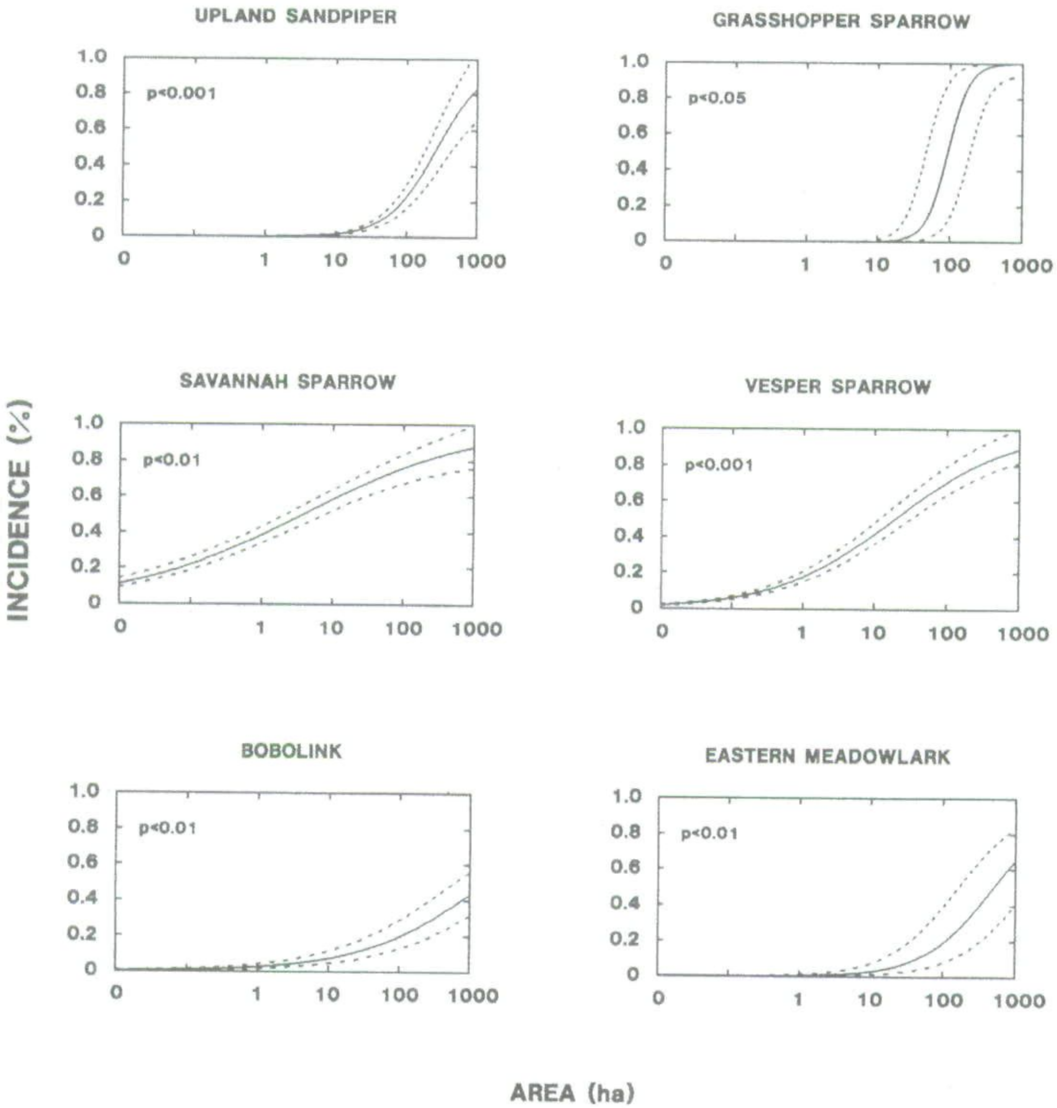

FIG. 1. Frequency of occurrence of six species of grassland birds in grasslands of different sizes in coastal Maine (Vickery et al. 1994; reprinted with permission from Blackwell Publishing).

have increased by >200% as a result of these management changes (Melvin 1994, Jones and Vickery 1997).

Prescribed fire is used primarily for two reasons: habitat management of rare plant (Vickery 2002a, b) and animal assemblages and maintenance of commercial lowbush blueberry fields (Fig. 2). Prescribed fire is used on commercial blueberry barrens to prune blueberry plants, reduce litter, and reduce pest insect densities; in Maine, ~3,000 ha are burned annually (D. Yarborough pers. comm.). The size of fires on blueberry lands is not accurately recorded, but these ignitions are much larger than the prescribed burns on conservation lands, probably on the order of 20–100+ ha (P. Vickery pers. obs.).

The scale of "ecological" prescribed burns in northeastern North America for grassland management has been small; since 1990, <400 ha have been burned annually in New England, and burned areas were usually <15 ha (T. Maloney unpubl. data). Despite the small size of these burns, they can have important benefits

FIG. 2. Northern Blazing Star (*Liatris borealis novae-angliae*), one of the endemic perennials growing on eastern sandplain grasslands, at the Kennebunk Plains, York County, Maine. This grassland is an important breeding area for Upland Sandpipers, Grasshopper Sparrows, and numerous other grassland birds. (Photograph by P. D. Vickery.)

for grassland birds, at least locally. In an eight-year study on a 210-ha sandplain grassland in Kennebunk, Maine, densities of Savannah Sparrows, Grasshopper Sparrows, Bobolinks, and Eastern Meadowlarks declined for one year immediately following fire but then were quite high for the subsequent five to seven years (Vickery et al. 1999a). By contrast, Horned Larks and Vesper Sparrows preferred recently burned sites. Abundances of these two species and Upland Sandpipers generally declined with time since fire.

Although appropriate management of airfields and protected natural areas is important for the future of grassland birds in the Northeast, farmland remains the greatest potential source of habitat for many of these species (Shriver et al. 2005, Vickery et al. 2005). Providing farmers with economic incentives to manage their land for conservation as well as agricultural production could help sustain grassland bird populations while preserving historically important rural landscapes.

Southeastern Pine Savannas

We include southeastern pine savannas to emphasize that a wide variety of different habitat types support grassland birds, and because pine savannas were historically the dominant vegetation over vast expanses of the Southeast and are important native habitats for several declining grassland birds in eastern North America.

History of grasslands.—Pine lands occurred historically over 25 million hectares of the southeastern coastal plain (Fig. 3). Longleaf pine (*Pinus palustris*) savannas covered a vast expanse from extreme southeastern Virginia, south through Florida, and west through southern Mississippi, parts of Louisiana, and east Texas, and other pine savanna communities occurred in smaller patches farther inland and upland. The distribution of wiregrass (*Aristida stricta*) was more limited, extending north into North Carolina and west into southern Mississippi (Stout and Marion 1993).

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Pollen studies suggest that the southeastern coastal plain was dominated by pines for the past 5,000 years, and for 3,500 years before that by oak forest, scrub, and savanna with scattered bluestem prairie (Watts 1971).

Southeastern pine savannas are naturally pyrogenic systems. Longleaf pine flatwoods and sandhills probably burned at one- to three-year intervals (Stout and Marion 1993), whereas in areas dominated by other species of pine, including mixed pine–hardwood areas farther inland, and in semiprotected areas the fire intervals were longer (Stanturf et al. 2002). For instance, shortleaf pine (*P. echinata*) in the Ouachita Mountains of Arkansas generally burned at intervals of 4–6 years (Wilson et al. 1995) or 5–10 years (Ware et al. 1993), and even less frequently (6–15 years) on poorer-quality sites (Stanturf et al. 2002). Frequent ground fires apparently were the normal pattern in longleaf systems (Williamson and Black 1981, Platt et al. 1988); they were frequent and pervasive enough to qualify as an ecological driver under our definition. Occupying wetter depressions, slash pine and pond pine burn less frequently than longleaf stands, and pond pine is more subject to occasional crown fires (Abrahamson and Hartnett 1990, Stout and Marion 1993). The former system can be described as an understory fire regime and the latter as a mixed fire regime, which removes 20–80% of the canopy (Stanturf et al. 2002).

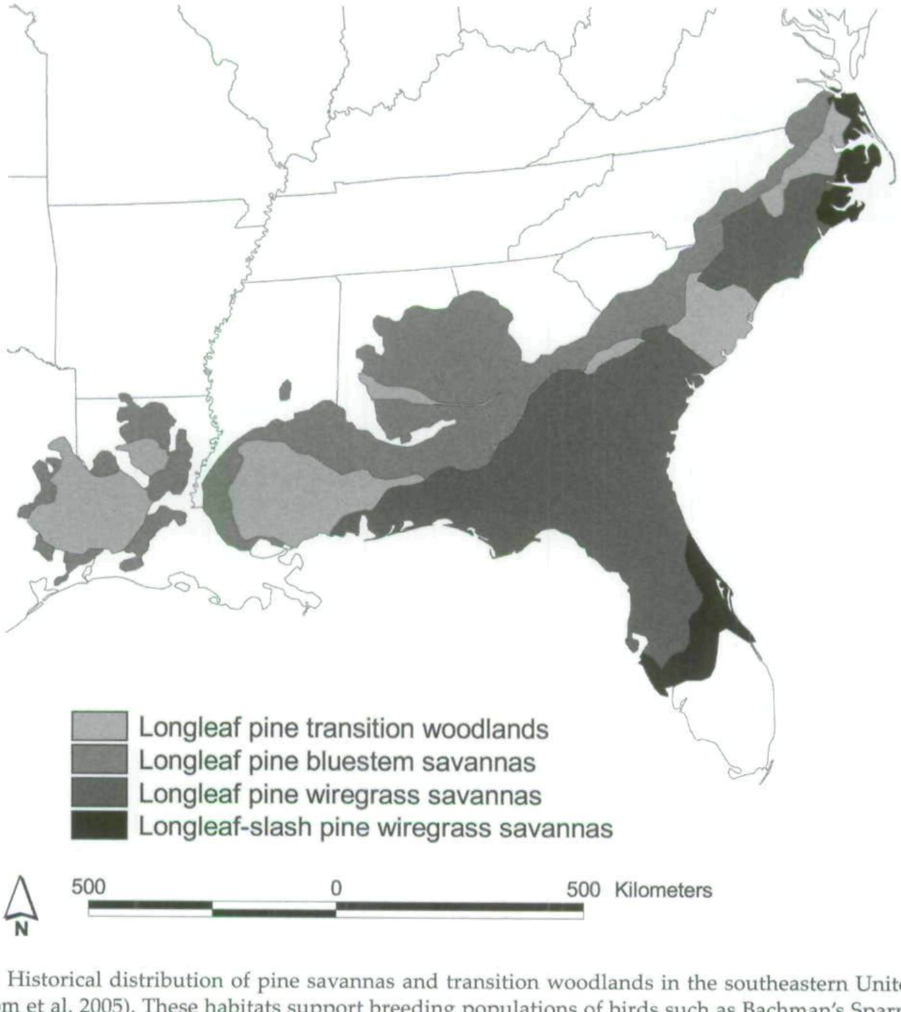

Fig. 3. Historical distribution of pine savannas and transition woodlands in the southeastern United States (Engstrom et al. 2005). These habitats support breeding populations of birds such as Bachman's Sparrows and Loggerhead Shrikes, and wintering populations of Loggerhead Shrikes and Henslow's Sparrows. (Reprinted from *Studies in Avian Biology* by permission of The Cooper Ornithological Society.)

al. 1997), and the channeling of more primary production toward food or fiber. In a broad sense, intensification would include conversion of rangeland to cropland, and the shift to the use of exotic grasses and forbs in pastures and hay meadows. A suite of factors associated with agricultural intensification tend to degrade grassland bird habitat: these include increased use of pesticides, removal of natural field edges, spring plowing, land drainage, replacement of mixed farms with farms dominated by one crop, harvesting or mowing earlier in the season when birds are still nesting, and higher stocking rates for livestock (Newton 1998). Murphy (2003) showed that population changes in grassland birds in eastern and central North America between 1980 and 1998 were highly correlated with changes in agricultural land use in their breeding areas. The most important factor was loss of rangeland, which was associated with negative population trends for 12 species of grassland birds. Rangeland is used for livestock production, but it generally is not managed as intensively as cropland or pasture and it is dominated by native species of plants, providing habitat for a diverse group of grassland birds (Peterjohn 2003). In the Midwest, population declines in several species of grassland birds are highly correlated with declines in the combined area of pasture and hay meadow (Herkert et al. 1996).

Our goal is to provide recommendations for halting and reversing the decline in grassland birds. In some cases, this may be accomplished by restoring natural grasslands, but in other cases it is more realistic to try to promote farming and ranching methods that make the land both economically productive and biologically diverse. In either case, it is important to understand the ecological processes that sustained grassland habitat before people began to modify the landscape. Here, we explore the main ecological processes that sustained grassland in several distinct regions of temperate North America. Instead of attempting to survey every type of grassland, we focus on some of the most widespread or well-studied systems to illustrate the relative importance of different ecological processes in different regions. The general conclusions derived from this analysis should be applicable to other grassland systems in North America and in other parts of the world where the biodiversity of grassland organisms is declining.

Scope of this Paper

We have decided to define grassland birds broadly, following Vickery et al. (1999b:5): "any species that has become adapted to and reliant on some variety of grassland habitat for part or all of its life cycle." We include species that use the grass stratum of open savanna habitats, such as the longleaf pine savannas of the southeastern United States or oak savannas on the edge of the tallgrass prairie.

Because we surveyed such a wide range of grassland habitats, we attempted to use ecological terms precisely and consistently to improve clarity. In regions where the dominant vegetation is forest, grassland ecologists emphasize the "disturbances" that remove woody plants to create and sustain grassland. They emphasize the importance of understanding the frequency, seasonality, and intensity of disturbances, and the size of disturbance patches. In prairie regions, where the dominant vegetation was originally grass, this terminology does not work well. The grassland was sustained by frequent or even continual processes such as drought, fire, and grazing, and prairie ecologists emphasize that the real "disturbance" was removing or modifying these processes (Evans et al. 1989). These more continual and pervasive ecological processes are called "ecological drivers" by prairie ecologists. We use the term "driver" for ecological processes that are continual and pervasive and the term "disturbance" for ecological events that are infrequent and episodic. We recognize that there is a gradient from continual to highly infrequent processes, so this distinction is not always clear-cut.

For each region, we describe the history and status of grassland birds and their habitats. This is not intended as a comprehensive review of the ecology of grassland birds in each region, however. Instead, we focus on the dominant ecological disturbances or drivers that sustained the most widespread types of grassland and savanna before European settlement, including a consideration of the extent to which these processes have been suppressed and replaced with artificial processes that sustain grassland. Our goal is to show how understanding the original ecological processes in a region can aid efforts to maintain or restore grassland habitat for birds.

Lightning strikes, which occur most frequently in late spring or early summer, were the primary source of fires before human settlement (Stout and Marion 1993). Native American burning occurred primarily in fall and winter (Ware et al. 1993), as does much recent prescribed burning (Platt et al. 1988). Near the coast, where topographic firebreaks were lacking, a single ignition likely burned large areas, on the order of 1,000 km^2. Farther inland and on moister soil, compartments were probably smaller and burned less frequently (Ware et al. 1993). In the Ouachita Mountains of Oklahoma, presettlement fires covered 300–800 ha (Masters et al. 1995).

Slight variations in topography and soil characteristics create variations in susceptibility to fire, resulting in extensive "interdigitation" of habitat types (Stout and Marion 1993). In contrast to prairie habitats, where time since last burn influences which suite of grassland bird species are seen on particular patches, grassland bird species of southeastern pine savannas all depend on frequent burns (i.e., every two to three years). Without fire, pine savannas rapidly succeed into hardwood forests, eliminating habitat for grassland birds (Stout and Marion 1993, Ware et al. 1993). Dry conditions combined with annual fire can create and maintain treeless grasslands (Ware et al. 1993), and these may be important for species, such as Grasshopper Sparrow, that do not tolerate a pine overstory. The dry prairies of Florida are similar to pine flatwoods but lack the pine overstory. The absence of trees may be a result of differences in hydrology, but this is not clear. At least some areas are maintained without trees because of unusually frequent burning, and clear-cutting and livestock grazing have also been shown to create treeless grasslands (Abrahamson and Hartnett 1990).

Grassland bird assemblage.—Although several bird species use the grassy component of southeastern pine savannas, these savannas are probably the dominant breeding habitat in the Southeast for only six species of grassland and savanna specialists: American Kestrel (*Falco sparverius*), Northern Bobwhite (*Colinus virginianus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), Loggerhead Shrike (*Lanius ludovicianus*), Eastern Bluebird (*Sialia sialis*), and Bachman's Sparrow (*Aimophila aestivalis*). Of these species, only Bachman's Sparrow is limited to the southeastern United States. American Kestrel, Red-headed Woodpecker, Loggerhead Shrike, and Eastern Bluebird all require open areas for foraging and trees for nesting, so their habitat requirements are met by savannas (Yosef 1996, Cade and Woods 1997, Gowaty and Plissner 1998, Smith et al. 2000, Smallwood and Bird 2002). Although commonly thought of as shrub nesters, Loggerhead Shrikes in pine savannas regularly nest high on limbs of mature longleaf pines (R. T. Engstrom pers. comm.). Some breeding species, such as Brown-headed Nuthatch (*Sitta pusilla*) and Red-cockaded Woodpecker (*Picoides borealis*), that are not known to use the grassland layer nevertheless seem to respond to changes in understory vegetation (Walters 1991, Wilson and Watts 1999).

Although not emphasized here, pine savannas provide important wintering habitat for some additional species, notably Henslow's Sparrow (Hamel 1992, Plentovich et al. 1999, Tucker and Robinson 2003), which prefers sites with greater herbaceous vegetation and less leaf litter (Carrie et al. 2002). Abundance of Henslow's Sparrow in winter is much greater on sites burned in the previous growing season, apparently because this stimulates production of grass seeds used as food (Bechtoldt and Stouffer 2005). Suppression of hardwood midstory is also important to wintering birds (Provencher et al. 2002a). Field Sparrow (*Spizella pusilla*) and Vesper Sparrow are found in pine savannas in winter, but primarily use early successional stages instead of sites with a mature pine overstory (Hamel 1992).

In the absence of fires, rapid encroachment of woody vegetation in these habitats leads to population declines of grassland birds (Engstrom et al. 2005). In north Florida, Bachman's Sparrows, Blue Grosbeaks (*Passerina caerulea*), Eastern Kingbirds (*Tyrannus tyrannus*), and Loggerhead Shrikes disappeared quickly (within five years) following fire exclusion (Engstrom et al. 1984, Brennan et al. 1998). In shortleaf pine–bluestem savanna in Arkansas, densities of ground–shrub foragers and ground-nesting birds were higher in stands that were treated by thinning, burning, or both than in unmanaged controls (Wilson et al. 1995). In Georgia, 29 of 46 breeding bird species showed significantly different habitat preferences for recently burned (1–3 years)

Northeastern Grasslands

History of grasslands.—Before European settlement, grasslands in temperate northeastern North America (defined as Pennsylvania, Ohio, New York, New Jersey, New England, eastern Ontario, and the Canadian Maritimes) were the result of natural disturbances such as fire, wind, disease, beaver (*Castor canadensis*) activity, flooding, and insect damage. These habitats are now more commonly a product of human disturbances, including farming and management of conservation areas to provide habitat for rare species (Askins 1999, 2000).

Fire has been an important disturbance mechanism in northeastern North America, especially in coastal areas that have sandy soils and support fire-adapted trees and vegetation such as pitch pine (*Pinus rigida*) and little bluestem (*Schizachyrium scoparium*). However, the historical frequency, intensity, and source of these ignitions are less clear (Patterson and Sassaman 1988, Parshall and Foster 2002). The presence of large sandplain grasslands along the coastal lowlands from New York to Maine before European settlement provides strong evidence that fires were frequent enough to maintain open habitats suitable for grassland birds (Vickery and Dunwiddie 1997, Askins 1999). The Hempstead Plains, a 24,000-ha grassland on Long Island, New York, that once supported a full complement of grassland birds, including the extinct Heath Hen (*Tympanuchus cupido cupido*; Askins 1997), was one of the most striking examples of these large grasslands.

Most of the pre-Columbian Northeast was heavily forested (Norment 2002): large openings that depended on fire were widely scattered, and many may have been created by periodic burning by Native Americans. Other forms of disturbance provided habitat for grassland birds, however. Until their widespread extirpation in the Northeast in the 18th century, beavers created large "beaver meadows," especially in flat floodplains. Before most rivers were dammed, frequent seasonal flooding also resulted in wet meadows in floodplains. These habitats would have been suitable for species of grassland birds, such as Bobolinks and Savannah Sparrows (*Passerculus sandwichensis*), that can nest in relatively small areas of grassland (Askins 1999). Presumably windthrows from hurricanes and other storms, tree diseases, and damage from infestations of insects such as spruce budworm (*Choristoneura fumiferana*) also helped create conditions that were favorable for extensive and intense fires that would have resulted in temporary grasslands (Runkle 1990).

The extent of grassland habitat in northeastern North America has changed drastically over the past 400 years, in conjunction with changing land-use practices. Population declines in grassland birds in the 20th century are the result of habitat loss resulting from forest succession, human development (Vickery and Dunwiddie 1997), and fire suppression (Patterson and Sassaman 1988, Vickery et al. 2005). In addition, more intensive agricultural practices, such as converting hay fields to alfalfa (*Medicago sativa*), have substantially reduced grassland bird habitat. Finally, earlier and more frequent mowing of remaining hay fields has made them less suitable for grassland birds because of destruction of nests (Bollinger and Gavin 1989, Jones and Vickery 1997).

Grassland bird assemblage.—Fifteen species of obligate grassland birds (*sensu* Vickery et al. 1999b) breed in northeastern North America. Horned Larks (*Eremophila alpestris*) and Vesper Sparrows (*Pooecetes gramineus*) prefer sparse vegetation with large amounts of bare ground. Grasshopper Sparrows (*Ammodramus savannarum*) typically select somewhat denser grassland vegetation, often with native bunchgrasses, such as little bluestem or poverty grass (*Danthonia spicata*; Bollinger 1995). Savannah Sparrows, Bobolinks, and Eastern Meadowlarks breed in a wider range of grasslands, including dense rhizomatous hay fields with exotic grasses such as timothy (*Phleum pratense*) (Wiens 1969, Vickery et al. 1999a, Shriver et al. 2005). Upland Sandpipers (*Bartramia longicauda*) tolerate a range of grassland conditions but appear to select sites with substantial heterogeneity (Vickery et al. 1994). Henslow's Sparrows (*A. henslowii*) and Short-eared Owls (*Asio flammeus*) generally prefer thicker, often moist grasslands (Holt and Leasure 1993, Herkert et al. 2002).

Between 1997 and 2000, a regional survey of breeding grassland birds in New England and New York estimated the occurrence and relative abundance of seven obligate grassland bird species at 1,140 sites (Shriver et al. 2005). Sites included hay fields, fallow fields, pastures, and unburned (>20 years) sites, 22 of these species occurring more frequently in recently burned sites (White et al. 1999). Species that were significantly more common in burned sites included Northern Flicker (*Colaptes auratus*), Prairie Warbler (*Dendroica discolor*), Bachman's Sparrow, Chipping Sparrow (*S. passerina*), Field Sparrow, Brown-headed Cowbird (*Molothrus ater*), and American Goldfinch (*Carduelis tristis*). So few nests were found on unburned sites that it was impossible to compare productivity.

Current habitat for grassland birds.—Loss of native habitat and fire suppression are major causes of population decline for grassland birds in the southeastern pine savanna region (Jackson 1988, Dunning and Watts 1990, Engstrom et al. 1996, Tucker et al. 1998). Urbanization has been the primary cause of the loss of forestland in the Southeast for the past two decades (Wear and Greis 2002). Native pine stands are also being rapidly replaced by pine plantations. Planted pine stands now occupy 48% of the pine lands in the region, compared to 1% in 1952 (Wear and Greis 2002). Most of these have been planted at densities that do not create savanna conditions, but this is changing.

Less than 2–3% of the original upland vegetation of the southeastern pine savannas remains intact (Noss 1989, Ware et al. 1993, Wear and Greis 2002), and even on these sites management may be inappropriate (Ware et al. 1993). Only 11% (21 million acres) of southern forestland is in public ownership. Most is managed by the U.S. Forest Service, but one-third of this area (7 million acres) is administered by other agencies, including state, county, municipal, and tribal governments (Fig. 4). The remaining 89% of the land is controlled by >5 million private landowners, 18% of whom own industrial forests (Wear and Greis 2002). Because most old-growth longleaf pine stands are privately owned, efforts to acquire land and to encourage private landowners to manage for endangered species have been important for conservation (Stout and Marion 1993, Ware et al. 1993). However, the largest remaining stands of longleaf pine occur on public land, with a few exceptions (including the Moody tract in south Georgia and Green Swamp in North Carolina; Wear and Greis 2002).

FIG. 4. Longleaf pine–wiregrass savanna, Eglin Air Force Base, Okaloosa County, Florida. This plot was photographed in April after a summer burn the previous June. (Photograph by Lori Blanc.)

airports, and military bases. Of the seven species surveyed, Savannah Sparrows and Bobolinks were most common, occurring on 72% and 69% of all sites, respectively. Eastern Meadowlarks were detected on 37% of the sites. Upland Sandpipers, Vesper Sparrows, Grasshopper Sparrows, and Henslow's Sparrows were generally uncommon and occurred on <20% of the sites.

Current habitat for grassland birds.—Privately owned agricultural land clearly represents the largest proportion of graminoid-dominated open land in northeastern North America. In 1997, there were 1,760,000 ha of open farmland in New England, of which ~720,000 ha were hay fields, pastures, and idle cropland (data from National Agricultural Statistics Service; see Acknowledgments). These habitats are most likely to provide suitable nesting habitat for grassland birds. Commercial lowbush blueberry (*Vaccinium angustifolium*) barrens, located primarily on sandy glacio-marine deltas in northeastern North America, constitute a unique type of agricultural landscape that is very important to grassland birds, especially Upland Sandpipers and Vesper Sparrows (Weik 1998, Shriver et al. 2005). The vegetation of the barrens comprises native grasses, shrubs, and trees that are adapted to frequent fires. Fire has been a regular component on some of these barrens for >1,700 years, and palynological evidence suggests that the habitat in these xeric areas was some form of grassland pine–shrub barren (Winne 1997). Presently managed for lowbush blueberry production by regular mowing and burning, these barrens occupy >50,000 ha, with 26,000 ha in Maine (D. Yarborough pers. comm.) and 26,700 ha in the Canadian Maritimes (K. McAloney pers. comm.).

