# Grasslands

*"The prairie, in all its expressions, is a massive, subtle place, with a long history of contradiction and misunderstanding. But it is worth the effort at comprehension. It is, after all, at the center of our national identity."*

William Least Heat Moon (1991)

Grasslands rank among the most biologically productive of all communities (Williams and Diebel 1996). Their high productivity stems from high retention of nutrients, efficient biological recycling, and a structure that provides for a vast array of animal and plant life (Estes et al. 1982). Grasses have contributed the hereditary material for the principal human food crops—rice, wheat, corn, and other grains. Worldwide production of such grain crops exceeds all other food crops combined. Grasslands also contribute immense value to watersheds and provide forage and habitat for large numbers of domestic and wild animals. Nevertheless, current levels of erosion in North America exceed the prairie soil's capacity to tolerate sediment and nutrient loss, thus threatening a resource essential to sustain future generations (Sampson 1981). Added to this threat is the potential for overgrazing by livestock and for other human activities to reduce the social and aesthetic values of grasslands and to restrict the commodities that grasslands can produce (National Research Council 1994), and the likelihood that severe degradation may be irreversible.

In North America, the prairie communities (about 1.5 million square kilometers) contain the majority of the continent's native grasslands (Fig. 1). Environmental features that describe the native North American grasslands embody similarity in vegetation, an abiotic environment to which the vegetation and structure respond, and the nature of the animal communities.

North American grasslands are similar in the general uniformity of their vegetation, dominance of grasses and grasslike plants, lack of shrubs, and absence of trees (Weaver 1968). The Great Plains grassland evolved in the rain shadow of the Rocky Mountains, where seasonal precipitation occurs mostly in spring and summer. From the Rocky Mountains east to the Mississippi River, the amount of precipitation increases and the frequency of droughts decreases (Simms 1988). Along a north-south gradient from central Texas to south-central Canada, the growing season becomes shorter, the average temperature decreases, and a greater proportion of annual precipitation occurs as snow. These broad-scale environmental gradients significantly influenced the evolutionary composition and distribution of prairie communities (Steinauer and Collins 1996; Weaver et al. 1996).

Many small and large grazing animals evolved on the North American prairie (Van Valkenburgh and Janis 1993), each with life-history and behavioral traits well adapted to the open character of prairie. For example, prairie dogs markedly affect the nutrient cycling, soil formation, and composition of grassland animal and plant communities (Miller et al. 1994). Moreover, it is important to realize that grasslands and their associated wildlife reflect events of the distant past (Knopf and Samson 1997). The incursion of animals—bison, elk, and others—into North America across land-bridges that once connected the Asian and North American continents is but one example of the role of past events. Thus, understanding how events of the distant past influenced both the isolation and interchange of plants and animals that interact with the more recent

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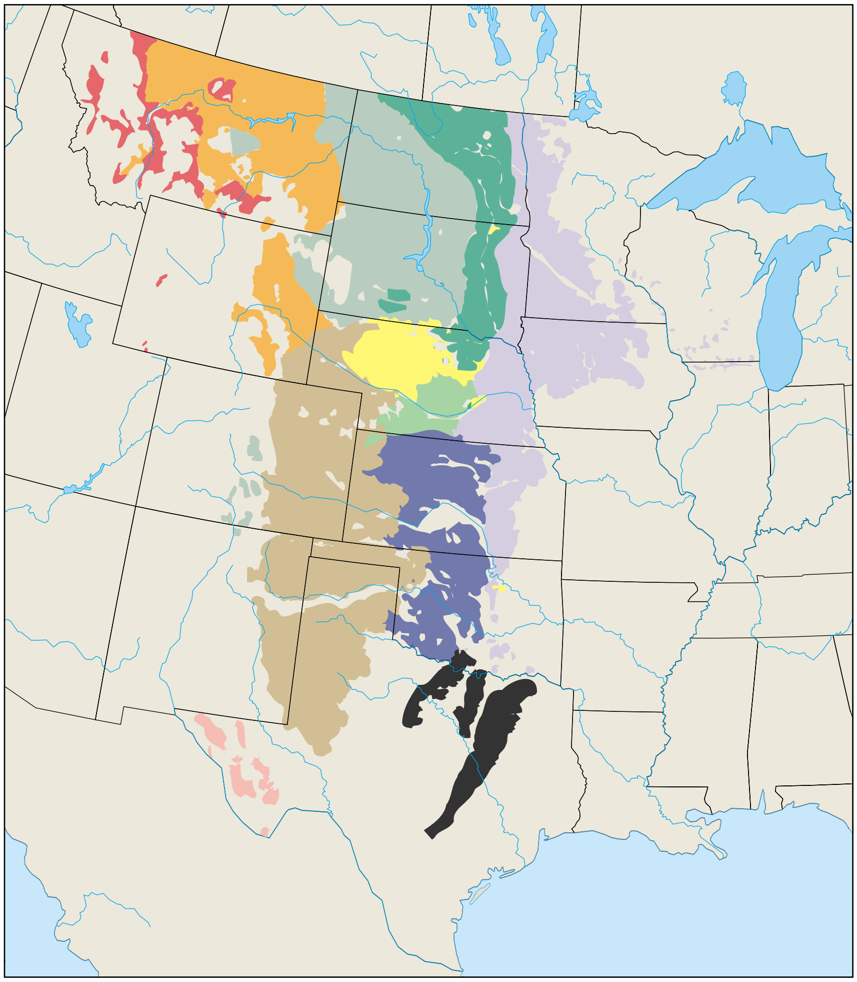

