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HISTORY OF GRASSLAND BIRDS IN EASTERN NORTH AMERICA

ROBERT A. ASKINS

Abstract. Until recently the severe decline in the populations of many species of grassland birds in eastern North America has aroused relatively little concern or conservation action. This response appears to be rooted in the perception that grassland birds invaded the East Coast from western grasslands after European settlers cleared the forest. Detailed historical accounts and analysis of pollen deposits, however, show that open grasslands existed on the East Coast of North America at the time of European settlement. Extensive grasslands resulted from burning and agricultural clearing by Native Americans. Natural disturbances, such as wildfire and beaver (*Castor canadensis*) activity, produced grasslands even before Native Americans cleared the forest. The presence of specialized grassland birds in Pleistocene deposits and in the earliest ornithological collections from eastern North America, and the existence of distinctive eastern populations of the Greater Prairie-Chicken (*Tympanuchus cupido*), Henslow's Sparrow (*Ammodramus henslowii*), and Savannah Sparrow (*Passerculus sandwichensis*), indicate that grassland birds are an ancient component of biological diversity on the heavily forested East Coast of North America.

LA HISTORIA DE LAS AVES DE PASTIZAL EN EL ESTE DE NORTEAMÉRICA

Sinopsis. Hasta hace poco tiempo, la declinación severa de las poblaciones de muchas especies de aves de pastizal en el este de América del Norte ha causado poco interés o acción de conservación. Esta respuesta se basa en la percepción de que las aves de pastizal invadieron la costa este de América del Norte de los pastizales occidentales después de la tala del bosque por los colonos europeos. Sin embargo, relatos históricos detallados y análisis de depósitos de polen indican que pastizales abiertos existían en la costa este de América del Norte en la época de la colonización europea. Quemadas y desbrozos agrícolas de los indígenas norteamericanos se tradujeron en pastizales extensivos. Disturbios naturales, como los hechos por incendios y castores (*Castor canadensis*), produjeron pastizales antes de que los indígenas talaran el bosque. La presencia de aves de pastizal especialistas en los depósitos pleistocenos y en las colecciones ornitológicas más antiguas del este de América del Norte, y la existencia de poblaciones orientales distintivas de *Tympanuchus cupido*, el Gorrión de Henslow (*Ammodramus henslowii*), y el Gorrión Sabanero (*Passerculus sandwichensis*), indican que las aves de pastizal forman una parte antigua de la diversidad biológica en la arbolada costa este de América del Norte.

Key Words: beaver; bird populations; disturbance; eastern grasslands; grassland birds.

Many grassland bird species were common or even abundant along the East Coast through most of the nineteenth century, but their numbers diminished noticeably between the late nineteenth and mid-twentieth centuries. Griscom (1949) described the Upland Sandpiper (*Bartramia longicauda*), Bobolink (*Dolichonyx oryzivorus*), Eastern Meadowlark (*Sturnella magna*), and Grasshopper Sparrow (*Ammodramus saviarum*) as formerly common but declining in Massachusetts. Forbush (1925:449) mourned the virtual disappearance of the Upland Sandpiper from New England: "our children's children may never see an Upland Plover in the sky or hear its rich notes on the summer air. Its cries are among the most pleasing and remarkable sounds of rural life."

Although the decline of grassland birds was obvious to any careful observer, it is only in recent decades that we have been able to calculate the precise rate and extent of these population changes. The best evidence for this comes from the Breeding Bird Survey, a system of roadside

routes scattered throughout the United States and southern Canada where birds are counted each year (Peterjohn 1994). The results for all of the survey routes east of the Mississippi River indicate that since 1966, when the surveys began, the abundance of 14 of the 19 species of grassland and savanna birds in eastern North America has declined significantly (Table 1). Some have shown rapid population changes. Between 1966 and 1994, for example, Grasshopper Sparrows decreased at a rate of 6% per year, whereas the annual rates of decline were 3% for Vesper Sparrows (*Pooecetes gramineus*), 9% for Henslow's Sparrows (*Ammodramus henslowii*), and 3% for Eastern Meadowlarks. In contrast, only 2 of 40 species of forest-dwelling migratory birds—a group that has received considerable attention from conservationists—decreased at a rate of more than 2% per year during approximately the same period (Askins 1993).