Federal, state, and municipal grasslands account for a small fraction of the total grassland habitat in northeastern North America. Despite the small proportion of public grassland habitat, some of these sites support large numbers of regionally threatened grassland birds. Because of their size, many airports in the Northeast are important for grassland birds, especially species such as Upland Sandpipers and Grasshopper Sparrows that require large areas of continuous grassland (Melvin 1994, Jones and Vickery 1997; Fig. 1).

Although of recent origin, reclaimed surface mines in eastern North America provide extensive grassland habitat (Whitmore and Hall 1978). For example, in Pennsylvania, there are ~35,000 ha of reclaimed surface mines that support high densities of grassland birds, including Grasshopper Sparrows and Henslow's Sparrows (Mattice et al. 2005). Reclaimed grasslands are also found in West Virginia, Virginia, Ohio, and Indiana (Bajema et al. 2001, DeVault et al. 2002). Nest success of grassland birds in a relatively small reclaimed surface mine in West Virginia was apparently too low to sustain their populations (Wray et al. 1982), but preliminary results of research in larger reclaimed surface-mine grasslands in Indiana indicate that grassland birds were reproducing successfully (DeVault et al. 2002). Also, Henslow's Sparrows had similar nest-success rates on reclaimed mine sites and nonmined sites in Kentucky (Monroe and Ritchison 2005). Additional studies are needed in the Northeast to determine whether reclaimed surface mines can provide good breeding habitat for grassland birds.

Managing habitat for grassland birds.—Presently, grassland habitat in northeastern North America is created and maintained primarily as a result of three types of habitat management: mowing, livestock grazing, and prescribed burning. In New England, hay fields and pastures compose the largest proportion of open land, and traditionally these fields have been mowed or grazed. The ~355,000 ha of hay fields in New England are cut one or more times annually. Although hay fields make up >50% of the grassland habitat in the Northeast, early and frequent mowing schedules are likely to make many of these hay fields substantial population sinks (Bollinger and Gavin 1992).

Livestock grazing is an important form of habitat management that affects grassland birds. In New York, Smith (1997) found that moderate grazing with stocking rates of 0.12–0.24 head of cattle per hectare provided adequate habitat for Henslow's and Grasshopper sparrows in the Finger Lakes National Forest.

Modifications in habitat management practices at military and municipal airports have clearly benefited grassland birds. These practices include deferred mowing schedules and reduced vehicular traffic in grassland areas. For example, at Westover Air Reserve Base, Chicopee, Massachusetts, populations of Upland Sandpipers and Grasshopper Sparrows

Because human activity has removed much of the naturally pyrogenic vegetation and introduced numerous firebreaks such as roads, there is little opportunity for lightning-ignited fires to burn with the frequency or to the extent they did historically. Ware et al. (1993:483) aptly described the situation as "finer and finer partitioning of the landscape into fire-protected compartments," putting the savanna ecosystem "in immediate danger of extinction." Consequently, implementing artificial disturbances is essential for maintaining the native bird fauna of the southeastern pine savannas.

Managing habitat for grassland birds.—Methods that prevent or remove encroachment of a hardwood understory are required to maintain suitable habitat for grassland-dependent species in pine savannas. Both thinning and prescribed burning are known to maintain habitat for grassland species in Arkansas (Wilson et al. 1995). An experimental comparison of burning, mechanical, and herbicide control of hardwood midstory in Florida longleaf pine demonstrated positive responses of most early-successional species to all these techniques (Provencher et al. 2002b, 2003). However, burning is usually significantly more cost-effective than other techniques (Provencher et al. 2002a). In general, some disturbance is required every two to three years, with a range of one to five years. Pine-grassland restoration for Red-cockaded Woodpeckers increased avian species richness and abundance and favored grassland birds and bird species of very high management concern (Conner et al. 2002, Tucker et al. 2003, Wood et al. 2004). Grazing and browsing by cattle or deer did not have major effects on understory plants in longleaf pine–bluestem savannas in Alabama, but clearcutting did (Brockway and Lewis 2003). In North Carolina, fire-suppressed stands had substantially reduced populations of Bachman's Sparrows, Red-headed Woodpecker, Prairie Warbler, Brown-headed Nuthatch, and other pine savanna species, compared with sites managed with prescribed fire (Allen et al. 2006). Besides creating desired habitat conditions, recent fire can reduce use of a stand by raccoons, potentially resulting in increased nesting success in areas with reduced predator activity (Jones et al. 2004).

Unless there is active management to maintain desired understory conditions (including frequent burning and intensive thinning), pine plantations are unlikely to provide good habitat for grassland birds except in the first few years. For example, natural longleaf pine forests had two to four times higher densities of breeding birds in the ground-foraging and ground-nesting guilds compared with almost all age-classes of slash pine plantations (Repenning and Labisky 1985). In South Carolina, very young (2–6 years) longleaf pine plantations supported more bird species than mid-aged (>32 years) longleaf stands that regenerated from old fields, but no comparison was made with old-growth stands. Bachman's Sparrows, Loggerhead Shrikes, and Eastern Kingbirds were detected on these sites (Krementz and Christie 1999).

Changes since the turn of the 21st century in pine plantation management, however, may create much more suitable habitat for grassland birds. Increasing prices for sawtimber as compared with pulpwood have made large trees much more valuable. Consequently, standard planting densities for loblolly pine (*Pinus taeda*) and slash pine (*P. elliottii*) plantations are now 500 trees acre^{-1}, down from 900 trees acre^{-1} a decade ago, allowing much more light to penetrate the understory (T. R. Fox pers. comm., Virginia Tech Department of Forestry). Following one or more thinnings at about age 12–16, to 200–300 trees acre^{-1}, or, in the case of intensively managed plantations, only 80–100 trees acre^{-1} (Visser and Stampfer 2003), combined with mechanical and chemical treatment to remove hardwood competition, these stands can support the grassy understory required by grassland birds. Given not only increased thinnings, but also the reduction of rotation lengths for southern pines under intensive management to only 18–25 years (Fox et al. 2004), many of these stands probably will provide suitable habitat for longer periods and at increasingly frequent intervals.

Although all the species described here respond positively to burning, Eastern Bluebirds, American Kestrels, and Red-headed Woodpeckers risk losing cavity trees to fire. The tradeoff between the creation of new snags through burning and the loss of existing cavity trees to fire is a challenge faced by land managers. Expertise of fire crews experienced at burning near active Red-cockaded Woodpecker cavities could be useful in planning prescribed burns to improve habitat for other cavity-nesting species. Once a frequent fire regime is

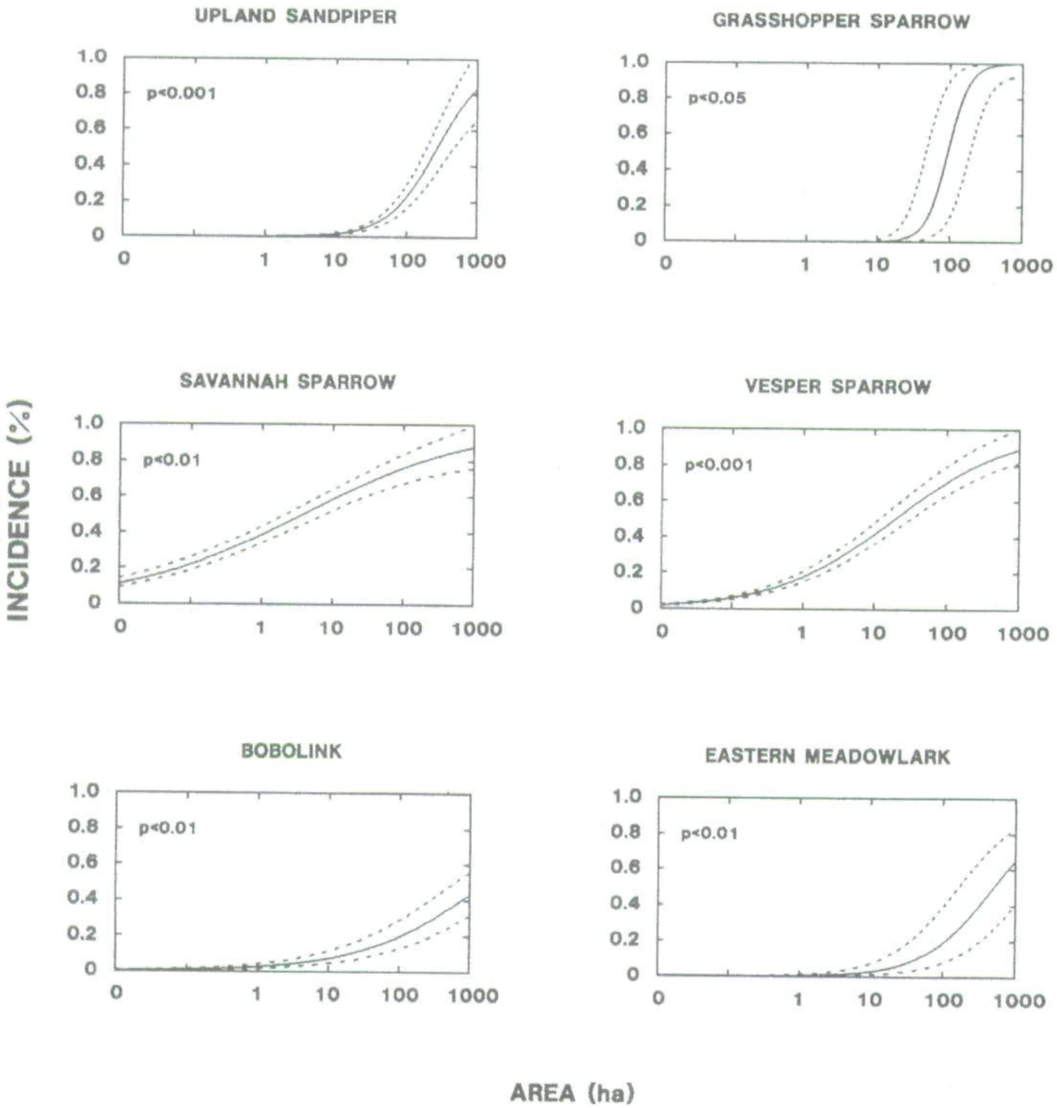

FIG. 1. Frequency of occurrence of six species of grassland birds in grasslands of different sizes in coastal Maine (Vickery et al. 1994; reprinted with permission from Blackwell Publishing).

have increased by >200% as a result of these management changes (Melvin 1994, Jones and Vickery 1997).

Prescribed fire is used primarily for two reasons: habitat management of rare plant (Vickery 2002a, b) and animal assemblages and maintenance of commercial lowbush blueberry fields (Fig. 2). Prescribed fire is used on commercial blueberry barrens to prune blueberry plants, reduce litter, and reduce pest insect densities; in Maine, ~3,000 ha are burned annually (D. Yarborough pers. comm.). The size of fires on blueberry lands is not accurately recorded, but these ignitions are much larger than the prescribed burns on conservation lands, probably on the order of 20–100+ ha (P. Vickery pers. obs.).

The scale of "ecological" prescribed burns in northeastern North America for grassland management has been small; since 1990, <400 ha have been burned annually in New England, and burned areas were usually <15 ha (T. Maloney unpubl. data). Despite the small size of these burns, they can have important benefits established and fuel loads are reduced, the risk of burning cavity trees during a prescribed fire declines dramatically.

Bachman's Sparrow is the species closest to being a pine-savanna endemic. It drops out of pine forests within four to five years after burning (Engstrom et al. 1984, Dunning 1993, Tucker et al. 2004) but can nest in recent clearcuts one to seven years after replanting. Current practices including fire suppression and intensive forest management usually do not allow suitable understory conditions for this species to develop. However, intensively managed mid-aged (17–28 years old) slash pine plantations supported Bachman's Sparrow populations if burned regularly (within two to four years; Tucker et al. 1998), though this practice is relatively uncommon (Fox et al. 2004). Bachman's Sparrow abundance was positively related to relative volume of grass but did not respond to season of burn (Tucker et al. 1998, Tucker et al. 2004). Sand pine (*P. clausa*) plantations >20 years old supported fewer birds than several native habitats (Tucker et al. 2003). Dunning (1993) gives a good review of the response of this species to forest management activities, mentioning that heavy thinning in 45- to 60-year-old pine plantations also provided suitable habitat.

Bachman's Sparrow was one of the few bird species to respond positively to restoration of native groundcover in old-field longleaf-pine stands (Rutledge and Conner 2002). Wintering Bachman's Sparrows occurred with greater relative abundance at sites with native groundcover (Cox and Jones 2004). Estimates of survival rates did not differ between young longleaf pine plantations and mid-aged longleaf pine forests growing on old fields (Krementz and Christie 1999), but no data were available from old-growth, fire-maintained stands. Bachman's Sparrow productivity in Florida dry prairie was not sufficient to maintain populations (Perkins et al. 2003) and probably required influx from pine savannas. In longleaf habitat, breeding productivity decreased with number of years since burn but was not related to season of burn (Tucker et al. 2006). Home-range size on the Savannah River Site in South Carolina was significantly larger (which often indicates lower habitat quality) in mature pine stands than in two-year-old and four-year-old pine stands (Stober and Krementz 2006). Bachman's Sparrows may have trouble colonizing isolated patches, so attention should be paid to distribution of suitable habitat across the landscape (Pulliam et al. 1992, Dunning et al. 1995).

Effective management for grassland birds in southeastern pine savannas will require a diversity of approaches. The paucity of work on demography of grassland birds in different habitats prevents clear evaluation of alternative practices. Protection of existing old-growth areas should be a priority, because native understories are difficult to restore and old-growth pine savannas may provide benefits as yet unidentified. Management to favor a grassy understory is obviously essential, and this may be accomplished effectively through burning, mowing, and mechanically or chemically removing hardwood or dense pine canopy. When it is possible to mimic natural fire regimes by burning during the growing season, this is desirable, especially given that growing-season burns are known to increase seed production of native grasses; but when growing-season burns are not possible, it is better to have winter burns than to go long periods without burning. Recently implemented practices in pine plantations may recreate the savanna-like conditions of native habitats. Although harvest rotations are too short to support cavity nesters such as Red-cockaded or Red-headed woodpeckers, there may be an increase in populations of grassland birds in these habitats if the current focus on sawtimber production continues. Although grassland birds native to northeastern North America may have evolved to disperse among ephemeral patches of early-successional habitat, the dominance of grassy vegetation in the Southeast for several millennia suggests that southeastern grassland birds may lack this ability. Managing for large contiguous patches may, therefore, be more critical in the Southeast. Priorities for research include studying demography and dispersal of birds in old-growth pine savannas and comparing these with other habitats. Responses of grassland birds to burn season, invasion of exotic plants, and brood parasitism are also important research topics.

Tallgrass Prairie

History of grasslands.—The tallgrass prairie region of North America extended from southern Manitoba to southern Texas and east

FIG. 2. Northern Blazing Star (*Liatris borealis novae-angliae*), one of the endemic perennials growing on eastern sandplain grasslands, at the Kennebunk Plains, York County, Maine. This grassland is an important breeding area for Upland Sandpipers, Grasshopper Sparrows, and numerous other grassland birds. (Photograph by P. D. Vickery.)

for grassland birds, at least locally. In an eight-year study on a 210-ha sandplain grassland in Kennebunk, Maine, densities of Savannah Sparrows, Grasshopper Sparrows, Bobolinks, and Eastern Meadowlarks declined for one year immediately following fire but then were quite high for the subsequent five to seven years (Vickery et al. 1999a). By contrast, Horned Larks and Vesper Sparrows preferred recently burned sites. Abundances of these two species and Upland Sandpipers generally declined with time since fire.

Although appropriate management of airfields and protected natural areas is important for the future of grassland birds in the Northeast, farmland remains the greatest potential source of habitat for many of these species (Shriver et al. 2005, Vickery et al. 2005). Providing farmers with economic incentives to manage their land for conservation as well as agricultural production could help sustain grassland bird populations while preserving historically important rural landscapes.

Southeastern Pine Savannas

We include southeastern pine savannas to emphasize that a wide variety of different habitat types support grassland birds, and because pine savannas were historically the dominant vegetation over vast expanses of the Southeast and are important native habitats for several declining grassland birds in eastern North America.

History of grasslands.—Pine lands occurred historically over 25 million hectares of the southeastern coastal plain (Fig. 3). Longleaf pine (*Pinus palustris*) savannas covered a vast expanse from extreme southeastern Virginia, south through Florida, and west through southern Mississippi, parts of Louisiana, and east Texas, and other pine savanna communities occurred in smaller patches farther inland and upland. The distribution of wiregrass (*Aristida stricta*) was more limited, extending north into North Carolina and west into southern Mississippi (Stout and Marion 1993).

to Indiana, with a historical area of 60 million hectares (Samson and Knopf 1994). Major ecological drivers in the tallgrass prairie region were fire, grazing, and drought. Fire played a major role in the formation and maintenance of tallgrass prairie (Axelrod 1985, Steinauer and Collins 1996; Fig. 5). Estimates of historical fire frequency in tallgrass prairie range from two to five years, but return intervals probably varied widely (Bragg 1982, Steinauer and Collins 1996). Naturally ignited prairie fires (primarily caused by lightning) occurred from March through December but were most common in mid- to late summer (Bragg 1982, McClain and Elzinga 1994). Up to half of all fires in the tallgrass prairie region, however, may have been set by Native Americans (Moore 1972, Higgins 1986).

Grazers and browsers that historically inhabited tallgrass prairie included bison (*Bison bison*), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and many small vertebrates and invertebrates. The extent to which herbivores, especially bison, grazed tallgrass prairie is unclear (Steinauer and Collins 1996). The greatest numbers of bison historically occurred in the mixed-grass prairie region (McDonald 1981), and grazing frequency and intensity were probably greatest in the western portions of the tallgrass prairies close to the mixed grass region. One possible scenario for bison grazing in tallgrass prairie is many small herds in the dormant and early growing season, the majority migrating to mixed and short-grass areas as the growing season progressed (Steinauer and Collins 1996). The frequency, timing, and intensity of grazing by other herbivores in tallgrass prairie also are poorly known.

Droughts occur periodically in tallgrass prairie (Weaver 1954), though the frequency of such events is lower than in either mixed- or shortgrass prairies (Wiens 1974). Wiens (1974) estimated that unusually wet or dry years (deviation from long-term average by ≥25%) occur in tallgrass prairie about once every four years, and that extremely wet or dry years (deviation from long-term average by ≥50%) occur roughly once every 40 years. Drought affects tallgrass prairie plant production and

FIG. 5. Spring prescribed fire conducted in a native prairie remnant in northern Illinois (Grundy County). Fire is a major ecological driver in the tallgrass-prairie region of North America. Naturally occurring fires are now rare in the tallgrass region, and most prairie fires are set by range managers and conservationists seeking to maintain prairie habitats. (Photograph by Bill Glass.)

Pollen studies suggest that the southeastern coastal plain was dominated by pines for the past 5,000 years, and for 3,500 years before that by oak forest, scrub, and savanna with scattered bluestem prairie (Watts 1971).

Southeastern pine savannas are naturally pyrogenic systems. Longleaf pine flatwoods and sandhills probably burned at one- to three-year intervals (Stout and Marion 1993), whereas in areas dominated by other species of pine, including mixed pine–hardwood areas farther inland, and in semiprotected areas the fire intervals were longer (Stanturf et al. 2002). For instance, shortleaf pine (*P. echinata*) in the Ouachita Mountains of Arkansas generally burned at intervals of 4–6 years (Wilson et al. 1995) or 5–10 years (Ware et al. 1993), and even less frequently (6–15 years) on poorer-quality sites (Stanturf et al. 2002). Frequent ground fires apparently were the normal pattern in longleaf systems (Williamson and Black 1981, Platt et al. 1988); they were frequent and pervasive enough to qualify as an ecological driver under our definition. Occupying wetter depressions, slash pine and pond pine burn less frequently than longleaf stands, and pond pine is more subject to occasional crown fires (Abrahamson and Hartnett 1990, Stout and Marion 1993). The former system can be described as an understory fire regime and the latter as a mixed fire regime, which removes 20–80% of the canopy (Stanturf et al. 2002).

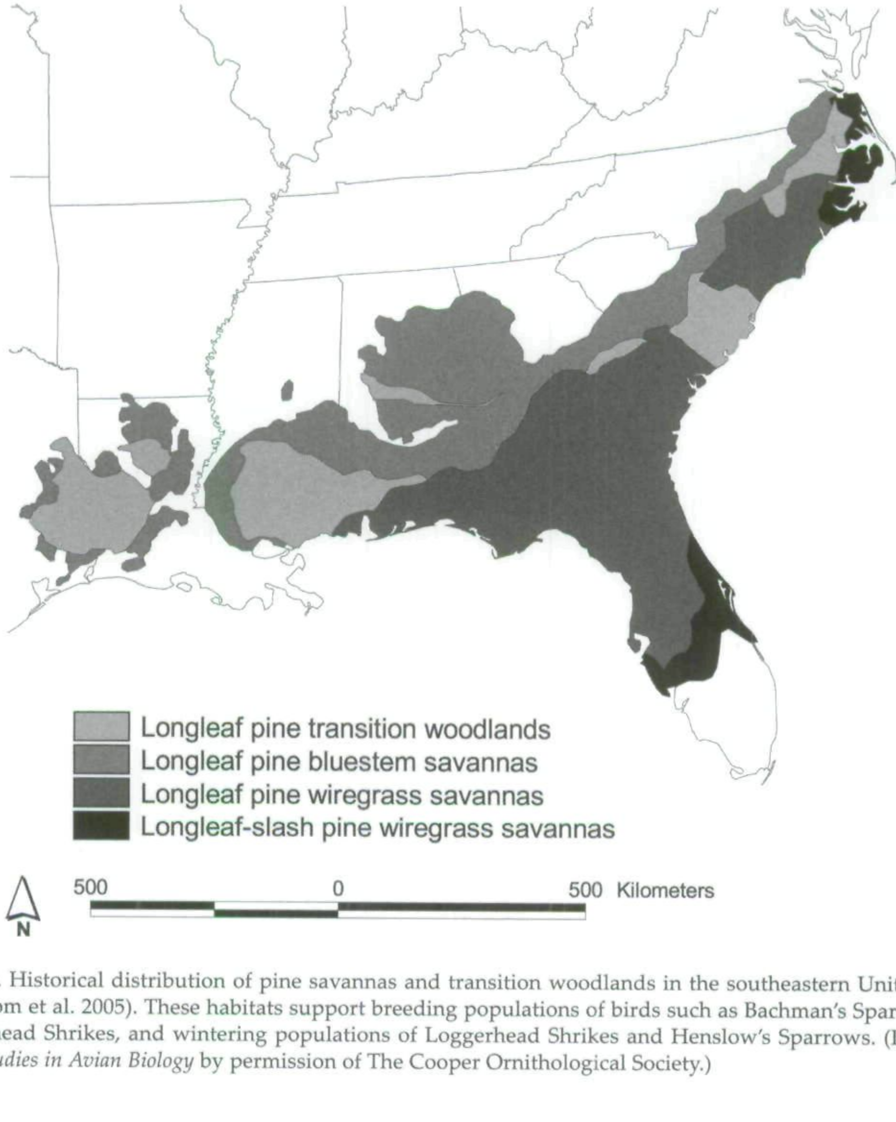

FIG. 3. Historical distribution of pine savannas and transition woodlands in the southeastern United States (Engstrom et al. 2005). These habitats support breeding populations of birds such as Bachman's Sparrows and Loggerhead Shrikes, and wintering populations of Loggerhead Shrikes and Henslow's Sparrows. (Reprinted from *Studies in Avian Biology* by permission of The Cooper Ornithological Society.)

diversity (Steinauer and Collins 1996), and this in turn has the potential to influence bird populations. Zimmerman (1992) found that March soil moisture was significantly correlated with total bird abundance in both burned and unburned Kansas tallgrass prairie, but that the abundance of a subset of core grassland-dependent species was related to March soil moisture in burned tallgrass prairie but not in unburned prairie. In Illinois, Henslow's Sparrow populations were found to be correlated with spring (January–April) precipitation, increasing in years when spring precipitation was greater than in the preceding year and declining in years when precipitation declined (Herkert and Glass 1999).

Grassland bird community.—Currently, 16 species of obligate grassland birds (Vickery et al. 1999b) breed in the tallgrass prairie region of North America. Characteristic species include Dickcissel (*Spiza americana*), Eastern Meadowlark, Bobolink, Henslow's Sparrow, Grasshopper Sparrow, Sedge Wren (*Cistothorus platensis*), Upland Sandpiper, and Greater Prairie-Chicken (*Tympanuchus cupido*) (Zimmerman 1993, 1996; Winter 1998; J. R. Herkert unpubl. data). Among these species, Henslow's Sparrows and Sedge Wrens prefer tall, dense vegetation, usually with a well-developed litter layer (Wiens 1969; Herkert et al. 2001, 2002); Dickcissels and Bobolinks prefer moderate to tall vegetation, also with well-developed litter (Wiens 1969, Skinner et al. 1984, Sample 1989, Bollinger 1995); Greater Prairie-Chickens, Eastern Meadowlarks, and Grasshopper Sparrows prefer vegetation of intermediate height (Wiens 1969, Vickery 1996, McCarthy et al. 1997); and Upland Sandpipers prefer short to moderate vegetation (Skinner et al. 1984, Sample 1989). Most tallgrass-prairie grassland birds also prefer areas with low levels of woody vegetation. Other species of birds commonly found in tallgrass prairies include Red-winged Blackbird (*Agelaius phoeniceus*), Common Yellowthroat (*Geothlypis trichas*), Mourning Dove (*Zenaida macroura*), Eastern Kingbird, American Goldfinch, Northern Bobwhite, and Field Sparrow. Most of the secondary species are associated with low to moderate levels of woody vegetation.