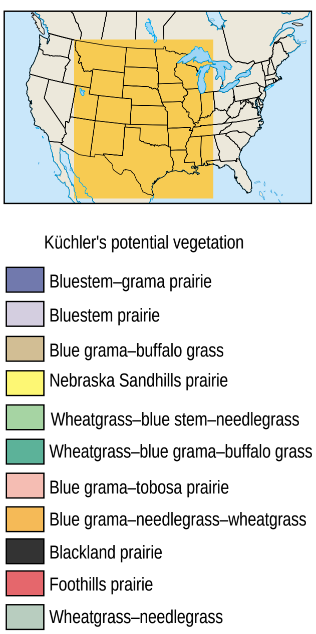


**Fig. 1.** The central grasslands, delineated by Küchler's potential vegetation types (Küchler 1964).

landscape is an essential step in interpreting any particular ecological community, including grasslands.

Understanding the biological resources of the Great Plains is difficult. The exact size of remaining grasslands in North America is unknown and difficult to estimate, and the community has undergone significant change since it was first described by early explorers and surveyors (Samson and Knopf 1994). Agriculture, urbanization, and mineral exploration have had both local and regional effects on biological resources. Invasions of nonindigenous plant species after fire suppression in the eastern, central, and southern prairies, as well as water developments in the western plains, have drastically altered grassland landscapes. Establishment of woodlots, shelterbelts, and tree-lined river and stream corridors within the prairie has contributed to a significant and ongoing loss of genetic diversity in North American grasslands (Knopf 1986).

This chapter highlights the status and trends of the main bodies of North American grasslands: the tall-grass prairie, the mixed-grass prairie, and the short-grass prairie. We feature the animals and plants dependent on native grassland and attempt to provide insight into the relationship between remaining native grassland and biological resources by reviewing available, current information and by describing threats.

## Prairie Past and Present

In the past, grassland dominated central North America (Fig. 2) and, during the warm, dry interglacial times, reached—as the prairie peninsula—into parts of Wisconsin, Illinois, Indiana, and eastern Ohio (Bazzaz and Parrish 1982). The main bodies of native grassland, now vastly altered, are the tall-grass prairie extending from Canada (Manitoba) and Minnesota south to Texas; the mixed-grass prairie from Canada, Montana, and North Dakota south to Texas; and the short-grass prairie extending from eastern Wyoming south to western Texas and eastern New Mexico. In the north, the natural grasslands are bordered on the west by coniferous forests of the Rocky Mountains and on the east by oak savannah (Anderson 1983) and aspen parkland in Manitoba and northwest Minnesota, with the transition from prairie to forest often abrupt (Great Plains Flora Association 1986). Across the Great Plains, coniferous and deciduous forest types meet only in the valley of the Niobrara River in north-central Nebraska, and isolated stands of both forest types occur in the Black Hills of South Dakota.

### Tall-grass Prairie

Tall-grass prairie (Fig. 3) is the wettest of the grassland provinces and is predominantly composed of sod-forming bunch grasses. Like other grasslands, the tall-grass prairie has species originally from different geographical sources (Simms 1988). Grassland groupings of the tall-grass prairie are the bluestem prairie from southern Manitoba through eastern North Dakota and western Minnesota south to eastern Oklahoma, and the wheatgrass, bluestem, and needlegrass area from south-central Canada through east-central North Dakota and South Dakota to southern Nebraska.

Three additional areas are associated with tall-grass prairie: the Crosstimbers, a band of grassland and oak savanna at the southern edge of the bluestem prairie in Kansas to the Trinity River in Texas (Küchler 1964), the Blackland Prairie south of the Crosstimbers (Gould 1962), and the rice prairies. The rice prairies are former coastal prairies that have been converted to rice production (Hobaugh et al. 1989). The original vegetation in rice prairies was mainly tall grass