Another indication that grassland birds in the eastern United States are in trouble comes from state lists of endangered and threatened species

TABLE 1. POPULATION TRENDS OF GRASSLAND AND SAVANNA SPECIALISTS IN NORTH AMERICA EAST OF THE MISSISSIPPI RIVER BETWEEN 1966 AND 1994

Species	% change per year	Statistical significance ^a	Number of routes
Grassland species ^b			
Northern Harrier (<i>Circus cyaneus</i>)	+2.1	*	227
Ring-necked Pheasant (<i>Phasianus colchicus</i>)	-2.2	—	522
Northern Bobwhite (<i>Colinus virginianus</i>)	-3.3	***	880
Upland Sandpiper (<i>Barramia longicauda</i>)	+1.2	—	201
Horned Lark (<i>Eremophila alpestris</i>)	0.0	—	642
Dickcissel (<i>Spiza americana</i>)	-4.3	***	269
Vesper Sparrow (<i>Pooecetes gramineus</i>)	-3.3	***	650
Lark Sparrow (<i>Chondestes grammacus</i>)	-6.9	*	39
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	-1.7	***	727
Grasshopper Sparrow (<i>Ammodramus saviannarum</i>)	-5.9	***	730
Henslow's Sparrow (<i>A. henslowii</i>)	-9.3	***	137
Bobolink (<i>Dolichonyx oryzivorus</i>)	-1.4	***	745
Eastern Meadowlark (<i>Sturnella magna</i>)	-3.4	***	1,330
Western Meadowlark (<i>S. neglecta</i>)	-7.2	***	174
Savanna species ^c			
Common Ground-Dove (<i>Columbina passerina</i>)	-3.4	***	127
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	-2.1	***	667
Eastern Bluebird (<i>Sialia sialis</i>)	+2.2	***	1,185
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	-4.3	***	379
American Goldfinch (<i>Carduelis tristis</i>)	-1.1	***	1,349

Note: Data are from the Breeding Bird Survey database, U.S. Fish and Wildlife Service (Sauer et al. 1995). Habitat classifications are based on DeGraaf and Rudis 1986, DeGraaf et al. 1991, and Askins 1993.

^a * P < 0.05, *** P < 0.001.

^b Species dependent on open habitats dominated by grass and forbs, with little woody vegetation.

^c Species found primarily in open grassland with scattered trees or shrubs.

(Vickery 1992). Of the 40 species listed as endangered, threatened, or of special concern in three or more northeastern states, 13 are grassland or savanna specialists and only 3 are forest specialists. For example, Upland Sandpiper, Northern Harrier (*Circus cyaneus*), Loggerhead Shrike (*Lanius ludovicianus*), and Grasshopper, Henslow's, and Vesper sparrows are listed in all or most of the New England states (Vickery 1992). The populations of many of these species have declined in other parts of the eastern United States, both in heavily forested areas along the East Coast and in the more agricultural Midwest (Herkert 1991, Bollinger and Gavin 1992).

What Mayfield (1988) called the "quiet decline" of grassland birds has attracted surprisingly little attention or concern from most government wildlife agencies and conservation organizations. This response is rooted in the widely held view that before Europeans cleared the land, unbroken forest stretched from the Atlantic to the Great Plains, leading to the general impression that grassland species invaded the eastern states from western savannas and prairies after the clearing of the forest for agriculture. For example, Whitcomb (1987) argued that this invasion of the eastern "neosavanna" created by agriculture has been a "failed experiment for

many of these species," which are now declining. The implication is that this is a return to ecosystems more similar to those before European settlement and therefore should not be a cause for concern. According to Whitcomb, these species could survive only with active management to preserve grassland "in a region where [grassland] is inappropriate as an equilibrium community" (Whitcomb 1987:165).

Many historians and botanists have depicted the landscape of the ancient East Coast of North America as carpeted with forest, a forest so continuous that a squirrel could travel from the Atlantic Ocean to the Mississippi River without touching the ground (Day 1953). Clearly forests in eastern North America were extensive, and in some areas they were essentially unbroken (Siccamo 1971, Lorimer 1977, Bormann and Likens 1979, Runkle 1990, Seischab and Orwig 1991). Since the early 1900s, however, some botanists have argued that the forest was not always continuous; in coastal areas and even in some inland areas, it was interrupted by scrubland, barrens, glades, and even, in places, prairielike grasslands (Day 1953). If this is true, then grassland birds would have had a place in the landscape before European settlement.

WERE THERE GRASSLANDS ON THE EAST COAST BEFORE EUROPEAN SETTLEMENT?

When Conrad (1935) visited Long Island's Hempstead Plains in the 1930s, much of the area was little bluestem (*Schizachyrium scoparius*) prairie, a yellow-green grassland dotted with the small, bright green hemispheres of wild indigo (*Baptista tinctoria*). In May the prairie was blue with the blossoms of birdfoot violets (*Viola pedata*). As Conrad pointed out, this grassland on the New York coast was remarkably similar to the tallgrass prairies of Iowa and Nebraska. Moreover, the Hempstead Plains had a rich community of grassland birds: Upland Sandpipers, Bobolinks, and Vesper and Grasshopper sparrows were all common there in the 1920s (Bull 1974).

European travelers described the Hempstead Plains as treeless in the 1600s (Harper 1911), so this grassland was not a product of European agriculture. The Hempstead Plains were characterized by thin soil resting on a porous foundation of quartz and granite pebbles (Conrad 1935, Cain et al. 1937), features that, in combination with periodic fires, appeared to favor the growth of grasses and herbs rather than trees and shrubs.