Current habitat for grassland birds.—Native tallgrass prairie has been greatly diminished range-wide, with only ~4% of presettlement tallgrass prairie now remaining (Samson and Knopf 1994). Losses have been highest in the eastern portion of the range, with Kansas (1.2 million hectares remaining), Texas (720,000 ha), and South Dakota (449,000 ha) currently possessing the greatest remaining acreage of presettlement prairie. Most of this is in private ownership, though several large conservation areas have been established, including Konza Prairie Long Term Ecological Research Site in Kansas (3,487 ha), The Nature Conservancy's Tallgrass Preserve in Oklahoma (15,384 ha), and the Tallgrass Prairie National Reserve in Kansas (4,410 ha).

A variety of nonnative grasslands, such as pasture and hay fields, now constitute a majority of the grassland habitat in the tallgrass region (Herkert et al. 1996), especially in the eastern portion of the area. These grasslands are almost exclusively privately held, and their acreage has declined sharply during the past 40 years (Herkert et al. 1996). Population declines of several species of grassland birds in the region, such as Grasshopper Sparrow, Eastern Meadowlark, Dickcissel, Bobolink, Western Meadowlark (*Sturnella neglecta*), and Savannah Sparrow, are strongly correlated with reductions in regional pasture and hay acreage (Herkert et al. 1996). New sources of habitat for grassland birds have been created during this period, however. Recent investigations of breeding birds in former strip-mines have shown that some of these areas can support relatively large populations of several characteristic tallgrass-prairie birds, including Grasshopper Sparrows, Eastern Meadowlarks, and Henslow's Sparrows (Bajema et al. 2001, Ingold 2002, Scott et al. 2002). Grasslands established by the Conservation Reserve Program (CRP; see below) in the tallgrass region also support good populations of prairie birds, including Bobolinks, Dickcissels, Grasshopper Sparrows, and Henslow's Sparrows (Best et al. 1997, Harroff 2001). Conservation Reserve Program grasslands have been planted to both native warm-season grasses and nonnative cool-season grasses. Species richness, overall abundance, and nest success appear to be similar in warm-season and cool-season CRP grasslands (e.g., Delisle and Savidge 1997, McCoy et al. 2001) and, in Iowa, species richness and densities of most common bird species were found to be similar in restored CRP grasslands and nearby tallgrass-prairie

Lightning strikes, which occur most frequently in late spring or early summer, were the primary source of fires before human settlement (Stout and Marion 1993). Native American burning occurred primarily in fall and winter (Ware et al. 1993), as does much recent prescribed burning (Platt et al. 1988). Near the coast, where topographic firebreaks were lacking, a single ignition likely burned large areas, on the order of 1,000 km^2. Farther inland and on moister soil, compartments were probably smaller and burned less frequently (Ware et al. 1993). In the Ouachita Mountains of Oklahoma, presettlement fires covered 300–800 ha (Masters et al. 1995).

Slight variations in topography and soil characteristics create variations in susceptibility to fire, resulting in extensive "interdigitation" of habitat types (Stout and Marion 1993). In contrast to prairie habitats, where time since last burn influences which suite of grassland bird species are seen on particular patches, grassland bird species of southeastern pine savannas all depend on frequent burns (i.e., every two to three years). Without fire, pine savannas rapidly succeed into hardwood forests, eliminating habitat for grassland birds (Stout and Marion 1993, Ware et al. 1993). Dry conditions combined with annual fire can create and maintain treeless grasslands (Ware et al. 1993), and these may be important for species, such as Grasshopper Sparrow, that do not tolerate a pine overstory. The dry prairies of Florida are similar to pine flatwoods but lack the pine overstory. The absence of trees may be a result of differences in hydrology, but this is not clear. At least some areas are maintained without trees because of unusually frequent burning, and clear-cutting and livestock grazing have also been shown to create treeless grasslands (Abrahamson and Hartnett 1990).

Grassland bird assemblage.—Although several bird species use the grassy component of southeastern pine savannas, these savannas are probably the dominant breeding habitat in the Southeast for only six species of grassland and savanna specialists: American Kestrel (*Falco sparverius*), Northern Bobwhite (*Colinus virginianus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), Loggerhead Shrike (*Lanius ludovicianus*), Eastern Bluebird (*Sialia sialis*), and Bachman's Sparrow (*Aimophila aestivalis*). Of these species, only Bachman's Sparrow is limited to the southeastern United States. American Kestrel, Red-headed Woodpecker, Loggerhead Shrike, and Eastern Bluebird all require open areas for foraging and trees for nesting, so their habitat requirements are met by savannas (Yosef 1996, Cade and Woods 1997, Gowaty and Plissner 1998, Smith et al. 2000, Smallwood and Bird 2002). Although commonly thought of as shrub nesters, Loggerhead Shrikes in pine savannas regularly nest high on limbs of mature longleaf pines (R. T. Engstrom pers. comm.). Some breeding species, such as Brown-headed Nuthatch (*Sitta pusilla*) and Red-cockaded Woodpecker (*Picoides borealis*), that are not known to use the grassland layer nevertheless seem to respond to changes in understory vegetation (Walters 1991, Wilson and Watts 1999).

Although not emphasized here, pine savannas provide important wintering habitat for some additional species, notably Henslow's Sparrow (Hamel 1992, Plentovich et al. 1999, Tucker and Robinson 2003), which prefers sites with greater herbaceous vegetation and less leaf litter (Carrie et al. 2002). Abundance of Henslow's Sparrow in winter is much greater on sites burned in the previous growing season, apparently because this stimulates production of grass seeds used as food (Bechtoldt and Stouffer 2005). Suppression of hardwood midstory is also important to wintering birds (Provencher et al. 2002a). Field Sparrow (*Spizella pusilla*) and Vesper Sparrow are found in pine savannas in winter, but primarily use early successional stages instead of sites with a mature pine overstory (Hamel 1992).

In the absence of fires, rapid encroachment of woody vegetation in these habitats leads to population declines of grassland birds (Engstrom et al. 2005). In north Florida, Bachman's Sparrows, Blue Grosbeaks (*Passerina caerulea*), Eastern Kingbirds (*Tyrannus tyrannus*), and Loggerhead Shrikes disappeared quickly (within five years) following fire exclusion (Engstrom et al. 1984, Brennan et al. 1998). In shortleaf pine–bluestem savanna in Arkansas, densities of ground–shrub foragers and ground-nesting birds were higher in stands that were treated by thinning, burning, or both than in unmanaged controls (Wilson et al. 1995). In Georgia, 29 of 46 breeding bird species showed significantly different habitat preferences for recently burned (1–3 years) remnants, except for Grasshopper and Savannah sparrows, which were more dense in restored grasslands (Fletcher and Koford 2002). The creation of a large acreage of grasslands by the CRP also seems to have benefited populations of some grassland bird species. For example, regional populations of Grasshopper and Henslow's sparrows increased following the creation of additional breeding grassland habitat by the CRP (Herkert 1997, 1998, 2007), which suggests that the availability of breeding habitat is influencing recent population trends for some tallgrass-prairie bird species and that large-scale grassland-restoration (such as that accomplished by the CRP) can help reverse recent population declines.

As grassland area declines, several species of grassland birds have been shown to be negatively affected by the subsequent reductions in patch size, in terms of both reduced abundance (Herkert 1994b, Helzer and Jelinski 1999, Winter and Faaborg 1999, Horn et al. 2002) and reduced nesting success (Johnson and Temple 1990, Winter and Faaborg 1999, Herkert et al. 2003) within small patches of grassland habitat. However, the influence of patch size on grassland birds may vary among years, regions, and species (Winter et al. 2006). Another consequence of reduced patch sizes is an increase in edge habitat. Many grassland birds avoid habitat edges (Lima and Valone 1991, Delisle and Savidge 1996, Helzer 1996, Fletcher and Koford 2003, Bollinger and Gavin 2004). However, woody edges appear to exert the strongest influence on grassland bird populations, reducing bird abundance and nest density and increasing rates of nest predation (Johnson and Temple 1986, 1990; Winter et al. 2000; Bollinger and Gavin 2004). Edge effects may be more pronounced and extend farther into grasslands with multiple edges (Fletcher 2005), so the negative effects of edges may be difficult to avoid in highly fragmented, edge-dominated landscapes (Renfrew et al. 2005).

Woody habitat edges in tallgrass prairie also have been shown to increase rates of nest parasitism by Brown-headed Cowbirds (Johnson and Temple 1990, Jensen and Finck 2004, Patten et al. 2006). However, regional cowbird abundance also influences cowbird parasitism rates in prairie birds; parasitism rates are highest in regions of high cowbird abundance (Herkert et al. 2003, Jensen and Cully 2005b). The effect of edge habitat on nest-parasitism rates in grassland birds may be more apparent in areas of low cowbird density than in areas with high cowbird densities (Jensen and Cully 2005a).

Woody encroachment is also having major effects on grassland birds in the tallgrass-prairie region. Woody species are increasing in cover and abundance in many areas of the tallgrass region (Briggs et al. 2002, Hoch et al. 2002, Heisler et al. 2003), and woody-plant expansion may be one of the greatest contemporary threats to mesic grasslands of the central United States (Briggs et al. 2005). This expansion is occurring because of altered fire and grazing regimes that provide the opportunity for recruitment of new individuals and of additional shrub and tree species (Briggs et al. 2005). Once established, woody cover tends to increase regardless of fire frequency, and infrequent fires accelerate the spread of some species (Briggs et al. 2005). This process is resulting in a new dynamic state of shrub–grass coexistence (Briggs et al. 2005), which has important implications for breeding birds. Landscape-level increases in woody vegetation are linked to regional population declines of grassland birds (Coppedge et al. 2001a, b), whereas local increases in woody vegetation have negative effects on patch-level abundance and nesting success for many grassland species (Johnson and Temple 1990, Hughes et al. 1999, Winter et al. 2000, Patten et al. 2006). Without drastic measures, such as mechanical removal of shrubs, it is unlikely that management of fire and grazing regimes alone will be sufficient to restore historical grass dominance in these ecosystems (Briggs et al. 2005).

Managing habitat for grassland birds.—Fire, grazing, and mowing are the three most common management techniques in the tallgrass region. In the western portion of the tallgrass region, Upland Sandpipers, Eastern Kingbirds, and Red-winged Blackbirds are most abundant in burned prairie, whereas Dickcissels, Grasshopper Sparrows, Eastern Meadowlarks, Henslow's Sparrows, and Brown-headed Cowbirds are most abundant in unburned grasslands (Zimmerman 1992, Powell 2006). Several species of facultative grassland birds (Vickery et al. 1999b) are also more common in unburned prairie because of their dependence on woody vegetation, which tends to be more common in unburned prairie (Briggs et al. 2002). These species include Bell's Vireo and unburned (>20 years) sites, 22 of these species occurring more frequently in recently burned sites (White et al. 1999). Species that were significantly more common in burned sites included Northern Flicker (*Colaptes auratus*), Prairie Warbler (*Dendroica discolor*), Bachman's Sparrow, Chipping Sparrow (*S. passerina*), Field Sparrow, Brown-headed Cowbird (*Molothrus ater*), and American Goldfinch (*Carduelis tristis*). So few nests were found on unburned sites that it was impossible to compare productivity.

Current habitat for grassland birds.—Loss of native habitat and fire suppression are major causes of population decline for grassland birds in the southeastern pine savanna region (Jackson 1988, Dunning and Watts 1990, Engstrom et al. 1996, Tucker et al. 1998). Urbanization has been the primary cause of the loss of forestland in the Southeast for the past two decades (Wear and Greis 2002). Native pine stands are also being rapidly replaced by pine plantations. Planted pine stands now occupy 48% of the pine lands in the region, compared to 1% in 1952 (Wear and Greis 2002). Most of these have been planted at densities that do not create savanna conditions, but this is changing.

Less than 2–3% of the original upland vegetation of the southeastern pine savannas remains intact (Noss 1989, Ware et al. 1993, Wear and Greis 2002), and even on these sites management may be inappropriate (Ware et al. 1993). Only 11% (21 million acres) of southern forestland is in public ownership. Most is managed by the U.S. Forest Service, but one-third of this area (7 million acres) is administered by other agencies, including state, county, municipal, and tribal governments (Fig. 4). The remaining 89% of the land is controlled by >5 million private landowners, 18% of whom own industrial forests (Wear and Greis 2002). Because most old-growth longleaf pine stands are privately owned, efforts to acquire land and to encourage private landowners to manage for endangered species have been important for conservation (Stout and Marion 1993, Ware et al. 1993). However, the largest remaining stands of longleaf pine occur on public land, with a few exceptions (including the Moody tract in south Georgia and Green Swamp in North Carolina; Wear and Greis 2002).

Fig. 4. Longleaf pine–wiregrass savanna, Eglin Air Force Base, Okaloosa County, Florida. This plot was photographed in April after a summer burn the previous June. (Photograph by Lori Blanc.)

(*Vireo bellii*), Brown Thrasher (*Toxostoma rufum*), Blue Grosbeak, and American Goldfinch (Zimmerman 1992). In the eastern portion of the tallgrass region, Bobolinks tend to be more abundant in recently burned areas, and Common Yellowthroat and Henslow's Sparrow are more abundant in unburned areas (Herkert 1994a, Johnson and Temple 1986, J. R. Herkert unpubl. data). Management response of breeding birds to prairie fires may also be influenced by other factors, such as prairie size. In Missouri tallgrass prairies, Winter (1998) reported that changes in Henslow's Sparrow density in response to fire were greater in large prairies than in small prairies. Because some birds respond positively and others negatively to fire, a rotational management program is usually suggested, whereby small portions of prairies are burned rotationally, with three to five years between burns (Zimmerman 1988, Herkert 1994c, Winter 1998; Fig. 6).

Grazing also has a significant effect on many grassland bird species; some species prefer grazed areas, and others avoid them. In Kansas tallgrass prairie, grazing by bison resulted in increased abundance of Upland Sandpipers and Grasshopper Sparrows and nearly eliminated Henslow's Sparrows (Powell 2006). In Missouri tallgrass prairie, moderate grazing (20–40% combined grass and forb cover at 25 cm) tended to favor populations of Grasshopper Sparrows, Greater Prairie-Chickens, and Eastern Meadowlarks, whereas heavy grazing (<20% combined grass and forb cover at 25 cm) favored Upland Sandpipers, Western Meadowlarks, and Horned Larks (Skinner et al. 1984). Henslow's Sparrows and Sedge Wrens are generally rare or absent in grazed grasslands. In south-central Illinois, light, late-season grazing of warm-season grasses resulted in higher densities of Eastern Meadowlarks, Dickcissels, and Grasshopper Sparrows compared with undisturbed warm-season fields (Walk and Warner 2000). Henslow's Sparrows, however, were more numerous in undisturbed fields in Illinois (Walk and Warner 2000).

Studies of the effects of grazing on nest success of birds in the tallgrass region have produced varying results. Some studies have found that grazing reduces nest success (Temple et al. 1999, Shochat et al. 2005, Sutter and Ritchison 2005), whereas others have found no difference in nest success between grazed and ungrazed areas (Zimmerman 1996, Klute et al. 1997). Sites managed with a combination of grazing and burning, however, have significantly lower nest success than unburned prairie (Zimmerman 1996, Shochat et al. 2005).

A promising new approach to tallgrass-prairie management involves burning discrete patches of prairie and then allowing free-ranging grazers (either bison or cattle) to selectively

FIG. 6. Midsummer picture (May 28) looking down the border of a spring prescribed fire in a tallgrass-prairie remnant in Illinois. The burned portion is on the left side of the photograph and the unburned portion on the right side; the residual vegetation is visible on the unburned portion. Fire removes residual vegetation and litter and is important in controlling woody invasion in tallgrass prairies. (Photograph by J. R. Herkert.)

Because human activity has removed much of the naturally pyrogenic vegetation and introduced numerous firebreaks such as roads, there is little opportunity for lightning-ignited fires to burn with the frequency or to the extent they did historically. Ware et al. (1993:483) aptly described the situation as "finer and finer partitioning of the landscape into fire-protected compartments," putting the savanna ecosystem "in immediate danger of extinction." Consequently, implementing artificial disturbances is essential for maintaining the native bird fauna of the southeastern pine savannas.

Managing habitat for grassland birds.—Methods that prevent or remove encroachment of a hardwood understory are required to maintain suitable habitat for grassland-dependent species in pine savannas. Both thinning and prescribed burning are known to maintain habitat for grassland species in Arkansas (Wilson et al. 1995). An experimental comparison of burning, mechanical, and herbicide control of hardwood midstory in Florida longleaf pine demonstrated positive responses of most early-successional species to all these techniques (Provencher et al. 2002b, 2003). However, burning is usually significantly more cost-effective than other techniques (Provencher et al. 2002a). In general, some disturbance is required every two to three years, with a range of one to five years. Pine-grassland restoration for Red-cockaded Woodpeckers increased avian species richness and abundance and favored grassland birds and bird species of very high management concern (Conner et al. 2002, Tucker et al. 2003, Wood et al. 2004). Grazing and browsing by cattle or deer did not have major effects on understory plants in longleaf pine–bluestem savannas in Alabama, but clearcutting did (Brockway and Lewis 2003). In North Carolina, fire-suppressed stands had substantially reduced populations of Bachman's Sparrows, Red-headed Woodpecker, Prairie Warbler, Brown-headed Nuthatch, and other pine savanna species, compared with sites managed with prescribed fire (Allen et al. 2006). Besides creating desired habitat conditions, recent fire can reduce use of a stand by raccoons, potentially resulting in increased nesting success in areas with reduced predator activity (Jones et al. 2004).

Unless there is active management to maintain desired understory conditions (including frequent burning and intensive thinning), pine plantations are unlikely to provide good habitat for grassland birds except in the first few years. For example, natural longleaf pine forests had two to four times higher densities of breeding birds in the ground-foraging and ground-nesting guilds compared with almost all age-classes of slash pine plantations (Repenning and Labisky 1985). In South Carolina, very young (2–6 years) longleaf pine plantations supported more bird species than mid-aged (>32 years) longleaf stands that regenerated from old fields, but no comparison was made with old-growth stands. Bachman's Sparrows, Loggerhead Shrikes, and Eastern Kingbirds were detected on these sites (Krementz and Christie 1999).

Changes since the turn of the 21st century in pine plantation management, however, may create much more suitable habitat for grassland birds. Increasing prices for sawtimber as compared with pulpwood have made large trees much more valuable. Consequently, standard planting densities for loblolly pine (*Pinus taeda*) and slash pine (*P. elliottii*) plantations are now 500 trees acre^{-1}, down from 900 trees acre^{-1} a decade ago, allowing much more light to penetrate the understory (T. R. Fox pers. comm., Virginia Tech Department of Forestry). Following one or more thinnings at about age 12–16, to 200–300 trees acre^{-1}, or, in the case of intensively managed plantations, only 80–100 trees acre^{-1} (Visser and Stampfer 2003), combined with mechanical and chemical treatment to remove hardwood competition, these stands can support the grassy understory required by grassland birds. Given not only increased thinnings, but also the reduction of rotation lengths for southern pines under intensive management to only 18–25 years (Fox et al. 2004), many of these stands probably will provide suitable habitat for longer periods and at increasingly frequent intervals.

Although all the species described here respond positively to burning, Eastern Bluebirds, American Kestrels, and Red-headed Woodpeckers risk losing cavity trees to fire. The tradeoff between the creation of new snags through burning and the loss of existing cavity trees to fire is a challenge faced by land managers. Expertise of fire crews experienced at burning near active Red-cockaded Woodpecker cavities could be useful in planning prescribed burns to improve habitat for other cavity-nesting species. Once a frequent fire regime is graze areas of burned and unburned prairie (Fuhlendorf and Engle 2004). This management approach has been shown to generate a more heterogeneous mosaic of grassland types that may enhance the diversity of grassland species by mimicking grazing patterns before European settlement (Fuhlendorf and Engle 2001).

The abundance of some grassland bird species, especially Bobolinks and Grasshopper Sparrows, is also high in recently hayed areas (Winter 1998, Swengel and Swengel 2001, J. R. Herkert unpubl. data), but studies comparing the relative merits of haying versus burning also produced conflicting results. In Missouri, Swengel and Swengel (2001) found that fields maintained by rotational haying every one to four years had higher densities of Henslow's Sparrows than fields maintained with spring burning. However, other studies indicate that haying can reduce densities of Henslow's Sparrows and other grassland species that prefer taller, more dense vegetation (Cully and Michaels 2000), and another study in Missouri prairies did not detect a difference in Henslow's Sparrow density in burned versus mowed prairies (Winter 1998). The timing of grassland cutting is another concern associated with mowing–haying of grasslands in the tallgrass region. Cutting during the nesting season is likely a bigger issue in agricultural grasslands, such as hay fields, than in prairie habitats, because agricultural grasslands are generally cut earlier and more frequently than prairies in the region, but haying in tallgrass prairies is also known to destroy nests (Winter 1998).

Shortgrass Prairie

History of grasslands.—The area currently designated "shortgrass prairie" was historically known as the Great Plains, because of the barrenness of the landscape. Beginning at the 100th meridian and extending to the Rocky Mountains, the grasses became short and the horizon treeless. The boundary between tallgrass and shortgrass prairie was a "feathered edge" that ran through eastern Nebraska, Kansas, and Oklahoma into central Texas. With the elimination of bison and prairie-dogs, mixed-grass prairie supplanted shortgrass prairie in this boundary zone because taller grass shaded out buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*). In the north, the shortgrass prairie extended into North and South Dakota and Montana along river valleys that were heavily grazed by bison. After bison were extirpated and cool-season grasses were introduced by ranchers, the tongues of shortgrass prairie in this northern region were supplanted by mixed-grass prairie, so we include this region in the "northern plains" section (below), along with the mixed-grass prairie of western Canada.

Drought was the primary ecological driver of this landscape. Unlike the tallgrass prairie (historically known as the true prairie) to the east of the 100th meridian, where fire was an important ecological driver, the shortgrass prairie was secondarily maintained by grazing (Fig. 7). The primary grazers were black-tailed prairie-dogs (*C. ludvicianus*), bison, and elk (wapiti), in that order. Pronghorn (*Antilocapra americana*), which selectively forage on forbs rather than grasses, were also present (Knopf and Samson 1997).

The historical frequency, intensity, and extent of grazing on the southern Great Plains are poorly understood. Elk occurred primarily on the eastern half of the Great Plains (eastern Nebraska, Kansas, and Oklahoma), where they foraged in small herds. Elk were apparently more frequent in the vicinity of riverbottom areas, where ranker grasses were present, and the effects of their grazing were probably not great, given the small size of the herds. Bison, on the other hand, grazed on the high plains in extensive herds, likely numbering at least in the tens of millions (Shaw 1995). Many authors refer to the annual movement patterns of bison creating a "grazing mosaic," though specific information on a regular patterning of movement is lacking. Because of the presence of large bison herds along the Missouri, Republican, Arkansas, Cimarron, and Canadian rivers (which served as water sources), much of what is today called "mixed-grass prairie" was shortgrass prairie historically (Hart 2001). Although it is tempting to attribute the development of the mixed-grass prairie to differential foraging by cattle as compared with bison, the reality is that the introduction of grazing practices (managing cattle stocking rates and seasonal timing) in which fences are used to control and standardize grazing pressure probably had a larger effect on bird habitats in the Great Plains (Samson et al. 2004) than the displacement established and fuel loads are reduced, the risk of burning cavity trees during a prescribed fire declines dramatically.

Bachman's Sparrow is the species closest to being a pine-savanna endemic. It drops out of pine forests within four to five years after burning (Engstrom et al. 1984, Dunning 1993, Tucker et al. 2004) but can nest in recent clearcuts one to seven years after replanting. Current practices including fire suppression and intensive forest management usually do not allow suitable understory conditions for this species to develop. However, intensively managed mid-aged (17–28 years old) slash pine plantations supported Bachman's Sparrow populations if burned regularly (within two to four years; Tucker et al. 1998), though this practice is relatively uncommon (Fox et al. 2004). Bachman's Sparrow abundance was positively related to relative volume of grass but did not respond to season of burn (Tucker et al. 1998, Tucker et al. 2004). Sand pine (*P. clausa*) plantations >20 years old supported fewer birds than several native habitats (Tucker et al. 2003). Dunning (1993) gives a good review of the response of this species to forest management activities, mentioning that heavy thinning in 45- to 60-year-old pine plantations also provided suitable habitat.

Bachman's Sparrow was one of the few bird species to respond positively to restoration of native groundcover in old-field longleaf-pine stands (Rutledge and Conner 2002). Wintering Bachman's Sparrows occurred with greater relative abundance at sites with native groundcover (Cox and Jones 2004). Estimates of survival rates did not differ between young longleaf pine plantations and mid-aged longleaf pine forests growing on old fields (Krementz and Christie 1999), but no data were available from old-growth, fire-maintained stands. Bachman's Sparrow productivity in Florida dry prairie was not sufficient to maintain populations (Perkins et al. 2003) and probably required influx from pine savannas. In longleaf habitat, breeding productivity decreased with number of years since burn but was not related to season of burn (Tucker et al. 2006). Home-range size on the Savannah River Site in South Carolina was significantly larger (which often indicates lower habitat quality) in mature pine stands than in two-year-old and four-year-old pine stands (Stober and Krementz 2006). Bachman's Sparrows may have trouble colonizing isolated patches, so attention should be paid to distribution of suitable habitat across the landscape (Pulliam et al. 1992, Dunning et al. 1995).

Effective management for grassland birds in southeastern pine savannas will require a diversity of approaches. The paucity of work on demography of grassland birds in different habitats prevents clear evaluation of alternative practices. Protection of existing old-growth areas should be a priority, because native understories are difficult to restore and old-growth pine savannas may provide benefits as yet unidentified. Management to favor a grassy understory is obviously essential, and this may be accomplished effectively through burning, mowing, and mechanically or chemically removing hardwood or dense pine canopy. When it is possible to mimic natural fire regimes by burning during the growing season, this is desirable, especially given that growing-season burns are known to increase seed production of native grasses; but when growing-season burns are not possible, it is better to have winter burns than to go long periods without burning. Recently implemented practices in pine plantations may recreate the savanna-like conditions of native habitats. Although harvest rotations are too short to support cavity nesters such as Red-cockaded or Red-headed woodpeckers, there may be an increase in populations of grassland birds in these habitats if the current focus on sawtimber production continues. Although grassland birds native to northeastern North America may have evolved to disperse among ephemeral patches of early-successional habitat, the dominance of grassy vegetation in the Southeast for several millennia suggests that southeastern grassland birds may lack this ability. Managing for large contiguous patches may, therefore, be more critical in the Southeast. Priorities for research include studying demography and dispersal of birds in old-growth pine savannas and comparing these with other habitats. Responses of grassland birds to burn season, invasion of exotic plants, and brood parasitism are also important research topics.