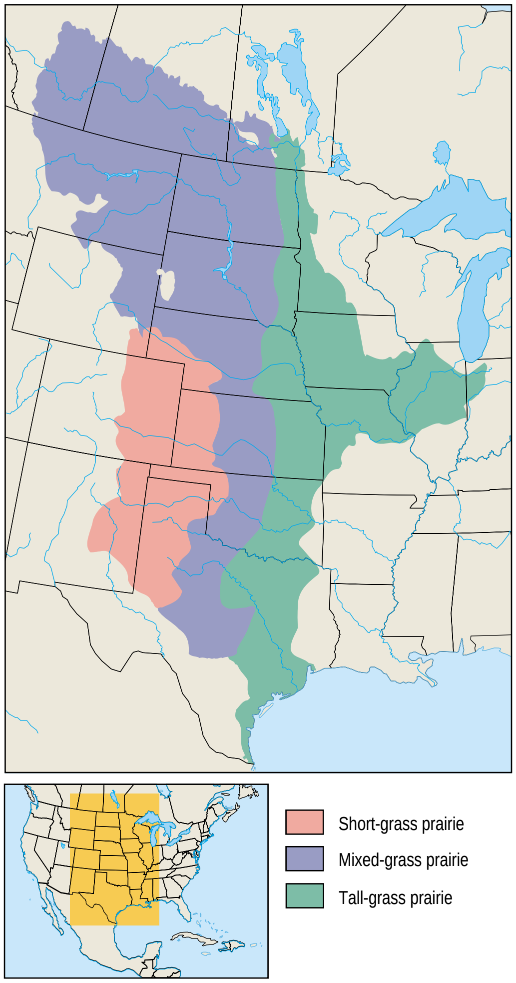


**Fig. 2.** Extent of historical (pre-European) tall-grass, mixed-grass, and short-grass prairies on the North American Great Plains.

and extended across 9,000 square kilometers, largely along the Texas coast and inland as much as 125 kilometers, and into Louisiana. Little coastal prairie remains; Attwater's Prairie Chicken National Wildlife Refuge in Texas is the single major remnant.

Since 1830 declines in the area of tall-grass prairie within specific states and provinces are estimated to be 82.6 to 99.9% (Table 1) and exceed those reported for any other major ecological community in North America (Samson and Knopf 1994). Iowa, for example, has barely 12,140 hectares remaining of its original 12 million hectares of tall-grass prairie. Less than 1% of the presettlement tall-grass prairie remains in Manitoba, Illinois, Indiana, and North Dakota. Minnesota and Missouri, states active in prairie conservation, work with less than 9% of the presettlement tall-grass prairie. Tall-grass prairie remains important to ranching in the Osage and Flint Hills of Kansas and in tracts in South Dakota, Oklahoma, and Texas.

Courtesy J. T. Lokemoen, USGS

**Fig. 3.** Tall-grass prairie.

## Mixed-grass Prairie

One can envision the short-grass and tall-grass prairies intergrading just east of an irregular line that runs from northern Texas through Oklahoma, Kansas, and Nebraska, northwestward into west-central North Dakota and South Dakota (Figs. 1 and 2). The perimeter is not well defined because of the array of

**Table 1.** Summary of the estimated past area, current area, and percent decline of tall-grass, mixed-grass, and short-grass prairies.

| Prairie type / Location | Past area (hectares)[a] | Current area (hectares)[a] | Decline (percent) |
|---|---|---|---|
| **Tall-grass** | | | |
| Manitoba | 600,000 | 300 | 99.9 |
| Illinois | 8,500,000 | 930 | 99.9 |
| Indiana | 2,800,000 | 404 | 99.9 |
| Iowa | 12,000,000 | 12,140 | 99.9 |
| Kansas | 6,900,000 | 1,200,000 | 82.6 |
| Minnesota | 7,300,000 | 30,000–60,000 | 99.2–99.6 |
| Missouri | 6,000,000 | 32,000 | 99.5 |
| Nebraska | 6,100,000 | 123,000 | 98.0 |
| North Dakota | 130,000 | 120 | 99.9 |
| Oklahoma | 5,200,000 | N/A[b] | N/A[b] |
| South Dakota | 2,600,000 | 20,000 | 99.2 |
| Texas | 7,200,000 | 720,000 | 90.0 |
| Wisconsin | 2,400,000 | 1,000 | 99.9 |
| **Mixed-grass** | | | |
| Alberta | 8,700,000 | 3,400,000 | 60.9 |
| Manitoba | 600,000 | 300 | 99.9 |
| Saskatchewan | 13,400,000 | 2,500,000 | 81.3 |
| Nebraska | 7,700,000 | 1,900,000 | 75.3 |
| North Dakota | 14,200,000 | 4,500,000 | 68.3 |
| Oklahoma | 2,500,000 | N/A[b] | N/A[b] |
| South Dakota | 1,600,000 | 480,000 | 70.0 |
| Texas | 14,100,000 | 9,800,000 | 30.5 |
| **Short-grass** | | | |
| Saskatchewan | 5,900,000 | 840,000 | 85.8 |
| Oklahoma | 1,300,000 | N/A[b] | N/A[b] |
| New Mexico | N/A[b] | 1,255,200 | N/A[b] |
| South Dakota | 179,000 | 116,350 | 35.0 |
| Texas | 7,800,000 | 1,600,000 | 79.5 |
| Wyoming | 3,000,000 | 2,400,000 | 20.0 |

[a] Estimates of past and current area based on information from The Nature Conservancy's Natural Heritage Data Center Network; Provinces of Alberta, Manitoba, and Saskatchewan; universities; and state conservation organizations.
[b] N/A means information is not available.

short-stature, intermediate, and tall-grass species that make up an ecotone between the short-grass and tall-grass prairies (Bragg and Steuter 1996). In general, the mixed-grass prairie is characterized by the warm-season grasses of the short-grass prairie to the west and the cool- and warm-season grasses, which grow much taller, to the east (Fig. 4). Because of this ecotonal mixing, the number of plant species found in mixed-grass prairies exceeds that in other prairie types. Estimated declines in area of native mixed-grass prairie, although less than those of the tall-grass, range from 30.5% in Texas to over 99.9% in Manitoba (Table 1).