The Plains once covered more than 20,000 ha, and for many years the area was used primarily for grazing sheep and racing horses (Svenson 1936, Stalter and Lamont 1987). Large areas of grassland remained in the 1930s, but after World War II these open areas were subdivided for housing or plowed for truck farms. Today only a few acres of this prairie survive: an 8-ha parcel belonging to Nassau County Community College and managed by The Nature Conservancy, and a 19-ha parcel managed as a nature preserve by Nassau County (Antenen et al. 1994). The smaller preserve has been maintained with controlled burning.

Although the Hempstead Plains may have been one of the largest and most distinctive grasslands on the East Coast, it was not the only one. Another grassland, the Montauk Downs, covered approximately 2,400 ha of eastern Long Island (Taylor 1923), and several large grasslands, called "glades," characterized a plateau in the Allegheny Mountains of western Pennsylvania (Whitney 1994). Also, in the 1600s a savanna where occasional large oaks (*Quercus*) broke an expanse of tall, wiry grass (probably bluestem) stretched for 24 km along the Quinnipiac River north of New Haven, Connecticut (Olmsted 1937). After decades of overgrazing, this area became the almost desertlike North Haven Sand Plains, and subsequently most of the

area was developed. Blueberry barrens, which are open expanses covered with lowbush blueberry (*Vaccinium angustifolium*) shrubs and grasses, still cover large areas in eastern Maine, where they are maintained by burning for blueberry production. Some of the largest East Coast populations of Upland Sandpipers, Vesper Sparrows, and other species of grassland birds breed on these barrens (Vickery et al. 1994).

Many of these grasslands may have resulted from the activities of Native Americans before European settlement. Early explorers and colonists frequently encountered open landscapes created by firewood harvesting, agricultural clearing, and burning to enhance hunting. For example, Giovanni da Verrazano described the area around Narragansett Bay (Rhode Island) in 1524 as open plains, without forests or trees, for many leagues inland (Day 1953). Samuel de Champlain and John Smith reported extensive areas of cleared land along the New England coast before Europeans colonized the area (Whitney 1994). Moreover, an early settler in Salem, Massachusetts, described "open plains, in some places five hundred acres. . .not much troublesome for to cleere for the plough to goe in" (Day 1953:331). These clearings were not restricted to coastal areas; accounts of early settlers indicate that river valleys had been cleared by Native Americans for farming and hunting (Patterson and Sassaman 1988).

Early assessments that Native American agriculture had relatively little effect on the landscape were based on population estimates after European settlement, but population densities were much higher before contact with Europeans triggered massive epidemics that killed a large proportion of the people in most tribes (Crosby 1972, Cronon 1983, Denevan 1992, Whitney 1994). As Kulikoff (1986:29) wrote regarding the Chesapeake Bay area, "though English settlers did not find a wilderness, they did create one"; extensive agricultural clearings reverted to forest as Native American populations declined. Pilgrims traveling through the area near Warren, Massachusetts, in 1621 "saw the remains of so many once occupied villages and such extensive formerly cultivated fields that they concluded thousands of people must have lived there before the plague" (Russell 1980: 24). Maps, drawings, and written accounts of the landscape around Native American settlements in the southeastern United States before European settlement provide evidence of extensive clearings created by farming and of "parklands" maintained by controlled burning (Hammett 1992). In New York and southern New England, relatively high population densities combined with slash-and-burn agriculture (Whitney 1994)

would have resulted in extensive areas of cleared land in the form of both active and abandoned fields. This would have produced a "mosaic of forests and fields in varying stages of succession" (Patterson and Sassaman 1988: 115). Another view is that Eastern tribes used large permanent agricultural fields from which tree stumps had been removed rather than temporary fields cut out of the forest for slash-and-burn agriculture (Doolittle 1992). This permanent farmland would have had to be rested occasionally, however, producing "weed-covered" fallow fields of the sort seen by Champlain near the site of Boston in 1605 (Doolittle 1992). Regardless of whether Native Americans used slash-and-burn or permanent-field agriculture, their activities would have produced open habitats (abandoned or fallow fields) that could have been used by grassland birds.

There also is good evidence that the Native Americans of the East Coast burned large areas to create open woodlands and grassland for hunting. For example, Roger Williams wrote in the 1640s that Native Americans in New England "burnt up all the underwoods in the Countrey, once or twice a yeare and therefore as Noble men in England possessed great Parkes . . . onely for their game" (Williams 1963:47). In 1818, B. Trumbull reported that the Native Americans of Connecticut "so often burned the country, to take deer and other wild game, that in many of the plain dry parts of it, there was but little small timber. Where the lands were thus burned there grew bent grass, or as some called it, thatch, two, three and four feet high" (Olmsted 1937:266). Native Americans in New York not only burned the woods each autumn to create a more open understory but also burned plains and meadows to improve hunting (Whitney 1994).