Tallgrass Prairie

History of grasslands.—The tallgrass prairie region of North America extended from southern Manitoba to southern Texas and east

FIG. 7. The shortgrass prairie, as seen here in Weld County, Colorado, evolved with intensive grazing pressure that results in native grasses with 90% of the biomass below ground to protect the individual plant when heavily cropped by species such as bison. Regrowth is rapid following summer rains. (Photograph by F. L. Knopf.)

of a native ungulate by a domestic ungulate (Hartnett et al. 1997).

The black-tailed prairie-dog is definitely underappreciated in its historical role as a grazer on the shortgrass prairie. This species occurred across all of Nebraska, Kansas, and Colorado. (Lewis and Clark collected the first specimen in eastern Nebraska.) In areas today considered mixed-grass prairie, bison preferentially forage on prairie-dog towns (colonies), further enhancing the pressure on taller grass species (Coppock et al. 1983). The sum effect was that the southern Great Plains were noted for their monotony of vista by Mark Twain and others, which further challenges the idea of a grazing mosaic (Hart and Hart 1997). The intense grazing pressure on the southern Great Plains favored a floristic homogeneity of the grasslands (Milchunas et al. 1988, Vinton and Collins 1997), so that the "mosaic" was dominated by a single type of grassland (shortgrass prairie), with smaller "decorative tile" inserts of tall grass and shrubs in areas with low grazing pressure because of soil conditions or availability of water.

Grassland bird assemblage.—Several species of grassland birds—Mountain Plover (*Charadrius montanus*), Baird's Sparrow (*Ammodramus bairdii*), Lark Bunting (*Calamospiza melanocorys*), McCown's Longspur (*Calcarius mccownii*), and Chestnut-collared Longspur (*C. ornatus*)—are endemic to the Central Grasslands of North America (Mengel 1970), so these species evolved within a grazed ecosystem. Some species (such as Mountain Plover and McCown's Longspur) occur in areas of intensive grazing, whereas others prefer ecotones of less intensive grazing (Lark Bunting and Chestnut-collared Longspur; Knopf 1996b). Still other species—such as Cassin's Sparrow (*Aimophila cassinii*)—are tolerant of, and probably require, shrub incursion into prairie.

Avian population declines from historical levels on the shortgrass prairie are intuitively obvious. Populations were certainly reduced to Indiana, with a historical area of 60 million hectares (Samson and Knopf 1994). Major ecological drivers in the tallgrass prairie region were fire, grazing, and drought. Fire played a major role in the formation and maintenance of tallgrass prairie (Axelrod 1985, Steinauer and Collins 1996; Fig. 5). Estimates of historical fire frequency in tallgrass prairie range from two to five years, but return intervals probably varied widely (Bragg 1982, Steinauer and Collins 1996). Naturally ignited prairie fires (primarily caused by lightning) occurred from March through December but were most common in mid- to late summer (Bragg 1982, McClain and Elzinga 1994). Up to half of all fires in the tallgrass prairie region, however, may have been set by Native Americans (Moore 1972, Higgins 1986).

Grazers and browsers that historically inhabited tallgrass prairie included bison (*Bison bison*), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and many small vertebrates and invertebrates. The extent to which herbivores, especially bison, grazed tallgrass prairie is unclear (Steinauer and Collins 1996). The greatest numbers of bison historically occurred in the mixed-grass prairie region (McDonald 1981), and grazing frequency and intensity were probably greatest in the western portions of the tallgrass prairies close to the mixed grass region. One possible scenario for bison grazing in tallgrass prairie is many small herds in the dormant and early growing season, the majority migrating to mixed and short-grass areas as the growing season progressed (Steinauer and Collins 1996). The frequency, timing, and intensity of grazing by other herbivores in tallgrass prairie also are poorly known.

Droughts occur periodically in tallgrass prairie (Weaver 1954), though the frequency of such events is lower than in either mixed- or shortgrass prairies (Wiens 1974). Wiens (1974) estimated that unusually wet or dry years (deviation from long-term average by ≥25%) occur in tallgrass prairie about once every four years, and that extremely wet or dry years (deviation from long-term average by ≥50%) occur roughly once every 40 years. Drought affects tallgrass prairie plant production and

FIG. 5. Spring prescribed fire conducted in a native prairie remnant in northern Illinois (Grundy County). Fire is a major ecological driver in the tallgrass-prairie region of North America. Naturally occurring fires are now rare in the tallgrass region, and most prairie fires are set by range managers and conservationists seeking to maintain prairie habitats. (Photograph by Bill Glass.)

as a result of the extensive fragmentation of the prairie as it was converted to agricultural crops, especially cereal grains, since the late 1800s. More recently, however, BBS data indicate continued, widespread declines of endemic grassland birds. The widespread nature of these declines across species argues for broad regional changes in the shortgrass prairie or across wintering areas since the mid-1960s (Knopf 1994).

The Mountain Plover is the most intensively studied of the endemic birds of the shortgrass prairie. The proposal to list it as a Threatened Species under the auspices of the Endangered Species Act (U.S. Fish and Wildlife Service 2002) identified five major threats to the continental population: (1) conversion of native grasslands to agriculture on the breeding grounds, (2) destruction of nests by certain agricultural practices, (3) historical conversion of native grasslands on wintering grounds, (4) consequences of rangeland management (standardized grazing, reduction of prairie-dog [*Cynomys* spp.] populations), and (5) conflicts arising from the development of mineral-extraction projects (Knopf and Wunder 2006). These threats, individually and cumulatively, surely influence populations of the other Central Grassland endemics as well.

Current habitat for grassland birds.—Unlike other areas of native grasslands in North America, the shortgrass prairie has a relatively large component of public lands. Following the devastation of the Dust Bowl, many parcels were repurchased by the federal government and assigned to the Soil Conservation Service. A total of 1,548,000 ha was subsequently turned over to the U.S. Forest Service in 1954, to be managed as 19 new national grasslands beginning in 1960 (West 1990). Seventeen of these national grasslands are on the historical southern Great Plains. Additional properties are managed by the Department of Interior through the Bureau of Indian Affairs (8,033,992 ha), Bureau of Land Management (4,930,503 ha), Bureau of Reclamation (275,190 ha), Fish and Wildlife Service (713,993 ha), and National Park Service (53,883 ha), and by the Department of Defense (1,434,136 ha). Collectively, ~6% of the historical southern Great Plains is in public ownership, with most of the acreage located disproportionately in the west. Substantial portions of these lands are suitable for grassland birds, and management for grassland species occurs with varying degrees of attention.

Managing habitat for grassland birds.—Ecological restoration methods have not been developed specifically for the shortgrass prairie as they have for the tallgrass (true) prairie. The CRP most closely approximates an effort to manage for grassland birds on the Great Plains, albeit secondarily. Under this program, farmers are paid to take land out of production to prevent soil erosion and to create wildlife habitat. A total of 8,044,346 ha of private lands is registered in the program across the 10-state area, with 4,708,301 ha in the current shortgrass-prairie region of the southern plains (Allen and Vandever 2005). Thus, grassland conservation is influenced more by CRP on private lands than by management of public lands within any single agency.

Despite the massive acreage enrolled in CRP, however, fields within most of the historical shortgrass prairies have been planted primarily to taller native or tame grasses that may have historically occurred in local patches, but not over broad areas. Whereas response to CRP by the more widespread grassland species has been favorable in the northern portion of the Great Plains (Johnson and Igl 1995), Central Grasslands endemic species that breed in the northern Great Plains and winter on the southern Great Plains have not colonized CRP fields, probably because these species require shortgrass habitats. Populations of species such as Baird's Sparrow, Lark Bunting, and Chestnut-collared Longspur have declined significantly during the CRP era (1986–2002; Sauer et al. 2003). The organization Environmental Defense is working with avian biologists, range ecologists, and federal agencies to help refine CRP management programs, including the proper grazing of Great Plains grasslands. To date, grazing of CRP lands has been permitted only within the context of drought ("disaster") relief, and not as a management tool.

Given that restoration practices have not been developed for the shortgrass prairie, management practices for birds in this region rely more on intuition and an understanding of natural history than on information derived from experiments on how bird populations are affected by habitat manipulation (Johnson and Igl 2001b). Fire was not a prevalent ecological driver in the shortgrass prairie. The endemic diversity (Steinauer and Collins 1996), and this in turn has the potential to influence bird populations. Zimmerman (1992) found that March soil moisture was significantly correlated with total bird abundance in both burned and unburned Kansas tallgrass prairie, but that the abundance of a subset of core grassland-dependent species was related to March soil moisture in burned tallgrass prairie but not in unburned prairie. In Illinois, Henslow's Sparrow populations were found to be correlated with spring (January–April) precipitation, increasing in years when spring precipitation was greater than in the preceding year and declining in years when precipitation declined (Herkert and Glass 1999).

Grassland bird community.—Currently, 16 species of obligate grassland birds (Vickery et al. 1999b) breed in the tallgrass prairie region of North America. Characteristic species include Dickcissel (*Spiza americana*), Eastern Meadowlark, Bobolink, Henslow's Sparrow, Grasshopper Sparrow, Sedge Wren (*Cistothorus platensis*), Upland Sandpiper, and Greater Prairie-Chicken (*Tympanuchus cupido*) (Zimmerman 1993, 1996; Winter 1998; J. R. Herkert unpubl. data). Among these species, Henslow's Sparrows and Sedge Wrens prefer tall, dense vegetation, usually with a well-developed litter layer (Wiens 1969; Herkert et al. 2001, 2002); Dickcissels and Bobolinks prefer moderate to tall vegetation, also with well-developed litter (Wiens 1969, Skinner et al. 1984, Sample 1989, Bollinger 1995); Greater Prairie-Chickens, Eastern Meadowlarks, and Grasshopper Sparrows prefer vegetation of intermediate height (Wiens 1969, Vickery 1996, McCarthy et al. 1997); and Upland Sandpipers prefer short to moderate vegetation (Skinner et al. 1984, Sample 1989). Most tallgrass-prairie grassland birds also prefer areas with low levels of woody vegetation. Other species of birds commonly found in tallgrass prairies include Red-winged Blackbird (*Agelaius phoeniceus*), Common Yellowthroat (*Geothlypis trichas*), Mourning Dove (*Zenaida macroura*), Eastern Kingbird, American Goldfinch, Northern Bobwhite, and Field Sparrow. Most of the secondary species are associated with low to moderate levels of woody vegetation.

Current habitat for grassland birds.—Native tallgrass prairie has been greatly diminished range-wide, with only ~4% of presettlement tallgrass prairie now remaining (Samson and Knopf 1994). Losses have been highest in the eastern portion of the range, with Kansas (1.2 million hectares remaining), Texas (720,000 ha), and South Dakota (449,000 ha) currently possessing the greatest remaining acreage of presettlement prairie. Most of this is in private ownership, though several large conservation areas have been established, including Konza Prairie Long Term Ecological Research Site in Kansas (3,487 ha), The Nature Conservancy's Tallgrass Preserve in Oklahoma (15,384 ha), and the Tallgrass Prairie National Reserve in Kansas (4,410 ha).

A variety of nonnative grasslands, such as pasture and hay fields, now constitute a majority of the grassland habitat in the tallgrass region (Herkert et al. 1996), especially in the eastern portion of the area. These grasslands are almost exclusively privately held, and their acreage has declined sharply during the past 40 years (Herkert et al. 1996). Population declines of several species of grassland birds in the region, such as Grasshopper Sparrow, Eastern Meadowlark, Dickcissel, Bobolink, Western Meadowlark (*Sturnella neglecta*), and Savannah Sparrow, are strongly correlated with reductions in regional pasture and hay acreage (Herkert et al. 1996). New sources of habitat for grassland birds have been created during this period, however. Recent investigations of breeding birds in former strip-mines have shown that some of these areas can support relatively large populations of several characteristic tallgrass-prairie birds, including Grasshopper Sparrows, Eastern Meadowlarks, and Henslow's Sparrows (Bajema et al. 2001, Ingold 2002, Scott et al. 2002). Grasslands established by the Conservation Reserve Program (CRP; see below) in the tallgrass region also support good populations of prairie birds, including Bobolinks, Dickcissels, Grasshopper Sparrows, and Henslow's Sparrows (Best et al. 1997, Harroff 2001). Conservation Reserve Program grasslands have been planted to both native warm-season grasses and non-native cool-season grasses. Species richness, overall abundance, and nest success appear to be similar in warm-season and cool-season CRP grasslands (e.g., Delisle and Savidge 1997, McCoy et al. 2001) and, in Iowa, species richness and densities of most common bird species were found to be similar in restored CRP grasslands and nearby tallgrass-prairie shortgrass species blue grama and buffalo grass are highly drought tolerant and maintain ~90% of their biomass below the surface. Thus, native shortgrass landscapes lack adequate fuel—because most of each plant is subterranean and because of intensive removal of aboveground tissues by herbivores and high levels of wind erosion of the litter layer during the dormant season—to carry a fire any distance, restricting the historical role of fire as an ecological driver and limiting the current efficacy of fire as a management tool to local use only.

Grazing is the principal management tool to promote the shortgrass species that evolved in this biome, especially as one approaches the Rocky Mountains. Grazing is as critical to the health of shortgrass prairie as it is in the Serengeti Plains of Africa (Sinclair and Norton-Griffiths 1979). Without grazing, shading by taller (native and exotic) grasses precludes establishment and growth of the historically dominant shortgrass species. Drought tolerance and grazing drive shortgrass-prairie health, and endemic grassland birds generally exploit niches created by different intensities of grazing at local and regional scales (Knopf 1996b; Fig. 8). Unfortunately, neither experimental nor rigorous observational data are available to make specific recommendations about how grazing can be managed to favor these species.

Management of shortgrass prairie for grassland birds faces one additional hurdle not encountered elsewhere in North America. Grazing on public lands is almost universally opposed by environmental organizations, on the basis of studies in desert, riparian, and forested landscapes of western North America. Numerous studies show, however, that many of the species characteristic of shortgrass prairies increase in density as grazing intensity increases (although this relationship depends on soil conditions and seasonal rainfall; Knopf 1996a). Where grazing by domestic stock is not permitted across broad landscapes, these endemic species will be threatened unless dense populations of native grazers are restored throughout these areas.

Northern Plains

History of grasslands.—The northern plains include southeastern Alberta, southern Saskatchewan, and southwestern Manitoba in Canada and much of Montana, North Dakota, South Dakota, and northeastern Wyoming in the United States. Shaped by glacial deposits, the northern plains are flat to rolling and are dotted with intermittent wetlands (prairie potholes). Precipitation is generally low, evaporation exceeds precipitation, and periodic droughts occur (Gauthier et al. 2003). Rainfall

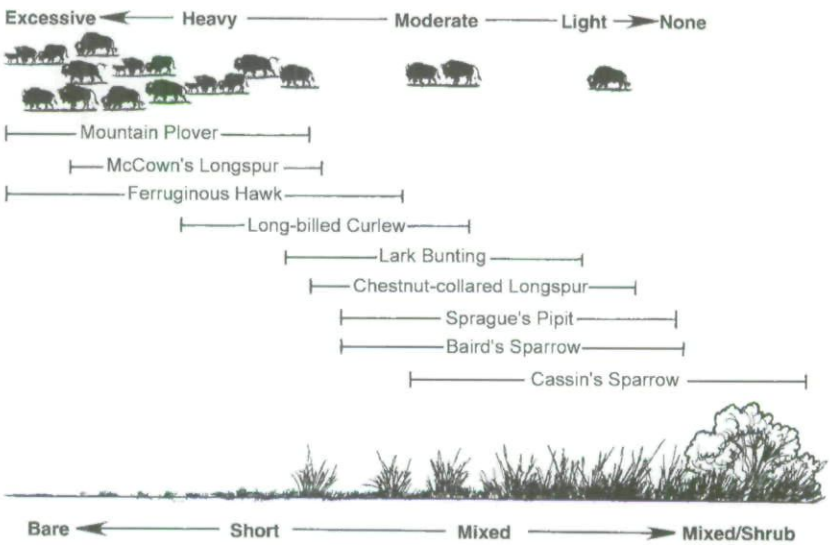

FIG. 8. Distribution of endemic birds of prairie uplands in relation to grassland type and historical grazing pressure across the central plains. (Reprinted from Knopf 1996b.)

remnants, except for Grasshopper and Savannah sparrows, which were more dense in restored grasslands (Fletcher and Koford 2002). The creation of a large acreage of grasslands by the CRP also seems to have benefited populations of some grassland bird species. For example, regional populations of Grasshopper and Henslow's sparrows increased following the creation of additional breeding grassland habitat by the CRP (Herkert 1997, 1998, 2007), which suggests that the availability of breeding habitat is influencing recent population trends for some tallgrass-prairie bird species and that large-scale grassland-restoration (such as that accomplished by the CRP) can help reverse recent population declines.

As grassland area declines, several species of grassland birds have been shown to be negatively affected by the subsequent reductions in patch size, in terms of both reduced abundance (Herkert 1994b, Helzer and Jelinski 1999, Winter and Faaborg 1999, Horn et al. 2002) and reduced nesting success (Johnson and Temple 1990, Winter and Faaborg 1999, Herkert et al. 2003) within small patches of grassland habitat. However, the influence of patch size on grassland birds may vary among years, regions, and species (Winter et al. 2006). Another consequence of reduced patch sizes is an increase in edge habitat. Many grassland birds avoid habitat edges (Lima and Valone 1991, Delisle and Savidge 1996, Helzer 1996, Fletcher and Koford 2003, Bollinger and Gavin 2004). However, woody edges appear to exert the strongest influence on grassland bird populations, reducing bird abundance and nest density and increasing rates of nest predation (Johnson and Temple 1986, 1990; Winter et al. 2000; Bollinger and Gavin 2004). Edge effects may be more pronounced and extend farther into grasslands with multiple edges (Fletcher 2005), so the negative effects of edges may be difficult to avoid in highly fragmented, edge-dominated landscapes (Renfrew et al. 2005).

Woody habitat edges in tallgrass prairie also have been shown to increase rates of nest parasitism by Brown-headed Cowbirds (Johnson and Temple 1990, Jensen and Finck 2004, Patten et al. 2006). However, regional cowbird abundance also influences cowbird parasitism rates in prairie birds; parasitism rates are highest in regions of high cowbird abundance (Herkert et al. 2003, Jensen and Cully 2005b). The effect of edge habitat on nest-parasitism rates in grassland birds may be more apparent in areas of low cowbird density than in areas with high cowbird densities (Jensen and Cully 2005a).

Woody encroachment is also having major effects on grassland birds in the tallgrass-prairie region. Woody species are increasing in cover and abundance in many areas of the tallgrass region (Briggs et al. 2002, Hoch et al. 2002, Heisler et al. 2003), and woody-plant expansion may be one of the greatest contemporary threats to mesic grasslands of the central United States (Briggs et al. 2005). This expansion is occurring because of altered fire and grazing regimes that provide the opportunity for recruitment of new individuals and of additional shrub and tree species (Briggs et al. 2005). Once established, woody cover tends to increase regardless of fire frequency, and infrequent fires accelerate the spread of some species (Briggs et al. 2005). This process is resulting in a new dynamic state of shrub–grass coexistence (Briggs et al. 2005), which has important implications for breeding birds. Landscape-level increases in woody vegetation are linked to regional population declines of grassland birds (Coppedge et al. 2001a, b), whereas local increases in woody vegetation have negative effects on patch-level abundance and nesting success for many grassland species (Johnson and Temple 1990, Hughes et al. 1999, Winter et al. 2000, Patten et al. 2006). Without drastic measures, such as mechanical removal of shrubs, it is unlikely that management of fire and grazing regimes alone will be sufficient to restore historical grass dominance in these ecosystems (Briggs et al. 2005).

Managing habitat for grassland birds.—Fire, grazing, and mowing are the three most common management techniques in the tallgrass region. In the western portion of the tallgrass region, Upland Sandpipers, Eastern Kingbirds, and Red-winged Blackbirds are most abundant in burned prairie, whereas Dickcissels, Grasshopper Sparrows, Eastern Meadowlarks, Henslow's Sparrows, and Brown-headed Cowbirds are most abundant in unburned grasslands (Zimmerman 1992, Powell 2006). Several species of facultative grassland birds (Vickery et al. 1999b) are also more common in unburned prairie because of their dependence on woody vegetation, which tends to be more common in unburned prairie (Briggs et al. 2002). These species include Bell's Vireo increases from west to east and south to north (from 20 cm in the west to ~45 cm in the east and north), which creates different prairie landscapes: small blocks of fescue, and large zones of mixed-grass, moist mixed-grass, and aspen (*Populus* spp.) parkland. Parkland is the transition zone between grassland and forest. Mixed-grass prairie is a combination of grasses of short and intermediate height, but the species of intermediate height contribute more biomass, except in heavily grazed areas. Shrubs may be scattered in the grass or form dense stands. The mixed-grass prairie is bordered by tall grass to the east and trees to the north.

Historically, lack of moisture and extreme variability in moisture maintained grass as the dominant vegetation (Samson et al. 2004), so it was the primary driver in this region. Amount of precipitation, in combination with soil quality and the secondary drivers of grazing and (to a lesser degree) fire, determined the extent of grass, the height and density of the standing crop of herbage, and amount of litter and shrub incursion. Because each factor varied temporally, spatially, or both, the historical northern plains were dynamic.

All the northern plains area was grazed intermittently by bison, pronghorn, and elk. Much of it was also grazed by lagomorphs, Richardson's ground squirrels (*Spermophilus richardsonii*), and black-tailed prairie-dogs. The large number of bison and their willingness to forage far from water meant that areas were probably grazed severely and fairly uniformly. However, particular sites had one to eight years of recovery before a herd returned (Malainey and Sherriff 1996). In contrast to the short-grass prairie, where grazing created a highly homogeneous stand, more localized grazing by bison in the northern plains probably resulted in a mosaic of large patches in all stages of renewal. Seasonal changes in amount and type of forage consumed by bison (Plumb and Dodd 1993) may have created other subtle differences between patches.

Fire was important in holding back tree and shrub invasion in the fescue, parkland, and moist mixed-grass. Intervals between fires varied with soil type, moisture, and grazing. The average return interval was probably 6 years in North Dakota (Madden et al. 1999) and areas with similar moisture, and 10 to 26 years in Montana (Umbanhowar 1996) and other dry sites. Burns were usually relatively small (Higgins 1984), and both human and lightning-caused fires contributed to the historical fire regime (Romo 2003). The lightning season was mid-May to mid-September, but fires set by First Nations people were most common in April, September, and October (Higgins 1986).

Grassland bird assemblage.—Twenty-six species of obligate grassland birds (*sensu* Vickery et al. 1999b) breed in the northern mixed-grass prairie. Nine of these are endemic to the Central Grasslands of North America (Mengel 1970). Twenty-two of the 25 obligate grassland species for which we have sufficient data on population trends (and 8 of 9 Central Grassland endemics) are declining (Sauer et al. 2005).

Even the tallest vegetation required by Central Grassland endemics is lower than that generally available in eastern grasslands. Sprague's Pipits (*Anthus spragueii*), and Baird's Sparrows need grasses 10–30 cm in height and avoid areas with taller grass cover, woody cover, or excessive litter (>4 cm depth; Robbins and Dale 1999, Green et al. 2002). Mountain Plovers use very short cover and are often associated with prairie-dog towns. McCown's and Chestnut-collared longspurs prefer low to moderately low cover. Many prairie birds need some heterogeneity. Marbled Godwits (*Limosa fedoa*) need different cover heights for feeding, nesting, and brood rearing (Ryan et al. 1984). Burrowing Owls need a mix of short and moderate grasses, but also need holes created by burrowing mammals for nesting and escape. Lark Buntings, Brewer's Sparrows (*Spizella breweri*) and Clay-colored Sparrows (*S. pallida*) require some shrubs. Ferruginous Hawk (*Buteo regalis*) can hunt and nest in a variety of grassland conditions with or without trees. Horned Larks and Western Meadowlarks tolerate a broad range of grassland conditions.

Current habitat for grassland birds.—The most obvious and important cause of bird population declines is habitat loss. Reduction in rangeland is followed by population declines in grassland birds (Murphy 2003), and populations generally are not declining in areas with more rangeland (Veech 2006). In Canada, ~14 million hectares (30%) of native grassland is still intact (Gauthier and Wiken 2003); the proportion remaining varies among provinces (Alberta, 43%; Saskatchewan, 24%; Manitoba, 21%) and by prairie type. In the United States, estimates for the historical and remaining cover of mixed grass

(*Vireo bellii*), Brown Thrasher (*Toxostoma rufum*), Blue Grosbeak, and American Goldfinch (Zimmerman 1992). In the eastern portion of the tallgrass region, Bobolinks tend to be more abundant in recently burned areas, and Common Yellowthroat and Henslow's Sparrow are more abundant in unburned areas (Herkert 1994a, Johnson and Temple 1986, J. R. Herkert unpubl. data). Management response of breeding birds to prairie fires may also be influenced by other factors, such as prairie size. In Missouri tallgrass prairies, Winter (1998) reported that changes in Henslow's Sparrow density in response to fire were greater in large prairies than in small prairies. Because some birds respond positively and others negatively to fire, a rotational management program is usually suggested, whereby small portions of prairies are burned rotationally, with three to five years between burns (Zimmerman 1988, Herkert 1994c, Winter 1998; Fig. 6).

Grazing also has a significant effect on many grassland bird species; some species prefer grazed areas, and others avoid them. In Kansas tallgrass prairie, grazing by bison resulted in increased abundance of Upland Sandpipers and Grasshopper Sparrows and nearly eliminated Henslow's Sparrows (Powell 2006). In Missouri tallgrass prairie, moderate grazing (20–40% combined grass and forb cover at 25 cm) tended to favor populations of Grasshopper Sparrows, Greater Prairie-Chickens, and Eastern Meadowlarks, whereas heavy grazing (<20% combined grass and forb cover at 25 cm) favored Upland Sandpipers, Western Meadowlarks, and Horned Larks (Skinner et al. 1984). Henslow's Sparrows and Sedge Wrens are generally rare or absent in grazed grasslands. In south-central Illinois, light, late-season grazing of warm-season grasses resulted in higher densities of Eastern Meadowlarks, Dickcissels, and Grasshopper Sparrows compared with undisturbed warm-season fields (Walk and Warner 2000). Henslow's Sparrows, however, were more numerous in undisturbed fields in Illinois (Walk and Warner 2000).