Courtesy F. L. Knopf, USGS

**Fig. 4.** Mixed-grass prairie in Nebraska Sandhills.

## Short-grass Prairie

The short-grass prairie extends east from the Rocky Mountains and south from Montana through the Nebraska panhandle and southeastern Wyoming into the high plains of Oklahoma, New Mexico, and Texas (Figs. 1 and 2.). The short-grass prairie landscape (Fig. 5) was one of relatively treeless stream bottoms and uplands dominated by blue grama and buffalo grass, two warm-season grasses that flourish under intensive grazing (Weaver et al. 1996). Buffalo grass reproduces both sexually and by tillering sprouts from the base of grass clumps. Unlike the more eastern species, short-grass prairie species remain digestible and retain their protein content when dormant.

Declines in short-grass prairie have generally been much less than those of tall-grass and mixed-grass prairies (Table 1). However, perhaps in no other system than short-grass prairie are historical and evolutionary impacts of grazing so apparent (Knopf 1996). Clearly, birds endemic to the short-grass prairie express life-history characteristics and habitat use in response to grazing (Fig. 6). The mountain plover responds to highly disturbed sites, the chestnut-collared longspur to moderately grazed areas, and the Baird's sparrow to sites with taller grasses. In the mid-1800's the numbers of individuals of native mammal species—bison, prairie dogs, pronghorn, elk, grizzly bears, and gray wolves—rivaled or exceeded those now in the African Serengeti (Howe 1994). Major antigrazing structures evolved in plants: thorns and spikes; thick or hard tissues difficult to bite, chew, or digest; and secondary compounds difficult to digest. These structures have arisen through the long coevolutionary association between plants and animals with grazing on grasslands.

At present, extensive areas of short-grass prairie are dominated by invasive perennial and annual species, whose presence is attributed to overgrazing by domestic livestock and dryland farming (Weaver et al. 1996). To the south, specifically the Texas high plains, much of the short-grass prairie is now farmland or shrubland invaded by prickly pear cacti and oaks. Only the short-grass prairie and, to a lesser extent, mixed-grass prairie remain in public ownership. These areas are largely on the national grasslands managed by the U.S. Forest Service.

## Prairie Wetlands

The northern prairie contains numerous wetlands (Fig. 7), including the glaciated prairie pothole region (Fig. 8), the Nebraska Sandhills, and the Rainwater Basin (Kresl et al. 1996; Mack 1996). The 770,000-square-kilometer prairie pothole region extends from Alberta, Saskatchewan, and Manitoba across northeastern Montana, then southeast through North Dakota and eastern South Dakota into western Minnesota and northwestern and central Iowa. This landscape is pockmarked with numerous small, shallow depressions that capture snowmelt and rainwater or are within reach of subsurface waters. Estimated losses of prairie pothole wetland range from 35% in South Dakota to 99% in Iowa with loss rates upwards of 1,300 hectares per year (Tiner 1984).

The Nebraska Sandhills is the largest dune area (5,260 square kilometers) in North America (Mack 1996). About 526,100 hectares of wetlands are scattered throughout the area. The rapid movement of groundwater creates a continuum among lakes, wetlands, and streams, thus an alteration in one area may easily affect vegetation and wetlands over a larger landscape. Wetlands in the sandhills range from shallow, extremely alkaline basins to deeper, freshwater lakes to spring-fed streams. They are economically valuable, particularly as a source of irrigation water.

Another wetland area dependent on capturing water runoff is the Rainwater Basin of south-central Nebraska (6,720 square kilometers). Throughout the basin, rainwater is caught by scattered wind-excavated depressions underlain by an impermeable clay pan. Since the late 1800's efforts have been under way to drain Rainwater Basin; today, fewer than 400 depressions remain of an estimated 4,000, and they account for 22% of the former area. Other large, alkaline wetlands in Kansas include the Jamestown marsh, Talmo marsh, Lincoln salt marsh, Cheyenne Bottoms, Quivira National Wildlife Refuge (including Big and Little Salt marshes), and Slate Creek salt marsh. A similar alkaline lake is the Great Salt Plains Reservoir in Alfalfa County, Oklahoma.

Effects of collective water loss on the northern prairie range from significant declines in waterfowl breeding populations (Bethke and Nudds 1995) to elimination of the flood storage value of natural wetlands. About half of the continental waterfowl production comes from the prairie pothole region. Nebraska's Rainwater Basin is the major spring staging area for the buff-breasted sandpiper and the greater white-fronted goose, and it provides migratory habitat for endangered species such as the whooping crane and interior least tern. In addition, about 45% of North America's shorebird population east of the Rocky Mountains may stop at Cheyenne Bottoms during spring migration, including 90% of the North American populations of the white-rumped sandpiper, stilt sandpiper, Baird's sandpiper, long-billed dowitcher, and Wilson's phalarope, and over half of all pectoral sandpipers, marbled godwits, and Hudsonian godwits.