Although fires were probably infrequent in most forests that were remote from Native American settlements (Russell 1983), fire and other disturbances near settlements provided extensive habitat for early successional species, including potential habitat for grassland birds. An analysis of charcoal deposits in the sediments of 11 lakes in New England demonstrated that before European settlement, fires were frequent in densely populated coastal areas but infrequent in inland and northern areas (Patterson and Sassaman 1988). Moreover, Winne's (1988) analysis of pollen and charcoal in lake sediments showed that the area around Pineo Pond in eastern Maine has been characterized by frequent, moderate fires and scrubby, fire-adapted vegetation for at least 900 yr. Today this area is dominated by blueberry barrens that are maintained by con-

trolled burning. These support a diversity of breeding grassland birds (Vickery et al. 1994).

The extent of forest clearing by Native Americans in the northeastern United States probably paled in comparison with the extensive agricultural fields created by the Moundbuilders, who lived along the Mississippi River and its tributaries in much of what is now the southeastern and midwestern United States. Moundbuilding cultures existed in the lower Mississippi River Valley as early as 1500 B.C. The early Moundbuilding cultures probably depended on a mixture of hunting, gathering of nuts, fishing, and small-scale farming based on native plants such as sunflower (*Helianthus*) and marsh elder (*Iva frutescens*; Shaffer 1992). Later, during the Mississippian Period, which lasted from A.D. 700 until the early 1700s, large-scale agriculture supported a dense population living in closely spaced villages. Corn (*Zea mays*) and beans (Leguminosae) from Mexico replaced indigenous crops, and large areas were cleared for farming (Shaffer 1992). The largest population center was Cahokia, located on the Mississippi River near its confluence with the Missouri River (Shaffer 1992). This center covered 800 ha, with 160 ha enclosed in a wooden palisade. The site was dotted with as many as 120 earthen mounds, the largest of which rose to 30 m and covered more than 6 ha. The mounds supported wooden buildings, and the area below the mounds was densely packed with rectangular thatched-roof houses where an estimated 15,000–38,000 people lived. Cahokia and the many villages and towns around it were supported by farming the American Bottom, a 324-km² strip of rich alluvial soil in the floodplain along the eastern bank of the Mississippi River. In A.D. 1000 there were 50 villages and 8 other large or medium-sized centers within 40 km of Cahokia.

There are no historical accounts of Cahokia because it was abandoned after A.D. 1200 (Shaffer 1992). Early Spanish visitors visited similar sites that were still occupied in the 1500s, however. A chronicler of Hernando de Soto's expedition (1539–1542) described a Moundbuilder town along the Mississippi River as being "in an open field, that for a quarter of a league over was all inhabited; and at the distance of from half a league to a league off were many other large towns, in which was a good quantity of maize, beans, walnuts [*Juglans*], and dried *Ameixas* [persimmons]" (Bourne 1904:149).

The Moundbuilding centers were abandoned long before Europeans settled the southeastern United States or Mississippi River Valley. This culture may have been destroyed by Old World diseases that swept inland from European outposts on the Florida and Gulf Coasts (Crosby

1986). Before the collapse of this agricultural society, however, there were extensive areas of open fields in many parts of the Southeast, especially the lower Mississippi River Valley.

GRASSLANDS BEFORE NATIVE AMERICAN AGRICULTURE

The patterns of Native American land use observed in the 1600s began to emerge about 2,000 yr ago (Smith 1989, 1995). Many species of grassland birds may have colonized cultivated areas after the initiation of Native American, rather than European, agriculture, and their current decline represents a return to conditions before humans began to substantially modify the vegetation of eastern North America.

Undoubtedly, many apparently "natural" open grasslands of eastern North America were the product of human activities. For example, historical accounts and analysis of the pollen record indicate that the extensive heathlands and sandplain grasslands on Nantucket Island, Massachusetts, resulted from the clearing of oak forest and grazing of sheep after Europeans settled that island (Dunwiddie 1989).

Some of the open habitats on the East Coast may predate disturbance by Native Americans or Europeans, however. Smaller shrubby and grassy openings in the eastern forest result from dam-building by beavers (*Castor canadensis*). After beavers exhaust the food supply around a pond, they move to another area. When the abandoned pond drains, the pond bed often becomes a "beaver meadow," a patch of shrubby vegetation or grassland. This meadow eventually is overgrown with young forest, and after 10–30 yr beavers may recolonize the site and initiate another cycle (Remillard et al. 1987).