Studies of the effects of grazing on nest success of birds in the tallgrass region have produced varying results. Some studies have found that grazing reduces nest success (Temple et al. 1999, Shochat et al. 2005, Sutter and Ritchison 2005), whereas others have found no difference in nest success between grazed and ungrazed areas (Zimmerman 1996, Klute et al. 1997). Sites managed with a combination of grazing and burning, however, have significantly lower nest success than unburned prairie (Zimmerman 1996, Shochat et al. 2005).

A promising new approach to tallgrass-prairie management involves burning discrete patches of prairie and then allowing free-ranging grazers (either bison or cattle) to selectively

FIG. 6. Midsummer picture (May 28) looking down the border of a spring prescribed fire in a tallgrass-prairie remnant in Illinois. The burned portion is on the left side of the photograph and the unburned portion on the right side; the residual vegetation is visible on the unburned portion. Fire removes residual vegetation and litter and is important in controlling woody invasion in tallgrass prairies. (Photograph by J. R. Herkert.)

are not available for all states. Samson and Knopf (1994) estimate that North and South Dakota historically had 13.9 and 1.6 million hectares of mixed grass, respectively, and that 28% of North Dakota prairie is intact.

Governments encouraged settlement by offering land and incentives to those willing to turn over the soil and plant crops. All but the poorest soils and steepest slopes were converted from grass to grain or introduced forage with associated roads, preferentially eliminating grassland with the greatest primary productivity. Grassland birds disappear or decline once the native cover is removed (Johnson and Schwartz 1993a, b; McMaster and Davis 2000) or replaced with hay (Dale et al. 1997, McMaster et al. 2005). Also, grassland birds nesting in crops (Lokemoen and Beiser 1997) or hay (Dale et al. 1997) have low productivity. Agricultural departments in both nations encouraged farmers to "improve" pastures by replacing native plant species with introduced species like crested wheatgrass (*Agropyron cristatum*). Several endemic bird species use planted pastures less frequently than native pasture because it is structurally different, particularly in the litter layer (Sutter and Brigham 1998, Davis and Duncan 1999). Chestnut-collared Longspurs sometimes find crested wheatgrass attractive but experience lower productivity than on native range (Lloyd and Martin 2005).

Although most habitat loss occurred during settlement, grassland continues to be converted to urban and suburban settlement (Hansen et al. 2005), and crops (Brown et al. 2005: fig. 2) or other cover. Exurban development (6–25 homes per square kilometer) is the fastest growing form of land use in the United States (Hansen et al. 2005), with settlement area increasing by ≤20% in some parts of the northern plains (Brown et al. 2005: fig. 2). Native species (including birds) have decreased reproduction and survival near houses, largely because development alters habitats and increases disturbance and predation (Hansen et al. 2005).

Changes in grassland conditions may be almost as important as loss of habitat. The remaining prairie has lost much of its dynamic nature. Fire has been suppressed, allowing trees and shrubs to invade grassland in all but the driest areas. For example, aspen is expanding at 0.5–5% year^{-1} on black soils in prairie Canada (Prairie Farm Rehabilitation Administration 2000). Many grassland bird species occur less frequently when woody cover increases (Robbins and Dale 1999, Green et al. 2002, Grant et al. 2004, Ahlering 2005) or avoid nesting near it (Davis 2005). Shrubs may provide cover for rodents that prey on nests of open-country birds (With 1994). Also, intensive livestock grazing can reduce the health and vigor of the plant community, resulting in range conditions (rated "poor" or "fair" for livestock) that are less likely to attract some endemic bird species (Robbins and Dale 1999; Fig. 9) and less able to sustain grassland birds during periods of drought (George et al. 1992). Reduced range condition is a serious and pervasive problem, with more than half of Canadian prairie grassland estimated to be in less than "good" condition (Prairie Farm Rehabilitation Administration 2000). In addition, because cattle are confined by fences, they may graze sites annually rather than periodically, creating a landscape with a far more uniform height and density of grass than would have resulted from periodic grazing by bison. Both of the extreme ends of the height-and-thickness spectrum are less common, as are the associated birds (Knopf 1994). For example, prairie-dog towns, characterized by very short vegetative cover and a high proportion of bare ground, occupy only a fraction of their original estimated distribution (Wuerthner 1997), which means reduced success for short-cover specialists such as Burrowing Owls (Desmond et al. 2000).

Additional factors (invasive plants, roads, energy extraction, and habitat fragmentation) have changed the quality of remaining habitats and are associated with declines in occupancy or productivity. Invasion by exotic plants (Wilson and Belcher 1989, Robbins and Dale 1999, Scheiman et al. 2003, Grant et al. 2004) reduces avian occupancy of grassland. Two common invaders, crested wheatgrass and smooth brome (*Bromus inermis*), result in changes to structure (e.g., amount of standing dead grass; Henderson and Naeth 2005) or function (e.g., litter decomposition rates; Ogle et al. 2003). Roads and trails are implicated in dispersal of exotic species (Larson et al. 2001). Roads are also associated with direct mortality of birds (e.g., 20–37% of Burrowing Owl mortality; Haug et al. 1993) as well as changes in habitat and ecological function (Forman 2000, Trombulak and Frissell 2000). Songbird graze areas of burned and unburned prairie (Fuhlendorf and Engle 2004). This management approach has been shown to generate a more heterogeneous mosaic of grassland types that may enhance the diversity of grassland species by mimicking grazing patterns before European settlement (Fuhlendorf and Engle 2001).

The abundance of some grassland bird species, especially Bobolinks and Grasshopper Sparrows, is also high in recently hayed areas (Winter 1998, Swengel and Swengel 2001, J. R. Herkert unpubl. data), but studies comparing the relative merits of haying versus burning also produced conflicting results. In Missouri, Swengel and Swengel (2001) found that fields maintained by rotational haying every one to four years had higher densities of Henslow's Sparrows than fields maintained with spring burning. However, other studies indicate that haying can reduce densities of Henslow's Sparrows and other grassland species that prefer taller, more dense vegetation (Cully and Michaels 2000), and another study in Missouri prairies did not detect a difference in Henslow's Sparrow density in burned versus mowed prairies (Winter 1998). The timing of grassland cutting is another concern associated with mowing–haying of grasslands in the tallgrass region. Cutting during the nesting season is likely a bigger issue in agricultural grasslands, such as hay fields, than in prairie habitats, because agricultural grasslands are generally cut earlier and more frequently than prairies in the region, but haying in tallgrass prairies is also known to destroy nests (Winter 1998).

Shortgrass Prairie

History of grasslands.—The area currently designated "shortgrass prairie" was historically known as the Great Plains, because of the barrenness of the landscape. Beginning at the 100th meridian and extending to the Rocky Mountains, the grasses became short and the horizon treeless. The boundary between tallgrass and shortgrass prairie was a "feathered edge" that ran through eastern Nebraska, Kansas, and Oklahoma into central Texas. With the elimination of bison and prairie-dogs, mixed-grass prairie supplanted shortgrass prairie in this boundary zone because taller grass shaded out buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*). In the north, the shortgrass prairie extended into North and South Dakota and Montana along river valleys that were heavily grazed by bison. After bison were extirpated and cool-season grasses were introduced by ranchers, the tongues of shortgrass prairie in this northern region were supplanted by mixed-grass prairie, so we include this region in the "northern plains" section (below), along with the mixed-grass prairie of western Canada.

Drought was the primary ecological driver of this landscape. Unlike the tallgrass prairie (historically known as the true prairie) to the east of the 100th meridian, where fire was an important ecological driver, the shortgrass prairie was secondarily maintained by grazing (Fig. 7). The primary grazers were black-tailed prairie-dogs (*C. ludvicianus*), bison, and elk (wapiti), in that order. Pronghorn (*Antilocapra americana*), which selectively forage on forbs rather than grasses, were also present (Knopf and Samson 1997).

The historical frequency, intensity, and extent of grazing on the southern Great Plains are poorly understood. Elk occurred primarily on the eastern half of the Great Plains (eastern Nebraska, Kansas, and Oklahoma), where they foraged in small herds. Elk were apparently more frequent in the vicinity of riverbottom areas, where ranker grasses were present, and the effects of their grazing were probably not great, given the small size of the herds. Bison, on the other hand, grazed on the high plains in extensive herds, likely numbering at least in the tens of millions (Shaw 1995). Many authors refer to the annual movement patterns of bison creating a "grazing mosaic," though specific information on a regular patterning of movement is lacking. Because of the presence of large bison herds along the Missouri, Republican, Arkansas, Cimarron, and Canadian rivers (which served as water sources), much of what is today called "mixed-grass prairie" was shortgrass prairie historically (Hart 2001). Although it is tempting to attribute the development of the mixed-grass prairie to differential foraging by cattle as compared with bison, the reality is that the introduction of grazing practices (managing cattle stocking rates and seasonal timing) in which fences are used to control and standardize grazing pressure probably had a larger effect on bird habitats in the Great Plains (Samson et al. 2004) than the displacement

Fig. 9. A fenceline contrast in mixed-grass prairie in southern Alberta, near the Little Bow River. The field on the left is managed with a rotational system for winter grazing. There is substantial between-season carryover, and the site is in good range health. It would sustain some individuals of many species, including generalists like Horned Lark and Western Meadowlark; a few species that like low cover, such as Chestnut-collared Longspur; and a variety of those needing moderate to relatively tall cover. The field on the right has been grazed intensively in a season-long system and would support mainly generalists and low-cover-specialist birds. (Photograph by Barry Adams, Alberta Sustainable Resource Development.)

numbers were 20–50% lower within 100 m of gravel roads in Saskatchewan (Sutter et al. 2000) and Wyoming (Ingelfinger 2001). Assuming a similar zone of effect, Forman (2000) estimated that 16.7% of rural areas in the United States are influenced by roads. The zone of effect may be larger, because grassland songbirds continued to increase with distance from roads out to 2 km (Koper and Schmiegelow 2006b). Energy extraction is a common but little-studied activity (Fig. 10). Birds can respond to well pads and pipelines themselves (Gratto-Trevor 2000) or to associated noise (Habib 2006), roads, invasive species, and traffic (Lyon and Anderson 2003). Greater Sage-Grouse (*Centrocercus urophasianus*) avoided high-density well areas (Holloran 2005), and disturbance at leks kept female Sharp-tailed Grouse (*Tympanuchus phasianellus*) from visiting (Baydack and Hein 1987).

Fragmentation of habitat involves many of the already-mentioned factors (range condition, invasive species, roads, and energy extraction) linked to impaired habitat function and quality but also includes edge, minimum area, and isolation effects on abundance and productivity. Fragmentation or area sensitivity has been implicated in some tallgrass situations, but findings vary by region and species (Johnson and Igl 2001a). Regionally, area sensitivity was documented in some species using North Dakota CRP (Johnson and Igl 2001a) and Saskatchewan native grass (Davis 2004) and planted cover (McMaster and Davis 2000). Abundance was better explained for most species by distance to edge than by patch size in Saskatchewan (Davis 2004) and Alberta (Koper and Schmiegelow 2006a). Abundance was unrelated to the amount of grassland in the surrounding landscape (McMaster et al. 2005, Koper and Schmiegelow 2006a). With a few exceptions (Grant et al. 2006), songbird nest success was not related to patch size (Davis 2003, Davis et al. 2006), distance to edge (Koper and Schmiegelow 2006a), or the nature of the surrounding landscape (McMaster

FIG. 7. The shortgrass prairie, as seen here in Weld County, Colorado, evolved with intensive grazing pressure that results in native grasses with 90% of the biomass below ground to protect the individual plant when heavily cropped by species such as bison. Regrowth is rapid following summer rains. (Photograph by F. L. Knopf.)

of a native ungulate by a domestic ungulate (Hartnett et al. 1997).

The black-tailed prairie-dog is definitely underappreciated in its historical role as a grazer on the shortgrass prairie. This species occurred across all of Nebraska, Kansas, and Colorado. (Lewis and Clark collected the first specimen in eastern Nebraska.) In areas today considered mixed-grass prairie, bison preferentially forage on prairie-dog towns (colonies), further enhancing the pressure on taller grass species (Coppock et al. 1983). The sum effect was that the southern Great Plains were noted for their monotony of vista by Mark Twain and others, which further challenges the idea of a grazing mosaic (Hart and Hart 1997). The intense grazing pressure on the southern Great Plains favored a floristic homogeneity of the grasslands (Milchunas et al. 1988, Vinton and Collins 1997), so that the "mosaic" was dominated by a single type of grassland (shortgrass prairie), with smaller "decorative tile" inserts of tall grass and shrubs in areas with low grazing pressure because of soil conditions or availability of water.

Grassland bird assemblage.—Several species of grassland birds—Mountain Plover (*Charadrius montanus*), Baird's Sparrow (*Ammodramus bairdii*), Lark Bunting (*Calamospiza melanocorys*), McCown's Longspur (*Calcarius mccownii*), and Chestnut-collared Longspur (*C. ornatus*)—are endemic to the Central Grasslands of North America (Mengel 1970), so these species evolved within a grazed ecosystem. Some species (such as Mountain Plover and McCown's Longspur) occur in areas of intensive grazing, whereas others prefer ecotones of less intensive grazing (Lark Bunting and Chestnut-collared Longspur; Knopf 1996b). Still other species—such as Cassin's Sparrow (*Aimophila cassinii*)—are tolerant of, and probably require, shrub incursion into prairie.

Avian population declines from historical levels on the shortgrass prairie are intuitively obvious. Populations were certainly reduced

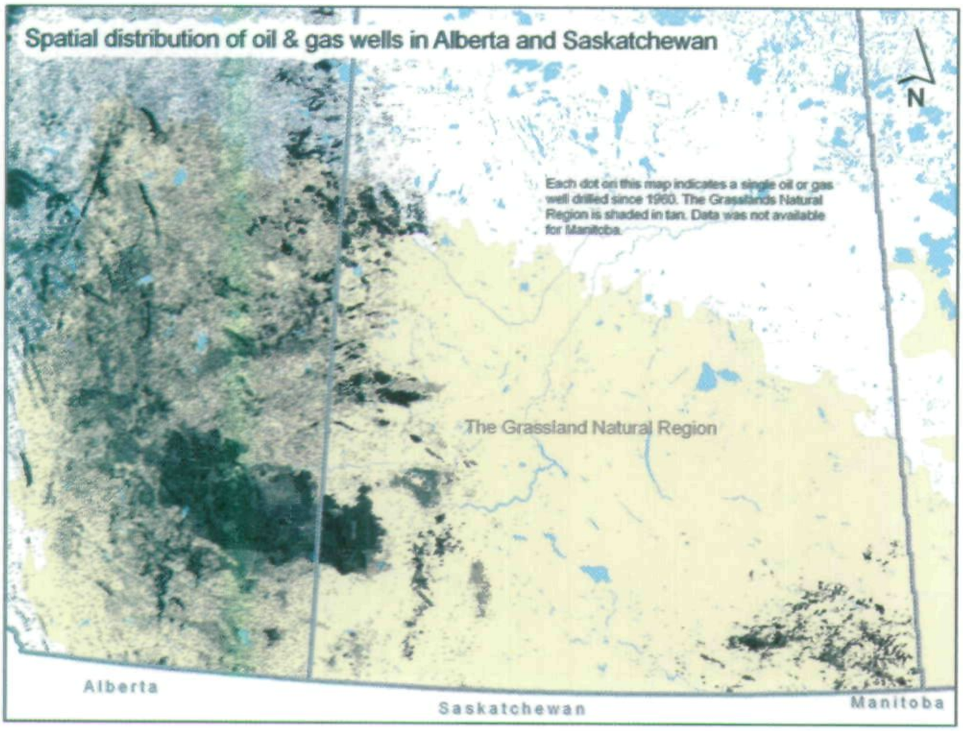

FIG. 10. Energy-extraction activity in one portion of the northern plains. Each small dot represents an oil or gas well (Source: Alberta Energy Utilities Board and Saskatchewan Industry and Resources). The extent of grassland appears as background (Natural Resources Canada, GeoGratis: www.geogratis.cgdi.gc.ca; map courtesy of Olaf Jensen, Canadian Wildlife Service).

et al. 2005, Davis et al. 2006), though nest parasitism increased with fragmentation in one study (Davis and Sealy 2000).

The last reason for declines is direct losses attributable to predation, field operations in crops or forage, road kills, air strikes (Dolbeer 2006), and pesticides (Mineau and Whiteside 2006). Fragmentation, roads, pesticides, grazing management (Desmond 2004), and invasion by exotics and shrub are also relevant during migration and on the wintering grounds.

Managing habitat for grassland birds.—According to Rodriguez (2002), the mechanisms driving declines may be complex, but the conservation effort can be simple: concentrate efforts where birds are most abundant and work from there. We know where high-abundance areas are, thanks to the BBS, Grassland Bird Monitoring (Dale et al. 2005), Conservation Data Centers, and individual research projects. These areas, not surprisingly, coincide with large stretches of grassland in eight "ecologically significant areas" identified by the Commission for Environmental Cooperation and The Nature Conservancy (Karl and Hoth 2005).

The most important goal of habitat management for grassland birds is to prevent further losses of native grasslands. About 30% of Canadian prairie grassland is in private hands, 7% is controlled by the federal government, and 63% is controlled by provincial, tribal, and other levels of government (Gauthier et al. 2003). Much public land is in community pastures or grazing leases. About 5.3% of the prairie is set aside for conservation, and most (63%) protected sites are >1,000 ha in size (Gauthier and Wiken 2002), which is the threshold for "minimum viable area" (Samson et al. 2004). Grassland ownership in the U.S. portion of the Great Plains is estimated to be 84% private, 7% federal (with the Bureau of Land Management and U.S. Forest Service managing the majority), and 9% state, municipal, county, or tribal government (Gauthier et al. 2003). Separate figures for the northern portion of the plains were not available. The northern plains are, in as a result of the extensive fragmentation of the prairie as it was converted to agricultural crops, especially cereal grains, since the late 1800s. More recently, however, BBS data indicate continued, widespread declines of endemic grassland birds. The widespread nature of these declines across species argues for broad regional changes in the shortgrass prairie or across wintering areas since the mid-1960s (Knopf 1994).

The Mountain Plover is the most intensively studied of the endemic birds of the shortgrass prairie. The proposal to list it as a Threatened Species under the auspices of the Endangered Species Act (U.S. Fish and Wildlife Service 2002) identified five major threats to the continental population: (1) conversion of native grasslands to agriculture on the breeding grounds, (2) destruction of nests by certain agricultural practices, (3) historical conversion of native grasslands on wintering grounds, (4) consequences of rangeland management (standardized grazing, reduction of prairie-dog [*Cynomys* spp.] populations), and (5) conflicts arising from the development of mineral-extraction projects (Knopf and Wunder 2006). These threats, individually and cumulatively, surely influence populations of the other Central Grassland endemics as well.

Current habitat for grassland birds.—Unlike other areas of native grasslands in North America, the shortgrass prairie has a relatively large component of public lands. Following the devastation of the Dust Bowl, many parcels were repurchased by the federal government and assigned to the Soil Conservation Service. A total of 1,548,000 ha was subsequently turned over to the U.S. Forest Service in 1954, to be managed as 19 new national grasslands beginning in 1960 (West 1990). Seventeen of these national grasslands are on the historical southern Great Plains. Additional properties are managed by the Department of Interior through the Bureau of Indian Affairs (8,033,992 ha), Bureau of Land Management (4,930,503 ha), Bureau of Reclamation (275,190 ha), Fish and Wildlife Service (713,993 ha), and National Park Service (53,883 ha), and by the Department of Defense (1,434,136 ha). Collectively, ~6% of the historical southern Great Plains is in public ownership, with most of the acreage located disproportionately in the west. Substantial portions of these lands are suitable for grassland birds, and management for grassland species occurs with varying degrees of attention.

Managing habitat for grassland birds.—Ecological restoration methods have not been developed specifically for the shortgrass prairie as they have for the tallgrass (true) prairie. The CRP most closely approximates an effort to manage for grassland birds on the Great Plains, albeit secondarily. Under this program, farmers are paid to take land out of production to prevent soil erosion and to create wildlife habitat. A total of 8,044,346 ha of private lands is registered in the program across the 10-state area, with 4,708,301 ha in the current shortgrass-prairie region of the southern plains (Allen and Vandever 2005). Thus, grassland conservation is influenced more by CRP on private lands than by management of public lands within any single agency.

Despite the massive acreage enrolled in CRP, however, fields within most of the historical shortgrass prairies have been planted primarily to taller native or tame grasses that may have historically occurred in local patches, but not over broad areas. Whereas response to CRP by the more widespread grassland species has been favorable in the northern portion of the Great Plains (Johnson and Igl 1995), Central Grasslands endemic species that breed in the northern Great Plains and winter on the southern Great Plains have not colonized CRP fields, probably because these species require shortgrass habitats. Populations of species such as Baird's Sparrow, Lark Bunting, and Chestnut-collared Longspur have declined significantly during the CRP era (1986–2002; Sauer et al. 2003). The organization Environmental Defense is working with avian biologists, range ecologists, and federal agencies to help refine CRP management programs, including the proper grazing of Great Plains grasslands. To date, grazing of CRP lands has been permitted only within the context of drought ("disaster") relief, and not as a management tool.

Given that restoration practices have not been developed for the shortgrass prairie, management practices for birds in this region rely more on intuition and an understanding of natural history than on information derived from experiments on how bird populations are affected by habitat manipulation (Johnson and Igl 2001b). Fire was not a prevalent ecological driver in the shortgrass prairie. The endemic many ways, decimated and their functioning impaired, but with 25–30% of the original grassland remaining and pieces as small as 18 ha of conservation value (Davis et al. 2006), we cannot hope to buy or otherwise secure all the remaining grassland through purchase or easement. Scrutiny and adjustment of policy and legislation at federal, state or provincial, and local levels are necessary to eliminate remaining incentives to break up grasslands.

Maintaining or rehabilitating the integrity of remaining grasslands is also critically important. Refuges and sanctuaries are the only sites likely to be managed at historically appropriate intervals. Sustained rest in mixed-grass prairie did not occur historically and is not beneficial for primary endemic grassland birds, because the increased height and thickness of grass, accumulated litter, or expanded shrub cover will render sites unattractive to specialized grassland birds. Application of natural drivers of grazing, and to a lesser degree burning, at appropriate intervals should maintain the broad variety of grassland conditions for the full suite of grassland birds historically associated with mixed-grass prairie. The variation in soil and moisture across the northern plains makes it impossible to offer blanket prescriptions (e.g., burn every six years, graze at a rate of 10 ha cow^{-1}) to benefit a given bird species (Kantrud 1981, B. C. Dale et al. unpubl. data). Madden et al. (2000) suggest using a range of acceptable vegetation measurements to guide management. Land managers then choose which management tool and application rate would create those conditions in their area.

Over much of this region, grazing is the land use most compatible with long-term maintenance of healthy grasslands and bird communities. Moderate or light grazing maintains or improves range condition (Holechek et al. 1999), and sites in good condition support more grassland bird species (George et al. 1992). Large fields are more likely to be heterogeneous, because of variety in topography and distance to water (B. C. Dale et al. unpubl. data, Renfrew and Ribic 2002, Fontaine et al. 2004, Koper and Schmiegelow 2006b).

Restoration of cover with regionally appropriate native grasses may be very beneficial, but, for economic reasons, it is not widespread. The total area in CRP in the northern plains region of the United States is 3,336,045 ha (Allen and Vandever 2005). The plant species and strains chosen are rarely native to the region. Grazing and haying are not permitted except under emergency circumstances. The total area in Canada's Permanent Cover Program (PCP) is 518,000 ha (Gauthier et al. 2003). Introduced plants are sown, and the cover may be grazed or hayed. Most endemic birds occur in low numbers in both programs (Johnson and Schwartz 1993a, b; McMaster and Davis 2000). A comparison of the densities or rankings of birds on CRP land (Johnson and Schwartz 1993a, b) with estimates on PCP land (D. G. McMaster unpubl. data) showed that six of eight primary endemics were more common on the latter. Only Lark Bunting was more common on CRP than on PCP land. Avian productivity is as good on CRP land as it is on Waterfowl Production Areas, however (Koford 1999). The PCP has been replaced by the Greencover Canada Program (Agriculture and Agri-Food Canada 2005) and will continue to allow agricultural use that benefits grassland birds. It could be improved with date restrictions on haying to increase productivity of birds (Dale et al. 1997, McMaster et al. 2005).

In summary, while pursuing opportunities for protection, we must concentrate most of our efforts on extensive activities like policy reform, farm programs, demonstration projects, marketing of "eco-products," and extension and other forms of education to encourage retention of native prairie and restoration of range condition while encouraging creation of new grass habitats and best practices on crops and tame forage. The U.S. Farm Bill and the new Canadian Agricultural Farm Policy (Agriculture and Agri-Food Canada 2005) are mechanisms for delivery of additional cover and Good Management Practice incentives. The latter offers a dynamic opportunity, because it incorporates farm planning and a series of practices (reviewed annually) whose costs are offset. As we obtain more information along the lines of Davis (2004) or Fletcher et al. (2006), we can target these activities more precisely and modify our advice, but we must not delay our collaborative activities until we have all the answers.

We need to work with other disciplines to make our biological findings economically relevant (Theobald et al. 2005). Good grazing management is consistent with profits for producers (Holechek et al. 1999, Prairie Farm Rehabilitation Administration 2000), shortgrass species blue grama and buffalo grass are highly drought tolerant and maintain ~90% of their biomass below the surface. Thus, native shortgrass landscapes lack adequate fuel—because most of each plant is subterranean and because of intensive removal of aboveground tissues by herbivores and high levels of wind erosion of the litter layer during the dormant season—to carry a fire any distance, restricting the historical role of fire as an ecological driver and limiting the current efficacy of fire as a management tool to local use only.

Grazing is the principal management tool to promote the shortgrass species that evolved in this biome, especially as one approaches the Rocky Mountains. Grazing is as critical to the health of shortgrass prairie as it is in the Serengeti Plains of Africa (Sinclair and Norton-Griffiths 1979). Without grazing, shading by taller (native and exotic) grasses precludes establishment and growth of the historically dominant shortgrass species. Drought tolerance and grazing drive shortgrass-prairie health, and endemic grassland birds generally exploit niches created by different intensities of grazing at local and regional scales (Knopf 1996b; Fig. 8). Unfortunately, neither experimental nor rigorous observational data are available to make specific recommendations about how grazing can be managed to favor these species.