Interior wetland from the edge of the prairie pothole region across the central Great Plains is associated with major river systems. The area has few natural lakes, the largest of which is Inman Lake (78 hectares) in central Kansas (Carlander et al. 1986). Climate and past events account for the interior wetland's habitat characteristics (Cross and Moss 1987). On the central Great Plains, such areas have been transformed from wide, unvegetated channels (Fig. 9) to the current extensive cottonwood–willow woodlands lining narrow channels (Johnson 1994). This transformation is a result of human alteration of natural flow regimes, cessation of prairie fires, and elimination of the bison (Currier 1982). Overall, the presettlement near-river mosaic of meadow, marsh, and drier upland grassland is now an open- to

Courtesy F. L. Knopf, USGS

**Fig. 5.** Short-grass prairie in Laramie Plain, Wyoming.

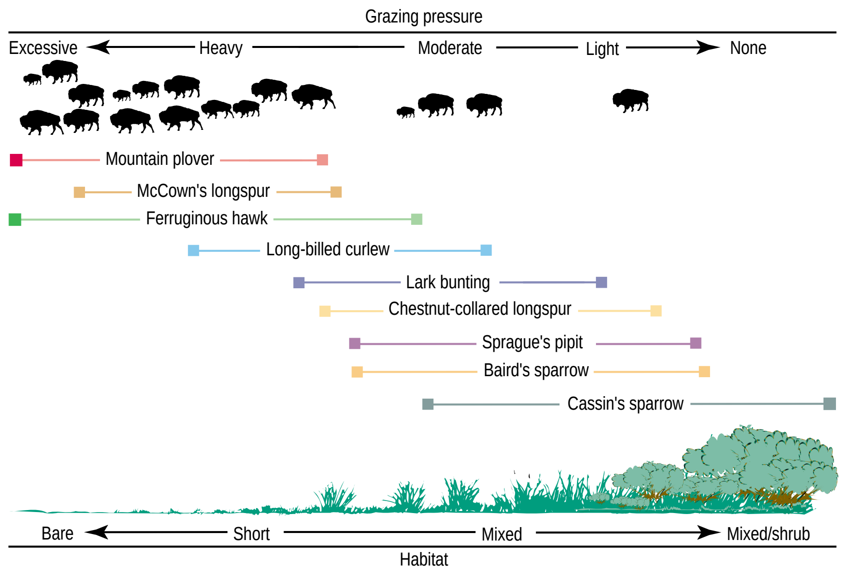


**Fig. 6.** Importance of coevolution between grazing and native prairie bird distributions and abundances (after Knopf 1996).

Courtesy USGS

**Fig. 7.** Prairie wetlands, showing the zonation of wetland plant communities.

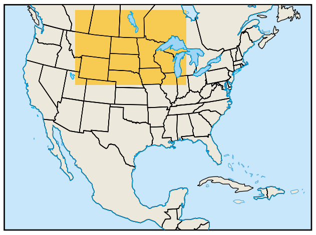

**Fig. 8.** The prairie pothole region (in green) of the northern Great Plains.

a.

Courtesy F. L. Knopf, USGS

b.

Courtesy F. L. Knopf, USGS

**Fig. 9.** a) Upper California Crossing, Oregon Trail, Fort Sedgwick (Ovid), Colorado, around 1900; b) Same locale, town of Ovid, in 1990.

closed-canopy woodland. Major changes in the habitat mosaic are expected in the future because secondary succession of woody vegetation will lead to a climax forest of regenerating stands of the nonindigenous Russian-olive along the Platte River and elsewhere across the entire central and western United States (Olson and Knopf 1986).

To the south are the Playa lakes. Upwards of 26,000 of these shallow, small wetlands dot the short-grass prairie in Texas and adjoining states, reaching northward to Colorado (Bolen et al. 1989). Because of evaporation, such lakes often are rimmed in a salty crust. Playa lakes have abundant populations of small, aquatic invertebrates (Carlander et al. 1986). At times, these lakes serve as vital waterfowl nesting and resting areas (U.S. Fish and Wildlife Service 1986) and as winter habitat for most North American sandhill cranes.

## Aquifers and Waterways

The High Plains aquifer (formerly called the Ogallala aquifer) consists of one or more geological units connected belowground under the central Great Plains. The aquifer is essential to agricultural, urban, and environmental resources, containing about 20% of the irrigated farmland in the High Plains and about 30% of the water used for irrigation (Huntzinger 1996). Precipitation is the principal source of natural groundwater recharge, but recharge can also result from seepage loss from streams and lakes. Natural discharge occurs as evaporation from plants and soils where the water table is near the surface or as seepage to springs. Over the long term, natural recharge should compensate discharge.