Although beaver meadows are largely restricted to flood plains, their total area was probably extensive before beavers were extirpated in most parts of eastern North America (Naiman et al. 1988). In Ontario's Algonquin Provincial Park, where beavers are protected, there is a high density of beaver ponds and meadows (Coles and Orme 1983). After beavers became reestablished at Quabbin Reservoir in Massachusetts in 1952, the population grew rapidly until the density reached 0.8 colony per kilometer of stream (Howard and Larson 1985). The impact of a dense beaver population can be considerable. In the Adirondack Mountains of New York, beaver dams created patches of disturbance that covered an average area of 7 ha, with a maximum area of 12 ha (Remillard et al. 1987). Bela Hubbard, who surveyed land in Michigan before European settlement, reported that one-fifth of the area within 19 km of what is now Detroit was covered with "marshy tracts or prairies which had

their origin in the work of the beaver" (Whitney 1994:304). Coles and Orme (1983:99) argued that ancient forests in England must have been "moth-holed with clearings wherever beaver were present." These "grassy meadows of relict pools" were also an important feature of the pre-settlement landscape of eastern North America. Although beaver meadows are generally too small to accommodate many species of specialized grassland birds, some other species (e.g., Eastern Meadowlark and Savannah Sparrow) occur in patches of grassland of similar size (5–10 ha; Herkert 1994, Vickery et al. 1994).

Many regions of the East were subject to disturbances that created large openings in the forest (Runkle 1990). Grassland, savanna, and grassy scrub were probably created by large fires, particularly fires that burned following hurricanes or tornadoes that periodically leveled forests. These catastrophic disturbances were probably most frequent in low-lying sandy areas on the coastal plain. In many regions farther inland, fires, windstorms, and other disturbances were infrequent, and consequently the forest canopy was almost continuous, with few large openings (Lorimer 1977). For example, the northern hardwood forest of western New York and of the White Mountains of New Hampshire probably formed an almost unbroken canopy (Bormann and Likens 1979, Seischab and Orwig 1991). Large grassy openings may have occurred in some of the river valleys in the interior, however. John Winthrop (Hosmer 1959:85) described how one of the first European expeditions to the White Mountains passed through "many thousands of acres of rich meadow" as it paddled birch-bark canoes up the Saco River in what is now Maine.

A LONGER VIEW: PLEISTOCENE STEPPE AND SAVANNA

When continental glaciers covered much of Canada and the northern United States, the regions immediately south of the glaciers were dominated by a spruce (*Picea*) parkland, a grassy savanna with scattered spruce trees (Webb 1988). Samples of pollen from lake sediments deposited 18,000–12,000 yr ago show that this savanna stretched westward from the Atlantic Coast to the Great Plains. Most species of deciduous trees, and presumably the closed forests where these species grow today, were restricted to the extreme southeastern United States (Webb 1988). Thus, in eastern North America there was a gradient from savanna in the north to dense forest in the south.

Vegetation zones shifted and changed as the glaciers retreated northward beginning about 12,000 yr ago. Spruce parkland largely disap-

peared, and a new gradient, from eastern forest to western prairie, gradually formed (Webb 1988). Before this transition occurred, however, the spruce parkland was occupied by a diversity of large open-country mammals; caribou (*Rangifer tarandus*), mastodons (*Mammot americanum*), and long-nosed peccaries (*Mylohyus nasutus*) are frequently found in fossil deposits from the time of the spruce parkland (Kurtén and Anderson 1980).

One of the best samples of spruce parkland animals comes from a site called New Paris No. 4 in Pennsylvania (Guilday et al. 1964). Approximately 11,000 yr ago, a deep sinkhole acted like a pitfall trap, collecting the skeletons of more than 2,700 animals that fell into the crevice and died. The mixture of small mammals and skeletal remains of Sharp-tailed Grouse (*Tympanuchus phasianellus*) at this site suggests that there was extensive grassland habitat in this region.

A better picture of the birdlife of the postglacial period comes from another site, the caves of Natural Chimneys in Virginia, where skeletons were deposited at about the same time as at the New Paris No. 4 site. The skeletons at Natural Chimneys were deposited in owl pellets, so both small mammals and birds were well represented (Guilday 1962). Although remains of these animals may have accumulated over a long period while the vegetation was changing, they provide a glimpse of the bird community of the spruce parkland. The bones of Sharp-tailed Grouse, Northern Bobwhite (*Colinus virginianus*), Upland Sandpiper, Red-headed Woodpecker (*Melanerpes erythrocephalus*), Black-billed Magpie (*Pica pica*), and Brown-headed Cowbird (*Molothrus ater*), along with other grassland vertebrates such as thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), point to a landscape with large amounts of open savanna or grassland. The remains of woodland species such as Red-bellied Woodpecker (*Melanerpes carolinus*), Eastern Wood-Pewee (*Contopus virens*), and Red-breasted Nuthatch (*Sitta canadensis*) in the same deposits suggest either that woodland and savanna were found in the area at the same time or that woodland invaded and replaced the savanna while the bones accumulated at Natural Chimneys. In either case, it is clear that grassland birds occurred in eastern North America before the spruce parkland receded and disappeared.