Management of shortgrass prairie for grassland birds faces one additional hurdle not encountered elsewhere in North America. Grazing on public lands is almost universally opposed by environmental organizations, on the basis of studies in desert, riparian, and forested landscapes of western North America. Numerous studies show, however, that many of the species characteristic of shortgrass prairies increase in density as grazing intensity increases (although this relationship depends on soil conditions and seasonal rainfall; Knopf 1996a). Where grazing by domestic stock is not permitted across broad landscapes, these endemic species will be threatened unless dense populations of native grazers are restored throughout these areas.

Northern Plains

History of grasslands.—The northern plains include southeastern Alberta, southern Saskatchewan, and southwestern Manitoba in Canada and much of Montana, North Dakota, South Dakota, and northeastern Wyoming in the United States. Shaped by glacial deposits, the northern plains are flat to rolling and are dotted with intermittent wetlands (prairie potholes). Precipitation is generally low, evaporation exceeds precipitation, and periodic droughts occur (Gauthier et al. 2003). Rainfall

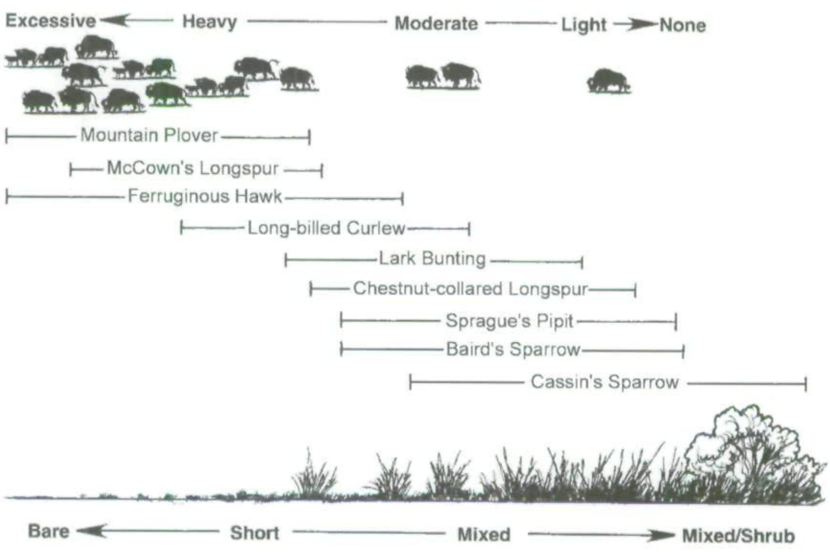

FIG. 8. Distribution of endemic birds of prairie uplands in relation to grassland type and historical grazing pressure across the central plains. (Reprinted from Knopf 1996b.)

and society benefits not only from increases in forage production but also from build-up of soil organic matter and sequestered atmospheric carbon (Conant et al. 2001). Minimum-tillage fields are better than conventional fields in terms of abundance, nest densities, and productivity of birds (Martin and Forsyth 2003) and offer producers improved economics through reduced field operations and maximum use of limited moisture. Conservation objectives can be achieved with little economic cost or conflict (Polasky et al. 2005).

Delivery of the North American Bird Conservation Initiative through North American Waterfowl Management Plan (NAWMP) joint ventures has been hailed as an opportunity for conserving grassland birds (Brennan and Kuvlesky 2005), but cover programs for waterfowl in the northern plains have limited benefits for high-priority grassland birds (Dale and McKeating 1996), and ducks do not always act as a conservation surrogate for other avian species in the mixed-grass prairie (Koper and Schmiegelow 2006b). The NAWMP's recent emphasis on protection of native habitats and on policy scrutiny is, however, beneficial to grassland birds. Also, the Prairie Conservation Action Plan functions as an important forum for engaging stakeholders and building on common goals related to maintaining healthy prairie (Nernberg and Ingstrup 2005).

Desert Grasslands

History of grasslands.—The grasslands of northern Mexico and the southwestern United States are generally referred to as "desert grasslands" (Rzedowski 1975, McClaran 1995; Fig. 11). The geographic extent of this grassland type basically coincides with the Chihuahuan Desert Ecoregion, which covers the Central Plateau of Mexico south to approximately the Transvolcanic belt and is bordered on the east and west by the Sierra Madre Oriental and Occidental, respectively, north to west Texas, southern New Mexico, and southeastern Arizona. As the name implies, the main ecological driver of desert grassland systems is drought. Fire, however, played a role in maintaining some areas of desert grasslands in the past (Humphrey 1958, Bahre 1991). The frequency of fires in prehistoric times is difficult to determine for desert and other grasslands, but several authors estimate that fires may have occurred at intervals of approximately 7–10 years. This estimate is based on indirect

Fig. 11. Desert grassland landscape with open-ground patches and shrubby elements of yucca in northern Chihuahua, Mexico. (Photograph by Profauna Chihuahua.)

increases from west to east and south to north (from 20 cm in the west to ~45 cm in the east and north), which creates different prairie landscapes: small blocks of fescue, and large zones of mixed-grass, moist mixed-grass, and aspen (*Populus* spp.) parkland. Parkland is the transition zone between grassland and forest. Mixed-grass prairie is a combination of grasses of short and intermediate height, but the species of intermediate height contribute more biomass, except in heavily grazed areas. Shrubs may be scattered in the grass or form dense stands. The mixed-grass prairie is bordered by tall grass to the east and trees to the north.

Historically, lack of moisture and extreme variability in moisture maintained grass as the dominant vegetation (Samson et al. 2004), so it was the primary driver in this region. Amount of precipitation, in combination with soil quality and the secondary drivers of grazing and (to a lesser degree) fire, determined the extent of grass, the height and density of the standing crop of herbage, and amount of litter and shrub incursion. Because each factor varied temporally, spatially, or both, the historical northern plains were dynamic.

All the northern plains area was grazed intermittently by bison, pronghorn, and elk. Much of it was also grazed by lagomorphs, Richardson's ground squirrels (*Spermophilus richardsonii*), and black-tailed prairie-dogs. The large number of bison and their willingness to forage far from water meant that areas were probably grazed severely and fairly uniformly. However, particular sites had one to eight years of recovery before a herd returned (Malainey and Sherriff 1996). In contrast to the short-grass prairie, where grazing created a highly homogeneous stand, more localized grazing by bison in the northern plains probably resulted in a mosaic of large patches in all stages of renewal. Seasonal changes in amount and type of forage consumed by bison (Plumb and Dodd 1993) may have created other subtle differences between patches.

Fire was important in holding back tree and shrub invasion in the fescue, parkland, and moist mixed-grass. Intervals between fires varied with soil type, moisture, and grazing. The average return interval was probably 6 years in North Dakota (Madden et al. 1999) and areas with similar moisture, and 10 to 26 years in Montana (Umbanhowar 1996) and other dry sites. Burns were usually relatively small (Higgins 1984), and both human and lightning-caused fires contributed to the historical fire regime (Romo 2003). The lightning season was mid-May to mid-September, but fires set by First Nations people were most common in April, September, and October (Higgins 1986).

Grassland bird assemblage.—Twenty-six species of obligate grassland birds (*sensu* Vickery et al. 1999b) breed in the northern mixed-grass prairie. Nine of these are endemic to the Central Grasslands of North America (Mengel 1970). Twenty-two of the 25 obligate grassland species for which we have sufficient data on population trends (and 8 of 9 Central Grassland endemics) are declining (Sauer et al. 2005).

Even the tallest vegetation required by Central Grassland endemics is lower than that generally available in eastern grasslands. Sprague's Pipits (*Anthus spragueii*), and Baird's Sparrows need grasses 10–30 cm in height and avoid areas with taller grass cover, woody cover, or excessive litter (>4 cm depth; Robbins and Dale 1999, Green et al. 2002). Mountain Plovers use very short cover and are often associated with prairie-dog towns. McCown's and Chestnut-collared longspurs prefer low to moderately low cover. Many prairie birds need some heterogeneity. Marbled Godwits (*Limosa fedoa*) need different cover heights for feeding, nesting, and brood rearing (Ryan et al. 1984). Burrowing Owls need a mix of short and moderate grasses, but also need holes created by burrowing mammals for nesting and escape. Lark Buntings, Brewer's Sparrows (*Spizella breweri*) and Clay-colored Sparrows (*S. pallida*) require some shrubs. Ferruginous Hawk (*Buteo regalis*) can hunt and nest in a variety of grassland conditions with or without trees. Horned Larks and Western Meadowlarks tolerate a broad range of grassland conditions.

Current habitat for grassland birds.—The most obvious and important cause of bird population declines is habitat loss. Reduction in rangeland is followed by population declines in grassland birds (Murphy 2003), and populations generally are not declining in areas with more rangeland (Veech 2006). In Canada, ~14 million hectares (30%) of native grassland is still intact (Gauthier and Wiken 2003); the proportion remaining varies among provinces (Alberta, 43%; Saskatchewan, 24%; Manitoba, 21%) and by prairie type. In the United States, estimates for the historical and remaining cover of mixed grass evidence such as presence and abundance of woody species (Griffiths 1910, Leopold 1924, Wright and Bailey 1980, Schmutz et al. 1985). Early Spanish explorers reported that fires were intentionally set by Native American tribes in desert grasslands in Mexico and the southwestern United States (Gentry 1957). Fire can have major effects on desert grasslands. It eliminates cover in the short term, but may reduce the density of woody species in the long term. Saab et al. (1995) argued that the suppression of fires in this system produced, through increased woody plant cover, the drastic changes in ecosystem structure and function currently observed throughout desert grasslands in Mexico and the southwestern United States. Dinerstein et al. (2000) estimated that grasslands have decreased between 25% and 50% because of the spread of shrublands in the region.

Grazing by native herbivores may have been even more important than fire in preventing woody shrubs from spreading in desert grasslands (Weltzin et al. 1997). The primary natural grazers of desert grasslands were black-tailed prairie-dogs in the United States and northern Mexico; Mexican prairie-dogs (*C. mexicanus*) in central Mexico; and, to a lesser extent, bison and pronghorn (Anderson 1982, Saab et al 1995). Bison are reported to have roamed the region intermittently, being present in a particular area only sporadically in some years, apparently as a result of irruption-type movements from the Great Plains. The net effect of these sporadic irruptions of bison on the native grasslands and overall landscape of the region is not known, but probably was not strong (Parmenter and Van Devender 1995, Monger et al. 1998). Also, pronghorn were found in large numbers in the southwestern United States (Parmenter and Van Devender 1995). Although pronghorn are primarily forb-foragers or browsers rather than grazers, in many areas of desert grasslands, the most abundant plant species can at times be forbs.

The frequency and intensity of grazing in desert grasslands before the introduction of large number of domestic grazers starting ~450 years ago is not well known, but it is clear from historical descriptions that prairie-dogs were mostly responsible for the overall structure of vast areas of desert grassland communities (Parmenter and Van Devender 1995). Until the 1930s, prairie-dog towns covered large stretches of grassland from trans-Pecos Texas to southeastern Arizona; for example, prairie-dog towns covered an estimated 2.5 million ha in New Mexico. Federal programs in the United States almost completely exterminated prairie-dogs from this region by the 1960s. Numerous prairie-dogs, however, are still found in grasslands in northwestern Mexico (Ceballos et al. 1993), where there have been few large-scale eradication programs. The largest prairie-dog complex in North America is found at Janos-Nuevo Casas Grandes in northwestern Chihuahua, Mexico; it covers an estimated 55,258 ha (with one colony covering 34,949 ha; Ceballos et al. 1993). The distribution of the Mexican prairie-dog in Coahuila, Nuevo Leon, San Luis Potosi, and Zacatecas has decreased significantly from an estimated 1,500 km^2 to only 290 km^2 in 1999 (Scott-Morales et al. 2004). Most of the destruction has resulted from conversion of prairie-dog colonies to agriculture production and continues to the present day.

Prairie-dogs have a substantial influence on grasslands. By constantly clipping the vegetation to maintain an unobstructed view of the landscape, they prevent shrub and other woody species from invading. Koford (1958: 59) found that eradication of prairie-dogs usually results in the spread of mesquite, converting grassland to shrubland, and that "many old timers in Texas and Oklahoma attribute the great increase in mesquite on grasslands during the past century to the extermination of prairie dogs." Thus, prairie-dog eradication may explain why so much of the desert grassland has been converted to mesquite scrub (Weltzin et al. 1997). By contrast, areas with prairie-dog colonies in Chihuahua have remained open grassland (Ceballos et al. 1993, Manzano-Fischer et al. 1999). The role of prairie-dogs in preventing shrub invasion is consistent with evidence that there was never enough fuel in desert grasslands to permit extensive burns (Van Auken 2000) and that mesquite is more resistant to fire damage than some species of semidesert grass, such as black grama (*Bouteloua eripoda*; Buffington and Herbel 1965).

Grassland bird assemblage.—Many of the grassland bird species that breed in the desert grasslands of Mexico and the southwestern United States also breed farther north in the prairies of the United States and Canada (Peterson and Robbins 1999). These include Horned are not available for all states. Samson and Knopf (1994) estimate that North and South Dakota historically had 13.9 and 1.6 million hectares of mixed grass, respectively, and that 28% of North Dakota prairie is intact.

Governments encouraged settlement by offering land and incentives to those willing to turn over the soil and plant crops. All but the poorest soils and steepest slopes were converted from grass to grain or introduced forage with associated roads, preferentially eliminating grassland with the greatest primary productivity. Grassland birds disappear or decline once the native cover is removed (Johnson and Schwartz 1993a, b; McMaster and Davis 2000) or replaced with hay (Dale et al. 1997, McMaster et al. 2005). Also, grassland birds nesting in crops (Lokemoen and Beiser 1997) or hay (Dale et al. 1997) have low productivity. Agricultural departments in both nations encouraged farmers to "improve" pastures by replacing native plant species with introduced species like crested wheatgrass (*Agropyron cristatum*). Several endemic bird species use planted pastures less frequently than native pasture because it is structurally different, particularly in the litter layer (Sutter and Brigham 1998, Davis and Duncan 1999). Chestnut-collared Longspurs sometimes find crested wheatgrass attractive but experience lower productivity than on native range (Lloyd and Martin 2005).

Although most habitat loss occurred during settlement, grassland continues to be converted to urban and suburban settlement (Hansen et al. 2005), and crops (Brown et al. 2005: fig. 2) or other cover. Exurban development (6–25 homes per square kilometer) is the fastest growing form of land use in the United States (Hansen et al. 2005), with settlement area increasing by ≤20% in some parts of the northern plains (Brown et al. 2005: fig. 2). Native species (including birds) have decreased reproduction and survival near houses, largely because development alters habitats and increases disturbance and predation (Hansen et al. 2005).

Changes in grassland conditions may be almost as important as loss of habitat. The remaining prairie has lost much of its dynamic nature. Fire has been suppressed, allowing trees and shrubs to invade grassland in all but the driest areas. For example, aspen is expanding at 0.5–5% year^{-1} on black soils in prairie Canada (Prairie Farm Rehabilitation Administration 2000). Many grassland bird species occur less frequently when woody cover increases (Robbins and Dale 1999, Green et al. 2002, Grant et al. 2004, Ahlering 2005) or avoid nesting near it (Davis 2005). Shrubs may provide cover for rodents that prey on nests of open-country birds (With 1994). Also, intensive livestock grazing can reduce the health and vigor of the plant community, resulting in range conditions (rated "poor" or "fair" for livestock) that are less likely to attract some endemic bird species (Robbins and Dale 1999; Fig. 9) and less able to sustain grassland birds during periods of drought (George et al. 1992). Reduced range condition is a serious and pervasive problem, with more than half of Canadian prairie grassland estimated to be in less than "good" condition (Prairie Farm Rehabilitation Administration 2000). In addition, because cattle are confined by fences, they may graze sites annually rather than periodically, creating a landscape with a far more uniform height and density of grass than would have resulted from periodic grazing by bison. Both of the extreme ends of the height-and-thickness spectrum are less common, as are the associated birds (Knopf 1994). For example, prairie-dog towns, characterized by very short vegetative cover and a high proportion of bare ground, occupy only a fraction of their original estimated distribution (Wuerthner 1997), which means reduced success for short-cover specialists such as Burrowing Owls (Desmond et al. 2000).

Additional factors (invasive plants, roads, energy extraction, and habitat fragmentation) have changed the quality of remaining habitats and are associated with declines in occupancy or productivity. Invasion by exotic plants (Wilson and Belcher 1989, Robbins and Dale 1999, Scheiman et al. 2003, Grant et al. 2004) reduces avian occupancy of grassland. Two common invaders, crested wheatgrass and smooth brome (*Bromus inermis*), result in changes to structure (e.g., amount of standing dead grass; Henderson and Naeth 2005) or function (e.g., litter decomposition rates; Ogle et al. 2003). Roads and trails are implicated in dispersal of exotic species (Larson et al. 2001). Roads are also associated with direct mortality of birds (e.g., 20–37% of Burrowing Owl mortality; Haug et al. 1993) as well as changes in habitat and ecological function (Forman 2000, Trombulak and Frissell 2000). Songbird

Lark, Savannah Sparrow, and Grasshopper Sparrow. Other species that nest in the Great Plains are winter residents in desert grasslands (e.g., Ferruginous Hawk, Mountain Plover, Long-billed Curlew (*Numenius americanus*), Vesper Sparrow, Lark Bunting, McCown's and Chestnut-sided longspurs, and Eastern and Western meadowlarks). Several species listed as birds of conservation concern by the U.S. Fish and Wildlife Service, such as Sprague's Pipit and Baird's Sparrow, are concentrated in this region during winter. A few grassland species are endemic or nearly endemic to the Chihuahuan Desert of northern Mexico and the adjacent United States (e.g., Botteri's Sparrow [*Aimophila botterii*] and Rufous-winged Sparrow [*A. carpalis*]). Populations of the northern Aplomado Falcon (*Falco femoralis septentrionalis*) have historically (Oberholser 1974) and recently (Young et al. 2004) been found in grasslands of the northern Chihuahuan Desert (Texas, New Mexico, and Chihuahua). The only avian species truly endemic to this grassland system is Worthen's Sparrow (*Spizella wortheni*; Phillips 1977), which is considered threatened by BirdLife International (Byers et al. 1995). It occupies shrubby grassland habitats and is found consistently, though in low densities, at the edges of prairie-dog colonies in Coahuila, Nuevo Leon, and San Luis Potosi (Garza de Leon et al. 2007).

Although large tracts of desert grassland remain, many species that nest and winter in this type of environment are declining. Results of the North American BBS indicate that many of the species that breed or spend the winter in desert grasslands have had overall population declines in North America since the mid-1960s (Knopf 1994). Population declines can be attributed to several factors, including loss and fragmentation of habitat. Loss of grasslands in this region is attributable not only to conversion to shrublands following elimination of natural grazers and fire, but also to the transformation of some areas for agricultural purposes. Prairie-dogs have long been persecuted by cattle ranchers in both Mexico and the United States, leading to their elimination in many regions and diminishing their influence in maintaining desert grasslands free of woody invaders. Even where prairie-dogs remain in some areas of Chihuahua, severe overgrazing by livestock results in a habitat with few grassland birds (Desmond 2004).

Desert grasslands are structurally short and support a lower avian species-richness than peripheral areas (Mengel 1970), which are the transition zones with more structurally complex environments imbedded in the grasslands, such as riparian woodlands, mountain slopes, and adjoining shrublands. Prairie-dog colonies support higher diversity and densities of shortgrass-prairie birds than adjacent grassland areas without prairie-dogs (Agnew et al 1986, Desmond 2004). Some species are particularly frequent in prairie-dog colonies (e.g., Mountain Plover and Ferruginous Hawk; Fig. 12), whereas others are common on prairie-dog colony edges (i.e., sparrows [*Spizella* spp.], Lark Buntings). Bird surveys in the Janos-Nuevo Casas Grandes prairie-dog complex of Chihuahua revealed that Horned Larks and Lark Buntings were abundant and that several other grassland specialists (Ferruginous Hawk, Mountain Plover, Long-billed Curlew, Burrowing Owl, longspurs [*Calcarius* spp.], and meadowlarks [*Sturnella* spp.]) were common (Manzano-Fischer et al. 1999).

With a few notable exceptions, shortgrass-dependent birds are the least understood of North American birds in both breeding and wintering areas (Phillips 1977). This is particularly true for northern Mexico, where detailed studies of desert grassland avifauna have taken place only during the past two decades except in a few areas, such as the Mapimi Biosphere Reserve. For example, breeding by Mountain Plovers was documented only recently in colonies of Mexican prairie-dogs in northern Mexico (Desmond and Chávez-Ramírez 2002, González Rojas et al. 2006).

The patterns of occurrence for individual species and large concentrations of birds in specific regions of the desert grassland are highly dynamic and highly variable from year to year (Raitt and Pimm 1977), probably because of the variability in rainfall patterns and food production. The same area may have large concentrations of winter-resident sparrows in some winters and none in other winters (Desmond 2004, F. Chávez-Ramírez pers. obs.). This pattern was observed in a Christmas Bird Count in northwestern Chihuahua, where counts of sparrows (*Spizella* spp.) varied from <2,000 to >13,000 in successive years (Dieni et al. 2003). Grassland bird communities are also characterized by high turnover rates between breeding

FIG. 9. A fenceline contrast in mixed-grass prairie in southern Alberta, near the Little Bow River. The field on the left is managed with a rotational system for winter grazing. There is substantial between-season carryover, and the site is in good range health. It would sustain some individuals of many species, including generalists like Horned Lark and Western Meadowlark; a few species that like low cover, such as Chestnut-collared Longspur; and a variety of those needing moderate to relatively tall cover. The field on the right has been grazed intensively in a season-long system and would support mainly generalists and low-cover-specialist birds. (Photograph by Barry Adams, Alberta Sustainable Resource Development.)

numbers were 20–50% lower within 100 m of gravel roads in Saskatchewan (Sutter et al. 2000) and Wyoming (Ingelfinger 2001). Assuming a similar zone of effect, Forman (2000) estimated that 16.7% of rural areas in the United States are influenced by roads. The zone of effect may be larger, because grassland songbirds continued to increase with distance from roads out to 2 km (Koper and Schmiegelow 2006b). Energy extraction is a common but little-studied activity (Fig. 10). Birds can respond to well pads and pipelines themselves (Gratto-Trevor 2000) or to associated noise (Habib 2006), roads, invasive species, and traffic (Lyon and Anderson 2003). Greater Sage-Grouse (*Centrocercus urophasianus*) avoided high-density well areas (Holloran 2005), and disturbance at leks kept female Sharp-tailed Grouse (*Tympanuchus phasianellus*) from visiting (Baydack and Hein 1987).

Fragmentation of habitat involves many of the already-mentioned factors (range condition, invasive species, roads, and energy extraction) linked to impaired habitat function and quality but also includes edge, minimum area, and isolation effects on abundance and productivity. Fragmentation or area sensitivity has been implicated in some tallgrass situations, but findings vary by region and species (Johnson and Igl 2001a). Regionally, area sensitivity was documented in some species using North Dakota CRP (Johnson and Igl 2001a) and Saskatchewan native grass (Davis 2004) and planted cover (McMaster and Davis 2000). Abundance was better explained for most species by distance to edge than by patch size in Saskatchewan (Davis 2004) and Alberta (Koper and Schmiegelow 2006a). Abundance was unrelated to the amount of grassland in the surrounding landscape (McMaster et al. 2005, Koper and Schmiegelow 2006a). With a few exceptions (Grant et al. 2006), songbird nest success was not related to patch size (Davis 2003, Davis et al. 2006), distance to edge (Koper and Schmiegelow 2006a), or the nature of the surrounding landscape (McMaster

FIG. 12. Mountain Plover in Mexican prairie-dog colony, La Soledad, Nuevo Leon, Mexico. Short grassland vegetation can be seen within prairie-dog colony in contrast to adjacent desert scrub. (Photograph by Rogelio Hernandez.)

and wintering periods (Webster 1964, Raitt and Pimm 1977, F. Chávez-Ramírez pers. obs.).

Current habitat for grassland birds.—Dinerstein et al. (2000) estimated that ~20% of the Chihuahuan Desert region is currently grassland. The largest expanses of contiguous desert grasslands are found in Arizona, New Mexico, and Texas, and the amount decreases southward through the Mexican states. The condition of the remaining tracts of grassland is variable but is generally poor because of continuous overgrazing. The best-conserved remaining blocks of desert grassland are in central Chihuahua. Most desert grassland areas are privately owned cattle ranches. In the United States, some desert grasslands are protected in reserves and experimental ranges (e.g., Jornada Experimental Range, Santa Rita Experimental Range, and Appleton-Whittle Research Ranch). Similar reserves and state or federal experimental ranges occur in Mexico (La Campana, Mapimi, and Cuatro Cienegas). However, combined, reserves and grassland research stations represent a small proportion of the area dominated by desert grasslands. In the United States, it is estimated that 7.9% of the Chihuahuan Desert (roughly equal to the extent of desert grasslands) is under some sort of protection (DellaSala et al. 2001). In Mexico, the estimated area under a protected designation within the Chihuahuan Desert is <2%. The actual area of protected grasslands is much less, because grasslands are the least represented of vegetation communities in these protected areas (F. Chávez-Ramírez pers. obs.). Also, most designated protected areas in Mexico allow livestock grazing.

In Mexico, a proportion of the grasslands and other rural lands is held as communal properties called *ejidos*. An *ejido* is generally defined as a population center whose inhabitants have common use of a designated area, generally rangeland or agricultural areas. Most *ejidos* are rural communities that use the land primarily for grazing cattle and goats, but also for small-scale agricultural plots. The proportion of land held as *ejidos* is greater in the southern Mexican states (40% in Durango, Zacatecas, and San Luis Potosi) than in the northern areas (15% in Chihuahua and Coahuila).