The development of the High Plains aquifer for irrigation (1940–1980) is evident in an average area-weighted, water-level decline of 3 meters (0.07 meters per year; Dugan et al. 1994). Declines vary with locale, exceeding 30 meters in some parts of the central and southern High Plains; 6 meters in southwestern Kansas, east-central New Mexico, and the Oklahoma and Texas panhandles; and 3 to 6 meters in northeastern Colorado, northwestern Kansas, and southwestern Nebraska. Since 1980, water levels in such areas have continued to decline but at a slower rate, the result of greater than normal precipitation (10 to 15 centimeters annually), water conservation practices (particularly minimum tillage), and reduction in irrigated land area (about 540,000 hectares, 1979 to 1991). The extreme southern plains of Texas and eastern and east-central Nebraska have experienced water-level rises of 1 to 3 meters (Dugan et al. 1994).

Agricultural use of nitrogen fertilizers is the largest source of nitrates in near-surface aquifers in the midcontinent (Koplin et al. 1994). Over 100,000 metric tons of pesticides (herbicides, insecticides, and fungicides) were applied in the midcontinent in 1991, often to control nonindigenous plants and animals. In spring and summer 1991, concentrations of several herbicides exceeded U.S. Environmental Protection Agency standards in about half of the streams sampled in the upper Missouri River basin (Huntzinger 1996). Effects of these pollutants on the quality of human life and on the integrity of the ecological community are largely unknown. The U.S. Environmental Protection Agency has initiated an effort to develop stressor information to help recognize areas where urban development, agricultural nonpoint pollution (pesticides, toxic chemicals, nutrient pollution), and agricultural development may exacerbate ecological decline.

The rivers of the Great Plains flow from west to east; extreme turbidity is the key characteristic of the larger rivers. Whereas most water in these rivers originates from western mountains, sediments originate from thunderstorm runoff on the Great Plains. In small channels, fine particles held in suspension produced quicksands, which inhibited crossings by early travelers and caused extreme turbidity during low flows. In summer, open-river water temperatures often exceed 30°C, the salinity level is high because of salt- and gypsum-laden groundwaters, rates of evaporation are high, and the flow velocity is moderate.

The larger Great Plains rivers have been subjected to dewatering for irrigation, other consumptive uses, and reservoir construction (Cross and Moss 1987). In virtually all these river systems, such dewatering has altered the timing and extent of flows, downstream temperatures, levels of dissolved nutrients, sediment transport and deposition, and the structure of plant and animal communities. Few major interior rivers still exhibit the conditions evident before agricultural development and water management had occurred.

On the Missouri River, once a free-flowing river of more than 3,700 kilometers (from Three Forks, Montana, to St. Louis, Missouri), reservoir construction in Montana, North Dakota, and South Dakota has virtually stopped sediment transport below major reservoirs, as it also has on the Platte and Kansas rivers (Huntzinger 1996). Sediment deposition is part of reservoir design but remains a maintenance concern. Because of the value of surface waters, there is increasing interstate interest in surface waters such as those of the Missouri River. Such surface waters are important to wildlife, fish, and recreation, as well as to navigation and water-supply interests that rely on reservoir resources.

Ecologically, the effect of water management reaches far to the south because sediment deposits are needed to sustain the Mississippi Delta. Unchannelized reaches of the Missouri River are near Bismarck, North Dakota and in southeastern South Dakota and northeastern Nebraska. Such reaches host a number of pearlymussel, fish, and bird species that are federally listed or are candidates for listing under the Endangered Species Act of 1973.

The basic features of most Great Plains streams, such as flow and substrate, are unknown (Matthews 1988). In general, streams in the south are characterized by irregular flow, small particle size in substrates, and a distinct wet–dry cycle. Drought may be a more extreme disturbance than either the wet–dry cycle or floods. Streams in the northern prairies are more consistent in flow and tend to have cobble substrates, and winter precipitation (snow) is released with spring thaw. Great Plains streams fall into three categories: the shallow stream with shifting sand beds; clear brooks, ponds, and marshes supported by seeps and springs; and residual pools of intermittent streams (Cross and Moss 1987). All three stream types are affected by dewatering of channels and stabilized flows.

## Soils

Grassland soils are fundamentally different from those found under a forest canopy (Simms 1988). Many factors—parent material, climate, time, and human intervention—influence grassland soil type and condition (Peterson and Cole 1996). For example, soil organic carbon, a significant influence on soil productivity, is greatest in the Northeast (cooler and wet) and lower in the Southwest (warmer and dry). Where evaporation is low, water is more likely to remain in the soil, increasing the rate of mineral weathering and allowing large amounts of nitrogen, phosphorus, and sulfur to accumulate in conjunction with carbon.

Managed agriculture began on the easternmost grasslands in the 1850's (Peterson and Cole 1996). Surface cover is reduced by agriculture, and soil structure is destabilized by reducing aggregate size—the result of mixing and grinding action by farm implements. Organic carbon loss is accelerated by agriculture, and cultivated crops (particularly in dryland areas) return little carbon to the soil. Few agricultural practices of the early settlers captured or retained moisture. The black-dust storms of the 1930's resulted from exposing vast areas of cultivated prairie soil to wind action and drought (Sampson 1981).