A site farther south, at Duck River, Tennessee, revealed that in the late Pleistocene typical coniferous forest species (Northern Hawk-Owl [*Surnia ulula*], Boreal Owl [*Aegolius funereus*], Northern Saw-whet Owl [*A. acadicus*], Gray Jay [*Perisoreus canadensis*], and Pine Grosbeak

[*Pinicola enucleator*]) lived alongside grassland species such as Sharp-tailed Grouse, Greater Prairie-Chicken (*Tympanuchus cupido*), Horned Lark (*Eremophila alpestris*), meadowlark (*Sturnella* sp.), pocket gopher (*Geomys* spp.), and thirteen-lined ground squirrel (Parmalee and Klippel 1982).

A key question is whether grassland birds could have survived the northward spread of closed-canopy forest over eastern North America after the continental glaciers melted. This is an issue not only for the current warm interglacial period but also for previous interglacial periods. In all previous interglacial periods and at the beginning of the current postglacial period, large browsers such as mastodons and giant ground sloths (*Megalonyx jeffersonii* and other species) may have created and maintained openings in the forest in much the same way as African elephants (*Loxodonta africana*) maintain open savannas in East Africa today (Dublin et al. 1990). European ecologists have recognized that giant herbivores, particularly the extinct relatives of elephants, probably opened the forest, creating glades, parklike woods, or even savannas in areas that would otherwise be dominated by dense forest (Andersson and Appelquist 1990, Puchkov 1992). Such openings would have supported a variety of animal and plant species that depend on grassy habitats. Through most of the past 1 million yr, as forests retreated and advanced in response to the shrinking and growing of glacial ice sheets, woodland habitats may have been modified and opened by giant herbivores. Only in the present interglacial did mastodons, ground sloths, and other giants disappear from North America, perhaps as a result of the invasion of the continent by people who had already developed efficient tools and strategies for hunting large animals (Martin and Klein 1984). Human activities such as burning and agricultural clearing subsequently may have substituted for giant herbivores in creating a mosaic of forest and openings (Andersson and Appelquist 1990), permitting open-country species to persist in eastern woodlands.

THE ORIGIN OF EASTERN GRASSLAND BIRDS

The common impression that many species of grassland birds spread eastward from the prairies of the Midwest to the newly cleared farmland of the East Coast is substantiated by several well-documented examples of range expansion. For example, the prairie subspecies of Horned Lark (*Eremophila alpestris praticola*) spread eastward from Illinois and Wisconsin, reaching Michigan and Ontario in the 1870s, New York in the 1880s, New England by 1891, and Penn-

sylvania and Maryland by 1910 (Forbush 1927, Thomas 1951, Hurley and Franks 1976). The Dickcissel (*Spiza americana*) spread eastward from the tallgrass prairies in the early 1800s, but its range contracted after 1850, and it eventually disappeared as a regular breeding bird along the East Coast (Hurley and Franks 1976). Western Meadowlarks (*Sturnella neglecta*) expanded east into Wisconsin and Michigan after 1900 (Lanyon 1956), and Lark Sparrows (*Chondestes grammacus*) spread eastward from the prairies into agricultural areas in the Ohio Valley, West Virginia, and western Maryland (Brooks 1938).

Although these eastward range expansions were well documented, there is no similar evidence for invasion of the East by the species that are most abundant and widespread in eastern grasslands. Upland Sandpipers, Grasshopper Sparrows, Bobolinks, Eastern Meadowlarks, and other common grassland birds were reported by the earliest ornithologists who systematically documented the distribution of birds on the eastern coast of North America. Alexander Wilson's *American Ornithology* (originally published between 1808 and 1814; Brewer 1839) and John James Audubon's *Ornithological Biography* (Audubon 1831–1849) were published more than 100 yr after most of the eastern seaboard had been cleared, so it is possible that grassland birds colonized the meadows and pastures created by Europeans long before their occurrence was initially documented. Some seventeenth-century European observers, such as John Josselyn (Lindholt 1988) and William Wood (Vaughan 1977), described gamebirds and the more conspicuous songbirds, but only a few species are recognizable because descriptions are sketchy and the names of British birds were frequently used for North American species. Mark Catesby's *Natural History of Carolina, Florida, and the Bahama Islands*, completed in 1747, includes descriptions and paintings of many species of eastern birds, including two species of grassland songbirds, Eastern Meadowlark and Bobolink (Feduccia 1985). It is not surprising, however, that there are relatively few descriptions of grassland songbirds from this period. Many grassland birds are small, inconspicuous, and dull colored, so they could have been overlooked by early observers.