A continual and gradual decline in grassland condition has occurred, with little concerted effort to reverse the trend. Efforts to increase productivity of desert grasslands have led to introduction of nonnative grasses, and efforts to restore highly degraded sites with native grassland species have not been successful (Griffiths 1907, Roundy and Biedenbender 1995). Land-reclamation efforts have been more successful when using nonnative grasses or native shrubs and cacti. Although successful establishment of native shrubs may reduce soil erosion and stabilize the soil, it has the net effect of converting areas previously dominated

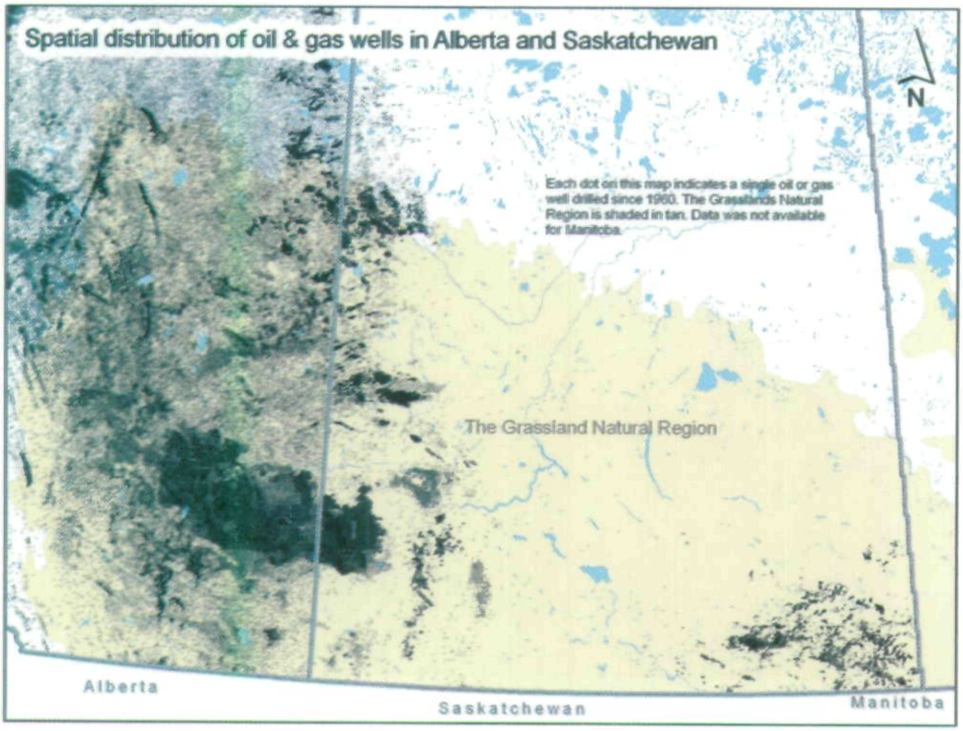

FIG. 10. Energy-extraction activity in one portion of the northern plains. Each small dot represents an oil or gas well (Source: Alberta Energy Utilities Board and Saskatchewan Industry and Resources). The extent of grassland appears as background (Natural Resources Canada, GeoGratis: www.geogratis.cgdi.gc.ca; map courtesy of Olaf Jensen, Canadian Wildlife Service).

et al. 2005, Davis et al. 2006), though nest parasitism increased with fragmentation in one study (Davis and Sealy 2000).

The last reason for declines is direct losses attributable to predation, field operations in crops or forage, road kills, air strikes (Dolbeer 2006), and pesticides (Mineau and Whiteside 2006). Fragmentation, roads, pesticides, grazing management (Desmond 2004), and invasion by exotics and shrub are also relevant during migration and on the wintering grounds.

Managing habitat for grassland birds.— According to Rodriguez (2002), the mechanisms driving declines may be complex, but the conservation effort can be simple: concentrate efforts where birds are most abundant and work from there. We know where high-abundance areas are, thanks to the BBS, Grassland Bird Monitoring (Dale et al. 2005), Conservation Data Centers, and individual research projects. These areas, not surprisingly, coincide with large stretches of grassland in eight "ecologically significant areas" identified by the Commission for Environmental Cooperation and The Nature Conservancy (Karl and Hoth 2005).

The most important goal of habitat management for grassland birds is to prevent further losses of native grasslands. About 30% of Canadian prairie grassland is in private hands, 7% is controlled by the federal government, and 63% is controlled by provincial, tribal, and other levels of government (Gauthier et al. 2003). Much public land is in community pastures or grazing leases. About 5.3% of the prairie is set aside for conservation, and most (63%) protected sites are >1,000 ha in size (Gauthier and Wiken 2002), which is the threshold for "minimum viable area" (Samson et al. 2004). Grassland ownership in the U.S. portion of the Great Plains is estimated to be 84% private, 7% federal (with the Bureau of Land Management and U.S. Forest Service managing the majority), and 9% state, municipal, county, or tribal government (Gauthier et al. 2003). Separate figures for the northern portion of the plains were not available. The northern plains are, in by grasslands into shrublands, leading to elimination of potential habitat for grassland birds. Most grassland-restoration experiments are conducted as research projects on small plots using expensive and labor-intensive methods, so it is unlikely that large restoration activities will be undertaken in the near future.

Managing habitat for grassland birds.—Management of desert grasslands focuses on its use as pasture for livestock. Low-intensity grazing does not appear to negatively affect the birds that depend on these grasslands, but higher-intensity grazing by cattle has a negative effect on grassland cover and on some species of grassland birds (Krueper et al. 2003, Desmond 2004). Any management recommendations for maintaining desert grasslands will have to focus on the intensity and level of grazing pressure and its effects on birds. More information is needed to adequately address the net effects of different levels and timing of livestock grazing on grassland birds in this area.

Governmental programs can promote the protection, conservation, or destruction of grasslands. Programs such as CRP are available only for the U.S. portion of the desert grassland; Mexico has no similar program. However, unlike in the northern plains, where grassland birds use CRP fields extensively (Johnson and Igl 1995), CRP fields in general have not provided additional habitats for shortgrass avian species. Mexico's perverse incentives have led to the conversion of grasslands to agricultural fields in areas with only marginal potential for agricultural production. Governmental programs in Mexico provide financial incentives to individuals for each new area opened for agricultural production for staple crops, regardless of the soil's potential for crop production.

Conservation of desert grasslands depends not only on the establishment and maintenance of protected areas devoted exclusively to grassland systems, but also on better management of grazing on private land. The historical evidence for dense populations of grazers (especially prairie-dogs, but also pronghorn and bison) suggests that restored desert grasslands could sustain moderate grazing. In fact, grazing by prairie-dogs could help maintain these grasslands, preventing the invasion of woody shrubs and trees. As Weltzin et al. (1997:761) argue, although growth of woody vegetation in desert grassland may be favored by such factors as reduction of fire frequency, long-term climate changes, and increasing concentrations of atmospheric carbon dioxide, "widespread eradication of prairie dogs may have been both necessary and sufficient to enable post-settlement increases in shrublands and woodlands." This contrasts with the widespread view that there were so few native grazers in desert grassland that this system cannot sustain grazing by domestic stock (Saab et al. 1995). The remaining prairie-dog colonies in Mexico should be protected and studied to determine whether grazing by prairie-dogs can help maintain desert grasslands, providing habitat for grassland birds and permitting sustainable cattle production. Grassland restoration in the southwestern United States may be difficult without the reintroduction of this keystone species (Miller et al. 1994).

General Implications for Grassland Bird Conservation

Although the grasslands and savannas we have discussed have distinctly different climates, vegetation, and bird assemblages, they share some of the same basic conservation problems. All these ecosystems have suffered from considerable habitat conversion, with almost complete loss of tallgrass prairies, northeastern coastal grasslands, and longleaf pine savannas. Tallgrass prairies were plowed to create cropland, longleaf pine savannas have been replaced with pine plantations and suburbs, and most of the coastal grasslands are now industrial and residential areas. Farming is also widespread in the mixed-grass and shortgrass prairies.

Even when grasslands have not been directly transformed into grain fields or suburban neighborhoods, they frequently have lost the basic ecological processes that sustained them (Vickery and Herkert 2001). In the northeastern coastal plain, southeastern pine flatlands, tallgrass prairies, and western aspen parklands, fire suppression led to the displacement of open, grass-dominated habitats by dense woody vegetation. Elimination of native grazers (especially prairie-dogs) and fire probably triggered a similar process in the desert grasslands, leading to the spread of mesquite scrub. In shortgrass and mixed-grass prairies, removal of grazers (both prairie-dogs and bison) and fire resulted in the spread of shrubs or a subtler shift in the density and dominant species of grasses and forbs.

many ways, decimated and their functioning impaired, but with 25–30% of the original grassland remaining and pieces as small as 18 ha of conservation value (Davis et al. 2006), we cannot hope to buy or otherwise secure all the remaining grassland through purchase or easement. Scrutiny and adjustment of policy and legislation at federal, state or provincial, and local levels are necessary to eliminate remaining incentives to break up grasslands.

Maintaining or rehabilitating the integrity of remaining grasslands is also critically important. Refuges and sanctuaries are the only sites likely to be managed at historically appropriate intervals. Sustained rest in mixed-grass prairie did not occur historically and is not beneficial for primary endemic grassland birds, because the increased height and thickness of grass, accumulated litter, or expanded shrub cover will render sites unattractive to specialized grassland birds. Application of natural drivers of grazing, and to a lesser degree burning, at appropriate intervals should maintain the broad variety of grassland conditions for the full suite of grassland birds historically associated with mixed-grass prairie. The variation in soil and moisture across the northern plains makes it impossible to offer blanket prescriptions (e.g., burn every six years, graze at a rate of 10 ha cow^{-1}) to benefit a given bird species (Kantrud 1981, B. C. Dale et al. unpubl. data). Madden et al. (2000) suggest using a range of acceptable vegetation measurements to guide management. Land managers then choose which management tool and application rate would create those conditions in their area.

Over much of this region, grazing is the land use most compatible with long-term maintenance of healthy grasslands and bird communities. Moderate or light grazing maintains or improves range condition (Holechek et al. 1999), and sites in good condition support more grassland bird species (George et al. 1992). Large fields are more likely to be heterogeneous, because of variety in topography and distance to water (B. C. Dale et al. unpubl. data, Renfrew and Ribic 2002, Fontaine et al. 2004, Koper and Schmiegelow 2006b).

Restoration of cover with regionally appropriate native grasses may be very beneficial, but, for economic reasons, it is not widespread. The total area in CRP in the northern plains region of the United States is 3,336,045 ha (Allen and Vandever 2005). The plant species and strains chosen are rarely native to the region. Grazing and haying are not permitted except under emergency circumstances. The total area in Canada's Permanent Cover Program (PCP) is 518,000 ha (Gauthier et al. 2003). Introduced plants are sown, and the cover may be grazed or hayed. Most endemic birds occur in low numbers in both programs (Johnson and Schwartz 1993a, b; McMaster and Davis 2000). A comparison of the densities or rankings of birds on CRP land (Johnson and Schwartz 1993a, b) with estimates on PCP land (D. G. McMaster unpubl. data) showed that six of eight primary endemics were more common on the latter. Only Lark Bunting was more common on CRP than on PCP land. Avian productivity is as good on CRP land as it is on Waterfowl Production Areas, however (Koford 1999). The PCP has been replaced by the Greencover Canada Program (Agriculture and Agri-Food Canada 2005) and will continue to allow agricultural use that benefits grassland birds. It could be improved with date restrictions on haying to increase productivity of birds (Dale et al. 1997, McMaster et al. 2005).

In summary, while pursuing opportunities for protection, we must concentrate most of our efforts on extensive activities like policy reform, farm programs, demonstration projects, marketing of "eco-products," and extension and other forms of education to encourage retention of native prairie and restoration of range condition while encouraging creation of new grass habitats and best practices on crops and tame forage. The U.S. Farm Bill and the new Canadian Agricultural Farm Policy (Agriculture and Agri-Food Canada 2005) are mechanisms for delivery of additional cover and Good Management Practice incentives. The latter offers a dynamic opportunity, because it incorporates farm planning and a series of practices (reviewed annually) whose costs are offset. As we obtain more information along the lines of Davis (2004) or Fletcher et al. (2006), we can target these activities more precisely and modify our advice, but we must not delay our collaborative activities until we have all the answers.

We need to work with other disciplines to make our biological findings economically relevant (Theobald et al. 2005). Good grazing management is consistent with profits for producers (Holechek et al. 1999, Prairie Farm Rehabilitation Administration 2000), Similarly, elimination of beavers resulted in the loss of floodplain meadows that supported grassland birds and other early-successional species in floodplains of the eastern forest. The suppression, alteration, or elimination of natural disturbances or ecological drivers can transform grassland as thoroughly as planting crops or building houses.

Similar processes seem to apply to the other North American grasslands that we did not discuss. The tule prairies of the Central Valley of California were maintained by the grazing of dense populations of tule elk (*Cervus elaphus nannodes*), giant kangaroo rats (*Dipodomys ingens*), and pronghorns (Knopf and Rupert 1995). The grasslands of the Great Valley of Virginia were heavily grazed by bison and elk and apparently frequently burned by Native Americans (Kercheval 1850). The seasonally flooded, open "prairies" of the Florida Everglades (where the endangered Cape Sable Seaside Sparrow [*Ammodramus maritimus mirabilis*]) lives) are generated by periodic wet-season burns (Kushlan et al. 1982). Midwestern oak savannas were also maintained by periodic burns (Curtis 1959).

In some ecosystems, such as longleaf pine savannas, tallgrass prairie, and desert grassland, changes in ecological processes can lead to rapid and substantial changes in vegetation structure that are not easily reversed (Westoby et al. 1989). For example, suppression of fire or removal of native grazers (or a combination of these factors) can cause a grassland to shift to a new stable state such as dense, woody vegetation. When the original ecological processes that characterized this system are restored (e.g., native grazers are reintroduced or prescribed burning is implemented), the vegetation may not return to its original state (Westoby et al. 1989, Briggs et al. 2005). Major restoration efforts, such as clearing shrubs and planting native grasses, may be needed in these cases.

The grasslands of North America have been transformed so profoundly that it is surprising that some of the more specialized species of grassland birds still persist. They were saved by their ability to adjust to artificial habitats. With the loss of prairies and savannas, many grassland birds became concentrated in farmland and ranchland where natural disturbances or ecological drivers were replaced with livestock grazing, mowing, prescribed burning, or plowing. Their future largely depends on how this private property is managed. Some traditional methods of farming and ranching maintained habitat for a diversity of grassland and savanna birds; rangeland, fallow fields, hay meadows, field edges, and orchards substituted for natural grasslands for many of these species. However, the steady progression to more efficient use of land for production of food and fiber has tended to reduce its suitability as breeding, migration, or winter habitat for most grassland specialists. This appears to be the main cause of recent sharp declines in populations of grassland birds.

Grassland birds became vulnerable when their natural habitats were destroyed or disrupted so that they became dependent on artificial habitats. Top priorities for conservation of grassland birds are preservation and restoration of remaining native grassland. A goal in all three of the countries that we have discussed here (Canada, the United States, and Mexico) should be removal of direct and indirect incentives in government agricultural programs for converting grassland to cropland. Moreover, the most intact natural grasslands should be protected as grassland reserves, as has been done in tallgrass-prairie landscapes by The Nature Conservancy and state agencies in Illinois and Missouri, and in mixed-grass prairies in Grasslands National Park and Canadian Forces Base (CFB) Suffield National Wildlife Area in Canada. Protecting extensive prairie-dog complexes and restoring their habitat in northern Mexico (at Janos-Nuevo Casas Grandes, Chihuahua, for example) is a particularly high priority, because it is no longer possible to study the ecological effects of extensive grazing by prairie-dogs in desert grasslands in the southwestern United States. These reserves could support source populations of grassland birds and, equally or more important, could provide sources of information about the natural processes that sustain habitats. The ultimate goal would be to re-establish these processes where they have been eliminated or inhibited. Where practical, managers should reintroduce fire to tallgrass prairies and longleaf pine savannas, allow beavers to dam streams and create beaver meadows, and re-establish the extensive grazing lawns maintained by prairie-dogs on shortgrass prairies and desert grasslands. The systematic destruction of keystone species such as beavers and prairie-dogs is one of the greatest and least-appreciated reasons and society benefits not only from increases in forage production but also from build-up of soil organic matter and sequestered atmospheric carbon (Conant et al. 2001). Minimum-tillage fields are better than conventional fields in terms of abundance, nest densities, and productivity of birds (Martin and Forsyth 2003) and offer producers improved economics through reduced field operations and maximum use of limited moisture. Conservation objectives can be achieved with little economic cost or conflict (Polasky et al. 2005).

Delivery of the North American Bird Conservation Initiative through North American Waterfowl Management Plan (NAWMP) joint ventures has been hailed as an opportunity for conserving grassland birds (Brennan and Kuvlesky 2005), but cover programs for waterfowl in the northern plains have limited benefits for high-priority grassland birds (Dale and McKeating 1996), and ducks do not always act as a conservation surrogate for other avian species in the mixed-grass prairie (Koper and Schmiegelow 2006b). The NAWMP's recent emphasis on protection of native habitats and on policy scrutiny is, however, beneficial to grassland birds. Also, the Prairie Conservation Action Plan functions as an important forum for engaging stakeholders and building on common goals related to maintaining healthy prairie (Nernberg and Ingstrup 2005).

Desert Grasslands

History of grasslands.—The grasslands of northern Mexico and the southwestern United States are generally referred to as "desert grasslands" (Rzedowski 1975, McClaran 1995; Fig. 11). The geographic extent of this grassland type basically coincides with the Chihuahuan Desert Ecoregion, which covers the Central Plateau of Mexico south to approximately the Transvolcanic belt and is bordered on the east and west by the Sierra Madre Oriental and Occidental, respectively, north to west Texas, southern New Mexico, and southeastern Arizona. As the name implies, the main ecological driver of desert grassland systems is drought. Fire, however, played a role in maintaining some areas of desert grasslands in the past (Humphrey 1958, Bahre 1991). The frequency of fires in prehistoric times is difficult to determine for desert and other grasslands, but several authors estimate that fires may have occurred at intervals of approximately 7–10 years. This estimate is based on indirect

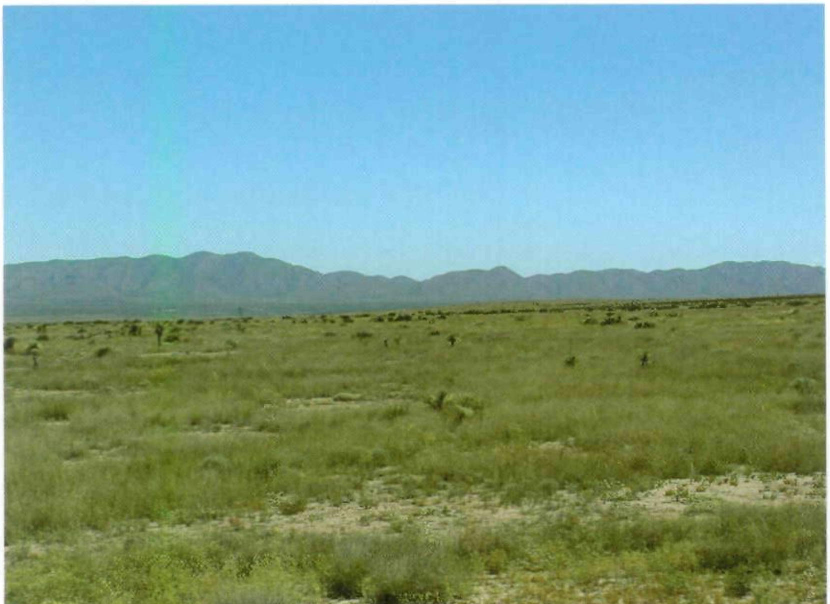

Fig. 11. Desert grassland landscape with open-ground patches and shrubby elements of yucca in northern Chihuahua, Mexico. (Photograph by Profauna Chihuahua.)

for the loss of biological diversity in grassland systems.

In many grassland and savanna systems, biological diversity depends on natural processes creating a patchwork of different types of vegetation across a large landscape. This patchwork is difficult to achieve in a small reserve or even in a system of small reserves, so creation and consolidation of large grassland reserves should be a high priority. The goal should be to establish reserves that are large enough to maintain the diversity of habitats and species characteristic of the full habitat mosaic that once characterized the region (the minimum dynamic area), an approach that currently guides conservation strategies of The Nature Conservancy in the Great Plains (Samson et al. 2004). This may require restoration or creation of natural grassland around existing grassland reserves, followed by reintroduction of natural drivers or disturbances. A large-scale strategy of this sort will require much greater cooperation among government agencies, nonprofit organizations, and private landowners. Large publicly owned grasslands are administered by different government agencies (Samson et al. 2004), but recently these agencies have begun to work together and to work with other land managers through conservation programs such as Partners in Flight, Prairie Partners, and Center for Environmental Cooperation. These programs have begun to focus on conservation of grassland ecosystems and to work across international boundaries to preserve breeding, migratory stopover, and wintering habitat of grassland birds in Canada, the United States, and Mexico.

Although protection and restoration of natural grasslands are important goals, they probably will not be sufficient for conservation of some species of grassland birds. It is unlikely that enough large grassland and savanna reserves can be established to maintain regional populations of grassland specialists. Fortunately, these species can potentially be supported on working land such as farms, ranches, airports, or commercial forests. For some habitats, such as tallgrass prairies and longleaf pine savannas, researchers can already provide specific recommendations for managing working land to support grassland birds and other grassland organisms. For other habitats, such as shortgrass prairies and desert grasslands, more research is needed to develop appropriate recommendations. We need to know more about the effects of livestock and native grazers in both of these systems, and about the relative roles of grazing and fire in desert grasslands. Where sustainable practices are profitable, education is the key to convincing private landowners to adopt measures that preserve or enhance biological diversity. The challenge is more difficult, however, when "bird-friendly" practices reduce economic productivity or where economic hardship pushes landowners into making unsustainable choices.

The PCP in Canada and the CRP in the United States provide payments to farmers who take land out of production and convert it to grassland to conserve soil and provide wildlife habitat. These programs have great potential for bird conservation, because they involve large areas of land. In some regions (particularly in the northern plains), fields in these programs provide good breeding habitat for grassland birds. In shortgrass prairie, however, CRP fields are usually planted in tall grass that does not attract endemic shortgrass-prairie birds. This problem is particularly acute in the United States, where grazing has not normally been permitted on CRP land. Both programs would be more effective if they were specifically designed to provide habitat for native grassland species, permitting grazing where it is appropriate and banning it where it is not; providing greater incentives to contribute to the establishment of large expanses of continuous grassland; and encouraging the planting and maintenance of native grass species. In this regard, the newly established Grassland Reserve Program of the 2002 U.S. Farm Bill may provide greater potential benefits for grassland birds because it protects existing grasslands (and therefore does not require the need to restore grass), and participants retain the right to graze, mow, or hay the land, subject to restrictions designed to protect nesting birds.

North Americans could develop incentives for conservation by emulating European programs that make birds (and other elements of biological diversity) a "farm product" (Musters et al. 2001). Incentive programs have become an integral part of the agricultural support system of the European Economic Community (Kleijn et al. 2004). Similar programs not only could sustain natural diversity and protect rural landscapes, but also could directly help support farmers and ranchers in North America. European nations evidence such as presence and abundance of woody species (Griffiths 1910, Leopold 1924, Wright and Bailey 1980, Schmutz et al. 1985). Early Spanish explorers reported that fires were intentionally set by Native American tribes in desert grasslands in Mexico and the southwestern United States (Gentry 1957). Fire can have major effects on desert grasslands. It eliminates cover in the short term, but may reduce the density of woody species in the long term. Saab et al. (1995) argued that the suppression of fires in this system produced, through increased woody plant cover, the drastic changes in ecosystem structure and function currently observed throughout desert grasslands in Mexico and the southwestern United States. Dinerstein et al. (2000) estimated that grasslands have decreased between 25% and 50% because of the spread of shrublands in the region.

Grazing by native herbivores may have been even more important than fire in preventing woody shrubs from spreading in desert grasslands (Weltzin et al. 1997). The primary natural grazers of desert grasslands were black-tailed prairie-dogs in the United States and northern Mexico; Mexican prairie-dogs (*C. mexicanus*) in central Mexico; and, to a lesser extent, bison and pronghorn (Anderson 1982, Saab et al 1995). Bison are reported to have roamed the region intermittently, being present in a particular area only sporadically in some years, apparently as a result of irruption-type movements from the Great Plains. The net effect of these sporadic irruptions of bison on the native grasslands and overall landscape of the region is not known, but probably was not strong (Parmenter and Van Devender 1995, Monger et al. 1998). Also, pronghorn were found in large numbers in the southwestern United States (Parmenter and Van Devender 1995). Although pronghorn are primarily forb-foragers or browsers rather than grazers, in many areas of desert grasslands, the most abundant plant species can at times be forbs.

The frequency and intensity of grazing in desert grasslands before the introduction of large number of domestic grazers starting ~450 years ago is not well known, but it is clear from historical descriptions that prairie-dogs were mostly responsible for the overall structure of vast areas of desert grassland communities (Parmenter and Van Devender 1995). Until the 1930s, prairie-dog towns covered large stretches of grassland from trans-Pecos Texas to southeastern Arizona; for example, prairie-dog towns covered an estimated 2.5 million ha in New Mexico. Federal programs in the United States almost completely exterminated prairie-dogs from this region by the 1960s. Numerous prairie-dogs, however, are still found in grasslands in northwestern Mexico (Ceballos et al. 1993), where there have been few large-scale eradication programs. The largest prairie-dog complex in North America is found at Janos-Nuevo Casas Grandes in northwestern Chihuahua, Mexico; it covers an estimated 55,258 ha (with one colony covering 34,949 ha; Ceballos et al. 1993). The distribution of the Mexican prairie-dog in Coahuila, Nuevo Leon, San Luis Potosi, and Zacatecas has decreased significantly from an estimated 1,500 km^2 to only 290 km^2 in 1999 (Scott-Morales et al. 2004). Most of the destruction has resulted from conversion of prairie-dog colonies to agriculture production and continues to the present day.

Prairie-dogs have a substantial influence on grasslands. By constantly clipping the vegetation to maintain an unobstructed view of the landscape, they prevent shrub and other woody species from invading. Koford (1958: 59) found that eradication of prairie-dogs usually results in the spread of mesquite, converting grassland to shrubland, and that "many old timers in Texas and Oklahoma attribute the great increase in mesquite on grasslands during the past century to the extermination of prairie dogs." Thus, prairie-dog eradication may explain why so much of the desert grassland has been converted to mesquite scrub (Weltzin et al. 1997). By contrast, areas with prairie-dog colonies in Chihuahua have remained open grassland (Ceballos et al. 1993, Manzano-Fischer et al. 1999). The role of prairie-dogs in preventing shrub invasion is consistent with evidence that there was never enough fuel in desert grasslands to permit extensive burns (Van Auken 2000) and that mesquite is more resistant to fire damage than some species of semidesert grass, such as black grama (*Bouteloua eripoda*; Buffington and Herbel 1965).