Several straightforward and well-documented relationships exist between plant productivity and soil organic material after native sod is cultivated. For example, soil productivity (indexed by corn grain yield) declined 71% and soil nitrogen 49% during a 28-year interval after cultivation began (Williams and Wolman 1986). Retention of organic matter—and thus the level of productivity—in grassland soils is only possible if the correct proportions of carbon, nitrogen, and phosphorus are present (Peterson and Cole 1996). Nitrogen fertilizers are used extensively to restore soil nitrogen levels, and more than 6.4 million metric tons of nitrogen fertilizers were applied to cropland in the Mississippi River basin in 1991 (Goolsby et al. 1993). In addition, removal of phosphorus in harvested plants and loss of organic phosphorus due to cultivation require fertilizer supplements to maintain productivity. Elevated concentrations of phosphorus may affect aquatic plant growth and reduce oxygen content in streams.

Soil formation is a slow, continuous process. About 2.5 centimeters of new topsoil is formed every 100 to 1,000 years, depending on climate, vegetation and other living organisms, topography, and the nature of the soil's parent material (Sampson 1981). Some soils, particularly where moisture is a limiting factor and growing seasons are short, may take 10,000 years to produce 2.5 centimeters of soil. On average, annual loss of topsoil in the United States is nearly three times greater than that being formed. Exact measurements of soil losses are difficult to obtain because soil eroded in one area is eventually deposited at another site (Peterson and Cole 1996). Smaller and lighter nutrient-rich organic soils are the most transportable, creating additional threat to the future productivity of prairie soils.

## Prairie Processes

Climate and fire (Fig. 10) are thought to be most important to the spread and maintenance of grasslands (Anderson 1990). The air mass originating in the Gulf of Mexico spreads high humidity and precipitation as it moves north. As it moves from west to east, the Pacific air mass passes over several mountain ranges, giving up most of its moisture and, as it meets the gulf air mass, creating a climate gradient across the Great Plains. The north–south gradient in temperature and moisture, largely influenced by snow cover to the north, is an effect of the polar air mass. Long-term response of vegetation to climate, particularly water availability, is illustrated by regional differences in species composition and height of native grasses: arid western short-grass prairie, central mixed-grass prairie, and eastern tall-grass prairie. As documented in past droughts, grassland distribution is controlled by extremes of climate variability. These forces are evident in the changing eastern edge of the prairie peninsula and, to a great extent, the annual productivity of grasslands.

Grassland plants have growing points protected from fire beneath the soil surface. Frequent fire is essential to maintaining native species diversity, and it affects other components, including nutrient cycling and productivity (Collins and Wallace 1990). On tall-grass prairie, the relationship between total plant species richness and the number of times a site is burned is important and positive (Collins 1991), at least on a small scale. Small animals create gaps and edges that influence tall-grass plant community structure and composition (Reichman et al. 1993). Recently burned tall-grass prairie has also provided stopover habitat for many long-distance migrant birds such as the lesser golden-plover and the now-endangered and possibly extinct Eskimo curlew. In the past, grazing was localized in these burned areas because of their greater productivity and the nutritive value of their forage (Risser 1990). Thus, the movement and impact of grazing animals on tall-grass prairie grasslands were bound to the spatial distribution of burned patches. For mixed-grass prairie, discussions of community composition and individual species should be set in a similar context of species patterns of both past grazing animals (ranging from bison to ants) and current grazing animals (domestic livestock) in relation to disturbance events (Umbanhowar 1992).

Grazing has direct and indirect effects at landscape and regional scales, which, in turn, interact with other small-scale and large-scale factors to heighten temporal and spatial diversity in grasslands (Gibson and Hulbert 1987; Risser 1990). A recent comparison of grazing over a global range of environments, however, suggests grazing is a factor in the conversion of grasslands to less desirable shrublands (Milchunas and Lauenroth 1993). Moreover, primary production on grasslands, largely the production of plant material, does not necessarily change when plant species composition changes. Current species-based management criteria by land management agencies, therefore, may lead to erroneous conclusions about the ability and future of grasslands to sustain productivity. Adequate assessment of the effects of grazing on grasslands, as with the effects of climate and fire, must be multiscaled and match management inferences and applications (Steinauer and Collins 1996).

Interactions among other factors, aside from climate, grazing, and fire, also influence grasslands (Burke et al. 1991). In the east, nitrogen normally restricts the annual production and composition of grasslands. In the semiarid west, the availability of nitrogen and water is important to composition and production. Long-term vegetative production on short-grass prairie is closely tied to precipitation (Lauenroth and Sala 1992). The most productive years are those when small precipitation events first stimulate


Courtesy F. L. Knopf, USGS

**Fig. 10.** Fire plays a major role in prairie dynamics.

nutrient availability, followed by large precipitation events that stimulate plant growth. Semiarid areas are thought of as especially variable in environmental conditions, particularly in precipitation, and the short-grass prairie is no exception. Effective grassland management requires understanding the effects of both the spatial and temporal patterns of precipitation on short-grass prairie.