Significantly, the East Coast populations of three species of grassland birds were distinctive enough from western populations to be considered separate subspecies. This suggests that these populations have existed in isolation in the East for many thousands of years, perhaps since unbroken grasslands reached from the Great Plains to the Atlantic during the last glacial period. The eastern Henslow's Sparrow (*Ammo-*

dramus henslowii susurrans) has a breeding range restricted to central New York and southern New England south to Virginia, eastern West Virginia, and North Carolina (Smith 1968). It is darker than the western subspecies, with a deeper bill and more buff on the underparts and more yellow in the wing (Smith 1968).

The "Ipswich" Sparrow (*Passerculus sandwichensis princeps*), a subspecies of the Savannah Sparrow, is also restricted to the East Coast (Wheelwright and Rising 1993). This population is so distinctive that it was considered a separate species until 1973. After reclassifying it as a subspecies of Savannah Sparrow, the American Ornithologists' Union (1957) recommended that it be designated by its vernacular name in quotes ("Ipswich" Sparrow). Vernacular names are only officially recognized for particularly distinctive subspecies (Stobo and McLaren 1975).

The "Ipswich" Sparrow was not described until 1868, when C. J. Maynard collected one in the coastal dunes at Ipswich, Massachusetts (Elliott 1968). Its breeding range on Sable Island, a 32-km-long island about 135 km off the coast of Nova Scotia, was not discovered until 1884.

"Ipswich" Sparrows spend both summers and winters in extremely open habitats. During the breeding season they are virtually restricted to low shrubby vegetation and stands of marram grass (*Ammophila breviligulata*) on Sable Island (Stobo and McLaren 1975). In winter they occur primarily in a narrow zone of dunes near Atlantic beaches from Nova Scotia to Florida, with the highest densities on relatively undeveloped barrier islands and sandy peninsulas between New Jersey and Virginia (Stobo and McLaren 1971).

The "Ipswich" Sparrow is adapted to living in the dunes and sandy scrub adjacent to the ocean. It is paler gray than other Savannah Sparrow subspecies, so it tends to be well camouflaged in the light-colored dune and beach areas where it lives (Stobo and McLaren 1975). Also, it averages 9% larger than other eastern subspecies of Savannah Sparrow, which might be an adaptation to feeding on the exceptionally large seeds of dune grasses such as marram grass and sea oats (*Uniola paniculata*; Stobo and McLaren 1975). Finally, unlike other Savannah Sparrow subspecies, the "Ipswich" Sparrow has a short tail, making it more similar to Grasshopper Sparrow, Seaside Sparrow (*Ammodramus maritimus*), and other sparrows that live in open habitats with few tall shrubs or trees. These specific adaptations indicate that grassy habitats must have existed along the outer beaches of the East Coast for a long time.

The now-extinct Heath Hen (*Tympanuchus cupido cupido*) was the eastern subspecies of the

Greater Prairie-Chicken. During the early years of European settlement, the Heath Hen was common or even abundant in open grasslands and scrublands on Long Island and around Boston, and it ranged along the coast from southern Maine as far south as Virginia (Gross 1932). Because it was an important game species, it was described by many early settlers. In the 1600s, William Wood, Thomas Morton, and other observers wrote that the Heath Hen was common in eastern Massachusetts (Forbush 1927, Gross 1932, Vaughan 1977). Heath Hens inhabited sandy scrub-oak plains, pine (*Pinus*) barrens, blueberry barrens, and other open habitats (Forbush 1927, Johnsgard 1983). In the nineteenth century they were common in the open grassland of the Hempstead Plains on Long Island (Bull 1974).

The abundance of Heath Hens at the time of European settlement, and the recognition of the Heath Hen and eastern populations of two other species of grassland birds as distinct subspecies, suggest that grassland birds inhabited the East Coast long before Europeans arrived or even before Native Americans started clearing the land for farming. This is consistent with the evidence on grassland plants. Several plant species are restricted to eastern grasslands (Mehrhoff 1997; P. Dunwiddie, pers. comm.), suggesting that they evolved in isolation from the grasslands of the Great Plains. Bushy rockrose (*Helianthemum dumosum*) is found from Massachusetts to Long Island; sandplain agalinis (*Agalinis acuta*) from Massachusetts to Maryland; and sickle-leaved golden aster (*Pityopsis* [*Chrysopsis*] *falcata*) from Massachusetts to New Jersey (Gleason and Cronquist 1991). In addition, a subspecies of northern blazing star (*Liatris scariosa* var. *novae-angliae*) is found only in eastern grasslands.

Because of the paucity of historical records of small birds in the 1600s and 1700s, it is likely that only carefully dated skeletal remains could provide definitive evidence of the occurrence of most species of grassland birds before European settlement. There is strong evidence, however, that extensive grasslands and savannas occurred in eastern North America at the time of European settlement. We also know that some grassland species were found in the spruce parkland of postglacial times, about 11,000 yr ago, and that distinctive eastern subspecies evolved in three grassland species. Therefore, it is reasonable to conclude that many open-country species are native to the region, not recent invaders from the western prairies. During the eighteenth and nineteenth centuries these species probably became much more abundant than they had been before Europeans cleared the land, but subsequently they may have declined far below the

level of abundance characteristic of the presettlement landscape. Many of these species are now in danger of regional extinction, and they deserve the same attention from conservationists as birds associated with eastern forests, marshes, and lakes.