Grassland bird assemblage.—Many of the grassland bird species that breed in the desert grasslands of Mexico and the southwestern United States also breed farther north in the prairies of the United States and Canada (Peterson and Robbins 1999). These include Horned have tried various types of programs since the 1970s, so North Americans can learn from both their successes and their failures.

In the United Kingdom, the steep decline in populations of farmland birds since the mid-1970s led to the adoption of "agri-environment schemes" to encourage farmers to manage their land to provide habitat for birds that require open fields (Vickery et al. 2004). Two majors approaches are used: Environmentally Sensitive Areas, in which farmers in a designated geographic region are paid to enhance landscape or biodiversity features; and the Countryside Stewardship Scheme (CSS), in which farmers in any region are compensated for adopting "good farming practices" that enhance biological diversity (such as delaying mowing to prevent destruction of nests and restrictions on grazing). Efforts to restore seminatural grassland have been hindered by two major problems: high nutrient concentrations because of intensive application of fertilizers in the past, and loss of the seed bank of grassland plants after many years of farming (Walker et al. 2004). British ecologists therefore have been concentrating on methods of "nutrient stripping" (removal of nutrients with such practices as intensive grazing and mowing) to reduce soil fertility so that a wide variety of grassland plants can coexist, and for sowing seeds of grassland plants to compensate for the missing seed bank.

Several studies have assessed the effects of efforts to provide habitat for grassland birds in Europe. In Devon, England, Peach et al. (2001) compared population trends of the Cirl Bunting (*Emberiza cirlus*) in fields managed under a CSS and in control fields. This species is a threatened grassland specialist that recently suffered a severe population decline in England. The CSS paid landowners to provide low-intensity grazed grassland as summer habitat and barley stubble as winter habitat. Densities of Cirl Buntings increased substantially on CSS land and remained stable on land not covered by this agreement, indicating that the program successfully enhanced habitat for this species. This management program was developed after intensive research on the ecology of Cirl Buntings and focused on a single region where this species was concentrated (Kleijn et al. 2004). However, less-focused agri-environment schemes have not demonstrably affected the rate of population declines in grassland birds in England (Vickery et al. 2004) or population densities of meadow birds in fields in The Netherlands (Kleijn et al. 2004). A more thorough understanding of the habitat requirements of these birds and a more coordinated effort to restore regional landscapes should help improve the success rate.

Another promising approach is to pay farmers for their success in supporting populations of target species. In a pilot program in The Netherlands, farmers were paid for every clutch of young produced by meadow-dependent birds (Musters et al. 2001). Such an intensive monitoring program is unrealistic for most of North America, but farmers, ranchers, and forest managers could be paid for sustaining populations of particular species. Landowners would then participate in improving habitat management methods and tailoring them to their own land.

The seminatural grasslands of Europe are the product of millennia of deforestation and livestock grazing and, in most cases, we have little basis for reconstructing the natural ecological processes that sustained the original habitats of grassland species. In North America, there is a better (if still imperfect) opportunity to restore natural grassland systems. Maintenance and restoration of natural grassland should have the highest conservation priority, because natural ecosystems can provide important insights about the habitat requirements of grassland species. These insights can then guide efforts to manage working land (especially farmland and ranchland) where most grassland birds nest and spend the nonbreeding season. If landowners are compensated for sustaining and enhancing biological diversity, efforts to save the distinctive species of open habitats could be compatible with efforts to support rural economies and landscapes. In the United States, the Conservation Security Program of the 2002 Farm Bill is a move in this direction; it is a voluntary program that will provide financial and technical assistance to landowners to promote conservation on private land including pasture and rangeland. Current economic pressures on producers of beef cattle to stockpile forage in pasture to replace hay cutting (e.g., Hitz and Russell 1998, Evers et al. 2004, Cuomo et al. 2005) may have important advantages for grassland birds, and these practices deserve further study. Another promising North American program is sponsored by the Colorado Division of Wildlife, which expended more than $1 million in 2004

Lark, Savannah Sparrow, and Grasshopper Sparrow. Other species that nest in the Great Plains are winter residents in desert grasslands (e.g., Ferruginous Hawk, Mountain Plover, Long-billed Curlew (*Numenius americanus*), Vesper Sparrow, Lark Bunting, McCown's and Chestnut-sided longspurs, and Eastern and Western meadowlarks). Several species listed as birds of conservation concern by the U.S. Fish and Wildlife Service, such as Sprague's Pipit and Baird's Sparrow, are concentrated in this region during winter. A few grassland species are endemic or nearly endemic to the Chihuahuan Desert of northern Mexico and the adjacent United States (e.g., Botteri's Sparrow [*Aimophila botterii*] and Rufous-winged Sparrow [*A. carpalis*]). Populations of the northern Aplomado Falcon (*Falco femoralis septentrionalis*) have historically (Oberholser 1974) and recently (Young et al. 2004) been found in grasslands of the northern Chihuahuan Desert (Texas, New Mexico, and Chihuahua). The only avian species truly endemic to this grassland system is Worthen's Sparrow (*Spizella wortheni*; Phillips 1977), which is considered threatened by BirdLife International (Byers et al. 1995). It occupies shrubby grassland habitats and is found consistently, though in low densities, at the edges of prairie-dog colonies in Coahuila, Nuevo Leon, and San Luis Potosi (Garza de Leon et al. 2007).

Although large tracts of desert grassland remain, many species that nest and winter in this type of environment are declining. Results of the North American BBS indicate that many of the species that breed or spend the winter in desert grasslands have had overall population declines in North America since the mid-1960s (Knopf 1994). Population declines can be attributed to several factors, including loss and fragmentation of habitat. Loss of grasslands in this region is attributable not only to conversion to shrublands following elimination of natural grazers and fire, but also to the transformation of some areas for agricultural purposes. Prairie-dogs have long been persecuted by cattle ranchers in both Mexico and the United States, leading to their elimination in many regions and diminishing their influence in maintaining desert grasslands free of woody invaders. Even where prairie-dogs remain in some areas of Chihuahua, severe overgrazing by livestock results in a habitat with few grassland birds (Desmond 2004).

Desert grasslands are structurally short and support a lower avian species-richness than peripheral areas (Mengel 1970), which are the transition zones with more structurally complex environments imbedded in the grasslands, such as riparian woodlands, mountain slopes, and adjoining shrublands. Prairie-dog colonies support higher diversity and densities of shortgrass-prairie birds than adjacent grassland areas without prairie-dogs (Agnew et al 1986, Desmond 2004). Some species are particularly frequent in prairie-dog colonies (e.g., Mountain Plover and Ferruginous Hawk; Fig. 12), whereas others are common on prairie-dog colony edges (i.e., sparrows [*Spizella* spp.], Lark Buntings). Bird surveys in the Janos-Nuevo Casas Grandes prairie-dog complex of Chihuahua revealed that Horned Larks and Lark Buntings were abundant and that several other grassland specialists (Ferruginous Hawk, Mountain Plover, Long-billed Curlew, Burrowing Owl, longspurs [*Calcarius* spp.], and meadowlarks [*Sturnella* spp.]) were common (Manzano-Fischer et al. 1999).

With a few notable exceptions, shortgrass-dependent birds are the least understood of North American birds in both breeding and wintering areas (Phillips 1977). This is particularly true for northern Mexico, where detailed studies of desert grassland avifauna have taken place only during the past two decades except in a few areas, such as the Mapimi Biosphere Reserve. For example, breeding by Mountain Plovers was documented only recently in colonies of Mexican prairie-dogs in northern Mexico (Desmond and Chávez-Ramírez 2002, González Rojas et al. 2006).

The patterns of occurrence for individual species and large concentrations of birds in specific regions of the desert grassland are highly dynamic and highly variable from year to year (Raitt and Pimm 1977), probably because of the variability in rainfall patterns and food production. The same area may have large concentrations of winter-resident sparrows in some winters and none in other winters (Desmond 2004, F. Chávez-Ramírez pers. obs.). This pattern was observed in a Christmas Bird Count in northwestern Chihuahua, where counts of sparrows (*Spizella* spp.) varied from <2,000 to >13,000 in successive years (Dieni et al. 2003). Grassland bird communities are also characterized by high turnover rates between breeding for its new Species Conservation Partnership Program to place conservation easements on ~8,100 ha of private land (K. Morgan pers. comm.). The Colorado program goes beyond concern for the shortgrass prairies to emphasize the whole prairie ecosystem and encompasses declining species of a wide range of taxa. The black-tailed prairie-dog is a key component of many easements because of its role as an ecological driver in this system. Similar revolutionary programs are needed to secure the ecological setting necessary to conserve the birds of native grasslands.

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FIG. 12. Mountain Plover in Mexican prairie-dog colony, La Soledad, Nuevo Leon, Mexico. Short grassland vegetation can be seen within prairie-dog colony in contrast to adjacent desert scrub. (Photograph by Rogelio Hernandez.)

and wintering periods (Webster 1964, Raitt and Pimm 1977, F. Chávez-Ramírez pers. obs.).

Current habitat for grassland birds.—Dinerstein et al. (2000) estimated that ~20% of the Chihuahuan Desert region is currently grassland. The largest expanses of contiguous desert grasslands are found in Arizona, New Mexico, and Texas, and the amount decreases southward through the Mexican states. The condition of the remaining tracts of grassland is variable but is generally poor because of continuous overgrazing. The best-conserved remaining blocks of desert grassland are in central Chihuahua. Most desert grassland areas are privately owned cattle ranches. In the United States, some desert grasslands are protected in reserves and experimental ranges (e.g., Jornada Experimental Range, Santa Rita Experimental Range, and Appleton-Whittle Research Ranch). Similar reserves and state or federal experimental ranges occur in Mexico (La Campana, Mapimi, and Cuatro Cienegas). However, combined, reserves and grassland research stations represent a small proportion of the area dominated by desert grasslands. In the United States, it is estimated that 7.9% of the Chihuahuan Desert (roughly equal to the extent of desert grasslands) is under some sort of protection (DellaSala et al. 2001). In Mexico, the estimated area under a protected designation within the Chihuahuan Desert is <2%. The actual area of protected grasslands is much less, because grasslands are the least represented of vegetation communities in these protected areas (F. Chávez-Ramírez pers. obs.). Also, most designated protected areas in Mexico allow livestock grazing.

In Mexico, a proportion of the grasslands and other rural lands is held as communal properties called *ejidos*. An *ejido* is generally defined as a population center whose inhabitants have common use of a designated area, generally rangeland or agricultural areas. Most *ejidos* are rural communities that use the land primarily for grazing cattle and goats, but also for small-scale agricultural plots. The proportion of land held as *ejidos* is greater in the southern Mexican states (40% in Durango, Zacatecas, and San Luis Potosi) than in the northern areas (15% in Chihuahua and Coahuila).

A continual and gradual decline in grassland condition has occurred, with little concerted effort to reverse the trend. Efforts to increase productivity of desert grasslands have led to introduction of nonnative grasses, and efforts to restore highly degraded sites with native grassland species have not been successful (Griffiths 1907, Roundy and Biedenbender 1995). Land-reclamation efforts have been more successful when using nonnative grasses or native shrubs and cacti. Although successful establishment of native shrubs may reduce soil erosion and stabilize the soil, it has the net effect of converting areas previously dominated

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by grasslands into shrublands, leading to elimination of potential habitat for grassland birds. Most grassland-restoration experiments are conducted as research projects on small plots using expensive and labor-intensive methods, so it is unlikely that large restoration activities will be undertaken in the near future.

Managing habitat for grassland birds.—Management of desert grasslands focuses on its use as pasture for livestock. Low-intensity grazing does not appear to negatively affect the birds that depend on these grasslands, but higher-intensity grazing by cattle has a negative effect on grassland cover and on some species of grassland birds (Krueper et al. 2003, Desmond 2004). Any management recommendations for maintaining desert grasslands will have to focus on the intensity and level of grazing pressure and its effects on birds. More information is needed to adequately address the net effects of different levels and timing of livestock grazing on grassland birds in this area.

Governmental programs can promote the protection, conservation, or destruction of grasslands. Programs such as CRP are available only for the U.S. portion of the desert grassland; Mexico has no similar program. However, unlike in the northern plains, where grassland birds use CRP fields extensively (Johnson and Igl 1995), CRP fields in general have not provided additional habitats for shortgrass avian species. Mexico's perverse incentives have led to the conversion of grasslands to agricultural fields in areas with only marginal potential for agricultural production. Governmental programs in Mexico provide financial incentives to individuals for each new area opened for agricultural production for staple crops, regardless of the soil's potential for crop production.

Conservation of desert grasslands depends not only on the establishment and maintenance of protected areas devoted exclusively to grassland systems, but also on better management of grazing on private land. The historical evidence for dense populations of grazers (especially prairie-dogs, but also pronghorn and bison) suggests that restored desert grasslands could sustain moderate grazing. In fact, grazing by prairie-dogs could help maintain these grasslands, preventing the invasion of woody shrubs and trees. As Weltzin et al. (1997:761) argue, although growth of woody vegetation in desert grassland may be favored by such factors as reduction of fire frequency, long-term climate changes, and increasing concentrations of atmospheric carbon dioxide, "widespread eradication of prairie dogs may have been both necessary and sufficient to enable post-settlement increases in shrublands and woodlands." This contrasts with the widespread view that there were so few native grazers in desert grassland that this system cannot sustain grazing by domestic stock (Saab et al. 1995). The remaining prairie-dog colonies in Mexico should be protected and studied to determine whether grazing by prairie-dogs can help maintain desert grasslands, providing habitat for grassland birds and permitting sustainable cattle production. Grassland restoration in the southwestern United States may be difficult without the reintroduction of this keystone species (Miller et al. 1994).

General Implications for Grassland Bird Conservation

Although the grasslands and savannas we have discussed have distinctly different climates, vegetation, and bird assemblages, they share some of the same basic conservation problems. All these ecosystems have suffered from considerable habitat conversion, with almost complete loss of tallgrass prairies, northeastern coastal grasslands, and longleaf pine savannas. Tallgrass prairies were plowed to create cropland, longleaf pine savannas have been replaced with pine plantations and suburbs, and most of the coastal grasslands are now industrial and residential areas. Farming is also widespread in the mixed-grass and shortgrass prairies.

Even when grasslands have not been directly transformed into grain fields or suburban neighborhoods, they frequently have lost the basic ecological processes that sustained them (Vickery and Herkert 2001). In the northeastern coastal plain, southeastern pine flatlands, tall-grass prairies, and western aspen parklands, fire suppression led to the displacement of open, grass-dominated habitats by dense woody vegetation. Elimination of native grazers (especially prairie-dogs) and fire probably triggered a similar process in the desert grasslands, leading to the spread of mesquite scrub. In shortgrass and mixed-grass prairies, removal of grazers (both prairie-dogs and bison) and fire resulted in the spread of shrubs or a subtler shift in the density and dominant species of grasses and forbs.

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Similarly, elimination of beavers resulted in the loss of floodplain meadows that supported grassland birds and other early-successional species in floodplains of the eastern forest. The suppression, alteration, or elimination of natural disturbances or ecological drivers can transform grassland as thoroughly as planting crops or building houses.

Similar processes seem to apply to the other North American grasslands that we did not discuss. The tule prairies of the Central Valley of California were maintained by the grazing of dense populations of tule elk (*Cervus elaphus nannodes*), giant kangaroo rats (*Dipodomys ingens*), and pronghorns (Knopf and Rupert 1995). The grasslands of the Great Valley of Virginia were heavily grazed by bison and elk and apparently frequently burned by Native Americans (Kercheval 1850). The seasonally flooded, open "prairies" of the Florida Everglades (where the endangered Cape Sable Seaside Sparrow [*Ammodramus maritimus mirabilis*]) lives) are generated by periodic wet-season burns (Kushlan et al. 1982). Midwestern oak savannas were also maintained by periodic burns (Curtis 1959).

In some ecosystems, such as longleaf pine savannas, tallgrass prairie, and desert grassland, changes in ecological processes can lead to rapid and substantial changes in vegetation structure that are not easily reversed (Westoby et al. 1989). For example, suppression of fire or removal of native grazers (or a combination of these factors) can cause a grassland to shift to a new stable state such as dense, woody vegetation. When the original ecological processes that characterized this system are restored (e.g., native grazers are reintroduced or prescribed burning is implemented), the vegetation may not return to its original state (Westoby et al. 1989, Briggs et al. 2005). Major restoration efforts, such as clearing shrubs and planting native grasses, may be needed in these cases.

The grasslands of North America have been transformed so profoundly that it is surprising that some of the more specialized species of grassland birds still persist. They were saved by their ability to adjust to artificial habitats. With the loss of prairies and savannas, many grassland birds became concentrated in farmland and ranchland where natural disturbances or ecological drivers were replaced with livestock grazing, mowing, prescribed burning, or plowing. Their future largely depends on how this private property is managed. Some traditional methods of farming and ranching maintained habitat for a diversity of grassland and savanna birds; rangeland, fallow fields, hay meadows, field edges, and orchards substituted for natural grasslands for many of these species. However, the steady progression to more efficient use of land for production of food and fiber has tended to reduce its suitability as breeding, migration, or winter habitat for most grassland specialists. This appears to be the main cause of recent sharp declines in populations of grassland birds.

Grassland birds became vulnerable when their natural habitats were destroyed or disrupted so that they became dependent on artificial habitats. Top priorities for conservation of grassland birds are preservation and restoration of remaining native grassland. A goal in all three of the countries that we have discussed here (Canada, the United States, and Mexico) should be removal of direct and indirect incentives in government agricultural programs for converting grassland to cropland. Moreover, the most intact natural grasslands should be protected as grassland reserves, as has been done in tallgrass-prairie landscapes by The Nature Conservancy and state agencies in Illinois and Missouri, and in mixed-grass prairies in Grasslands National Park and Canadian Forces Base (CFB) Suffield National Wildlife Area in Canada. Protecting extensive prairie-dog complexes and restoring their habitat in northern Mexico (at Janos-Nuevo Casas Grandes, Chihuahua, for example) is a particularly high priority, because it is no longer possible to study the ecological effects of extensive grazing by prairie-dogs in desert grasslands in the southwestern United States. These reserves could support source populations of grassland birds and, equally or more important, could provide sources of information about the natural processes that sustain habitats. The ultimate goal would be to re-establish these processes where they have been eliminated or inhibited. Where practical, managers should reintroduce fire to tallgrass prairies and longleaf pine savannas, allow beavers to dam streams and create beaver meadows, and re-establish the extensive grazing lawns maintained by prairie-dogs on shortgrass prairies and desert grasslands. The systematic destruction of keystone species such as beavers and prairie-dogs is one of the greatest and least-appreciated reasons

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for the loss of biological diversity in grassland systems.

In many grassland and savanna systems, biological diversity depends on natural processes creating a patchwork of different types of vegetation across a large landscape. This patchwork is difficult to achieve in a small reserve or even in a system of small reserves, so creation and consolidation of large grassland reserves should be a high priority. The goal should be to establish reserves that are large enough to maintain the diversity of habitats and species characteristic of the full habitat mosaic that once characterized the region (the minimum dynamic area), an approach that currently guides conservation strategies of The Nature Conservancy in the Great Plains (Samson et al. 2004). This may require restoration or creation of natural grassland around existing grassland reserves, followed by reintroduction of natural drivers or disturbances. A large-scale strategy of this sort will require much greater cooperation among government agencies, nonprofit organizations, and private landowners. Large publicly owned grasslands are administered by different government agencies (Samson et al. 2004), but recently these agencies have begun to work together and to work with other land managers through conservation programs such as Partners in Flight, Prairie Partners, and Center for Environmental Cooperation. These programs have begun to focus on conservation of grassland ecosystems and to work across international boundaries to preserve breeding, migratory stopover, and wintering habitat of grassland birds in Canada, the United States, and Mexico.

Although protection and restoration of natural grasslands are important goals, they probably will not be sufficient for conservation of some species of grassland birds. It is unlikely that enough large grassland and savanna reserves can be established to maintain regional populations of grassland specialists. Fortunately, these species can potentially be supported on working land such as farms, ranches, airports, or commercial forests. For some habitats, such as tallgrass prairies and longleaf pine savannas, researchers can already provide specific recommendations for managing working land to support grassland birds and other grassland organisms. For other habitats, such as shortgrass prairies and desert grasslands, more research is needed to develop appropriate recommendations. We need to know more about the effects of livestock and native grazers in both of these systems, and about the relative roles of grazing and fire in desert grasslands. Where sustainable practices are profitable, education is the key to convincing private landowners to adopt measures that preserve or enhance biological diversity. The challenge is more difficult, however, when "bird-friendly" practices reduce economic productivity or where economic hardship pushes landowners into making unsustainable choices.

The PCP in Canada and the CRP in the United States provide payments to farmers who take land out of production and convert it to grassland to conserve soil and provide wildlife habitat. These programs have great potential for bird conservation, because they involve large areas of land. In some regions (particularly in the northern plains), fields in these programs provide good breeding habitat for grassland birds. In shortgrass prairie, however, CRP fields are usually planted in tall grass that does not attract endemic shortgrass-prairie birds. This problem is particularly acute in the United States, where grazing has not normally been permitted on CRP land. Both programs would be more effective if they were specifically designed to provide habitat for native grassland species, permitting grazing where it is appropriate and banning it where it is not; providing greater incentives to contribute to the establishment of large expanses of continuous grassland; and encouraging the planting and maintenance of native grass species. In this regard, the newly established Grassland Reserve Program of the 2002 U.S. Farm Bill may provide greater potential benefits for grassland birds because it protects existing grasslands (and therefore does not require the need to restore grass), and participants retain the right to graze, mow, or hay the land, subject to restrictions designed to protect nesting birds.

North Americans could develop incentives for conservation by emulating European programs that make birds (and other elements of biological diversity) a "farm product" (Musters et al. 2001). Incentive programs have become an integral part of the agricultural support system of the European Economic Community (Kleijn et al. 2004). Similar programs not only could sustain natural diversity and protect rural landscapes, but also could directly help support farmers and ranchers in North America. European nations

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have tried various types of programs since the 1970s, so North Americans can learn from both their successes and their failures.

In the United Kingdom, the steep decline in populations of farmland birds since the mid-1970s led to the adoption of "agri-environment schemes" to encourage farmers to manage their land to provide habitat for birds that require open fields (Vickery et al. 2004). Two majors approaches are used: Environmentally Sensitive Areas, in which farmers in a designated geographic region are paid to enhance landscape or biodiversity features; and the Countryside Stewardship Scheme (CSS), in which farmers in any region are compensated for adopting "good farming practices" that enhance biological diversity (such as delaying mowing to prevent destruction of nests and restrictions on grazing). Efforts to restore seminatural grassland have been hindered by two major problems: high nutrient concentrations because of intensive application of fertilizers in the past, and loss of the seed bank of grassland plants after many years of farming (Walker et al. 2004). British ecologists therefore have been concentrating on methods of "nutrient stripping" (removal of nutrients with such practices as intensive grazing and mowing) to reduce soil fertility so that a wide variety of grassland plants can coexist, and for sowing seeds of grassland plants to compensate for the missing seed bank.

Several studies have assessed the effects of efforts to provide habitat for grassland birds in Europe. In Devon, England, Peach et al. (2001) compared population trends of the Cirl Bunting (*Emberiza cirlus*) in fields managed under a CSS and in control fields. This species is a threatened grassland specialist that recently suffered a severe population decline in England. The CSS paid landowners to provide low-intensity grazed grassland as summer habitat and barley stubble as winter habitat. Densities of Cirl Buntings increased substantially on CSS land and remained stable on land not covered by this agreement, indicating that the program successfully enhanced habitat for this species. This management program was developed after intensive research on the ecology of Cirl Buntings and focused on a single region where this species was concentrated (Kleijn et al. 2004). However, less-focused agri-environment schemes have not demonstrably affected the rate of population declines in grassland birds in England (Vickery et al. 2004) or population densities of meadow birds in fields in The Netherlands (Kleijn et al. 2004). A more thorough understanding of the habitat requirements of these birds and a more coordinated effort to restore regional landscapes should help improve the success rate.

Another promising approach is to pay farmers for their success in supporting populations of target species. In a pilot program in The Netherlands, farmers were paid for every clutch of young produced by meadow-dependent birds (Musters et al. 2001). Such an intensive monitoring program is unrealistic for most of North America, but farmers, ranchers, and forest managers could be paid for sustaining populations of particular species. Landowners would then participate in improving habitat management methods and tailoring them to their own land.

The seminatural grasslands of Europe are the product of millennia of deforestation and livestock grazing and, in most cases, we have little basis for reconstructing the natural ecological processes that sustained the original habitats of grassland species. In North America, there is a better (if still imperfect) opportunity to restore natural grassland systems. Maintenance and restoration of natural grassland should have the highest conservation priority, because natural ecosystems can provide important insights about the habitat requirements of grassland species. These insights can then guide efforts to manage working land (especially farmland and ranchland) where most grassland birds nest and spend the nonbreeding season. If landowners are compensated for sustaining and enhancing biological diversity, efforts to save the distinctive species of open habitats could be compatible with efforts to support rural economies and landscapes. In the United States, the Conservation Security Program of the 2002 Farm Bill is a move in this direction; it is a voluntary program that will provide financial and technical assistance to landowners to promote conservation on private land including pasture and rangeland. Current economic pressures on producers of beef cattle to stockpile forage in pasture to replace hay cutting (e.g., Hitz and Russell 1998, Evers et al. 2004, Cuomo et al. 2005) may have important advantages for grassland birds, and these practices deserve further study. Another promising North American program is sponsored by the Colorado Division of Wildlife, which expended more than $1 million in 2004

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for its new Species Conservation Partnership Program to place conservation easements on ~8,100 ha of private land (K. Morgan pers. comm.). The Colorado program goes beyond concern for the shortgrass prairies to emphasize the whole prairie ecosystem and encompasses declining species of a wide range of taxa. The black-tailed prairie-dog is a key component of many easements because of its role as an ecological driver in this system. Similar revolutionary programs are needed to secure the ecological setting necessary to conserve the birds of native grasslands.

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