CONSERVATION OF GRASSLAND BIRDS

Many of the original grasslands, such as beaver meadows and recently burned areas, were ephemeral. Other areas may have been disturbed frequently enough to create stable grasslands; the Hempstead Plains in New York and some of the barrens in eastern Maine are obvious candidates. Temporary grasslands are created much less frequently today because beavers are less abundant and fires are controlled, and most of the areas that may have been stable grasslands have been developed for agriculture or housing. The blueberry barrens of eastern Maine are an exception; these open habitats have been maintained in a seminatural state by controlled burning to sustain commercial blueberry production (Vickery et al. 1994).

With the exception of Maine's blueberry barrens and a few other areas remaining as seminatural open habitat for centuries, present-day habitats used by grassland birds along the East Coast are highly artificial. Populations of grassland species have diminished primarily because much of the farmland in the Northeast and parts of the Southeast has been abandoned and has reverted to forest, and because the remaining farmland is now managed more intensively for agricultural production (Hart 1968, Askins 1993). For example, hayfields have become less suitable as nesting habitat for Eastern Meadowlarks, Bobolinks, and some other grassland species because they are mowed earlier in the summer, before the end of the nesting season, and because they are rotated more frequently (Bollinger and Gavin 1992). In southern New England, most of the remaining populations of Grasshopper Sparrows and Upland Sandpipers are found in extensive mowed areas at airports and military airfields (Veit and Petersen 1993, Bevier 1994, Melvin 1994). The farmland once used by these species has either disappeared or become unsuitable for nesting.

Regional populations of grassland birds can be maintained with proper management of artificial grasslands such as fallow farmland and the mowed areas near airport runways. The Conservation Reserve Program (CRP), which pays farmers to take land out of production in order to manage it for conservation of soil and wildlife (Dunn et al. 1993), could potentially benefit grassland birds in the East as it already has in some western prairie regions (Johnson and

Schwartz 1993, Johnson and Igl 1995). However, most of the CRP land is concentrated in the northcentral United States (Rodenhouse et al. 1995), and abandoned farmlands in the East quickly become wooded, so a better approach might be to compensate farmers who use less intensive farming methods to create traditional hay meadows and other types of farmland that once sustained grassland birds. This approach has been successful in preserving open-country species in the Netherlands (Beintema 1988).

Relatively simple changes in airport management (e.g., removing woody vegetation and changing mowing schedules to avoid the nesting season) have sustained or improved habitat for grassland birds at Westover Air Reserve Base in Massachusetts (Melvin 1994), Bradley International Airport in Connecticut (Crossman 1989), and Floyd Bennett Field, a former naval air base on Long Island, New York (Lent and Litwin 1989). Habitat management at Westover resulted in substantial increases in the abundance of Grasshopper Sparrows and Upland Sandpipers between 1987 and 1994 (Melvin 1994).

Even when grassland birds are absent from an area, it should be possible to create habitat that will attract them. Probably because eastern grassland birds have always depended on patches of ephemeral habitat, they have a remarkable ability to find and colonize remote sites, even sites far from other bird populations of the same species. When a field in Lincoln, Massachusetts, was managed to maintain tall grass for nesting Bobolinks, in 1995 it attracted a breeding pair of Henslow's Sparrow, a species that has almost disappeared from Massachusetts, with no known breeding records in the preceding 20 yr (Ells 1995). Similarly, when abandoned strip mines in heavily forested areas of West Virginia were restored and seeded with grass, they were colonized by Horned Larks, Eastern Meadowlarks, and Savannah, Vesper, and Grasshopper sparrows (Whitmore and Hall 1978). These new grasslands were extremely isolated from other grasslands supporting grassland birds, but they still attracted breeding populations of several species.

Expending scarce resources to maintain meadows, fallow fields, and airfields may seem unwise to many conservationists who are accustomed to protecting forests and wilderness areas. Yet many species of birds, insects, plants, and other organisms depend on these grassland habitats. Artificial habitats are critical for many of these species because people have destroyed most of the native grassland habitat, including most of the midwestern tallgrass prairies where these species may have once been most abundant (Bollinger et al. 1990). People have not

only destroyed natural grasslands directly, but they also have interrupted or suppressed many of the natural processes of disturbance, such as fires and beaver activity, that once created the early successional habitats that grassland species need. In the near term, artificial grasslands represent our best hope for maintaining grassland species. These species are an important, and probably ancient, component of biological diversity along the East Coast of North America.

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