In prairie wetlands, disruption of natural processes such as fire has led to domination by robust, emergent plants, particularly in the prairie pothole region. Cattail, once rare on the Great Plains, has spread across thousands of prairie wetlands, as has purple loosestrife, a species native to Europe which is now threatening waterways across the United States (U.S. Congress, Office of Technology Assessment 1993; Malecki and Blossey 1994). In the past, climate, fire, and grazing controlled the diversity and abundance of vegetation in northern prairie wetlands. As environmental conditions changed, some plant populations have declined and others have increased. Belowground seed reserves favor those species with seeds that germinate under a wide range of conditions, such as cattail, purple loosestrife, and other nonindigenous species.

More is known about the effects of grazing than fire. Nodal rooting, or underground branching, and unpalatability are evident evolutionary responses of wetland plants to grazing. Under certain conditions grazing can increase species diversity and the development of intricate patterns and sharp boundaries among prairie wetland plant communities (Bakker and Ruyter 1981).

## Plant Assemblages

The Nature Conservancy, in a preliminary survey, has identified rare plant assemblages across the United States (Grossman et al. 1994). Of the 633 assemblages in the Great Plains, 107 (17%) are considered rare (Chaplin et al. 1996).

The 16 rare Great Plains forest assemblages are largely cottonwood and oak floodplain forests on the eastern and western edges of the plains (Grossman et al. 1994). The 20 rare canyon and mountain plant assemblages tend to be open pine, fir, and oak. The eight rare sparse woodland forests are primarily oak savannas on the eastern plains. The 19 rare shrubland assemblages include many sagebrush, hawthorn, and willow species.

Among 45 rare grassland assemblages on the Great Plains, 18 are found in tall-grass prairie, 13 in mixed-grass prairie, 7 in short-grass prairie, and 7 primarily in wetlands. Big bluestem is dominant in 9 of 18 rare tall-grass prairie communities, little bluestem in 3, and drop-seed species in 2. Similarly, little bluestem is common to 6 of 13 rare mixed-grass prairie communities, and sedges are important in 3. Buffalo grass, in part, distinguishes 5 of 8 rare short-grass prairie communities, and sedges are important to 2. The 7 remaining rare communities are dominated by forbs and embrace wetland plants.

## Invertebrates

A wide diversity of terrestrial insects exists on grasslands. For example, in two years of sampling on a 1,400-hectare area of tall-grass prairie in northeastern Oklahoma, 16 orders, 131 families, and more than 3,000 insect species were noted (Risser et al. 1981). More than 1,600 insect species are known from a short-grass prairie in Colorado (Kumar et al. 1976), and this list is incomplete. Inventories are rarely representative; some taxa are present in hot, dry years, others in wet years, and no single sampling method is adequate.

Other terrestrial invertebrates are also abundant. Smolik (1974) found 2 to 6 million soil nematodes per square meter to the depth of 60 centimeters in South Dakota mixed-grass prairie soil. Terrestrial invertebrates are important to the prairie community: they feed on plant tissue, pollen, nectar, and seeds; regulate numbers of other insects and plants; and recycle energy and nutrients (Risser et al. 1981). Underground, earthworms accelerate the decomposition and mineralization of soil organic matter and affect soil structure through burrowing and casting. The soil formation activities of native and nonindigenous earthworms vary considerably; the latter have a negative effect on soil turnover, at least in tall-grass prairie soils (James 1991). Nevertheless, in short-grass prairie soils, 90% of invertebrate energy cycling occurs belowground, less in tall-grass and mixed-grass prairies.

Preliminary lists of Lepidoptera (butterflies and moths) are available for Montana, North Dakota, Wyoming, Colorado, and New Mexico and are in progress in Texas (Powell 1995). Species numbers in a few selected Lepidoptera families vary from 181 in North Dakota to 520 in Texas, and numbers in Nebraska (254) and Oklahoma (228) rank high (Opler 1995). Several prairie butterflies—the Dakota skipper (Fig. 11), regal fritillary, tawny crescent, and

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**Fig. 11.** The Dakota skipper, a rare prairie butterfly.

# Tall-grass Prairie Butterflies and Birds

The destruction and degradation of North American prairie habitats, especially in the eastern tall-grass region, have considerably reduced the abundance of associated animals. The species most affected are those restricted to remaining prairie fragments. Prairie birds and butterflies often have specific habitat requirements, and reduction of the tall-grass prairie has caused serious declines in their populations. Because some species of prairie sparrows and butterflies have similar habitat requirements, trends in their populations are sometimes correlated.

## Prairie Sparrows

In eastern and central North America, birds nesting in grasslands and ground-nesting birds have declined more than birds of any other North American behavioral or ecological guild (Knopf 1994). Data from the U.S. Geological Survey Breeding Bird Survey illustrate that, between 1966 and 1993, Henslow's sparrows have declined 91% rangewide, grasshopper sparrows have been reduced by 66%, and dickcissels by 39% (Fig. 1). Henslow's sparrows and grasshopper sparrows are among the fastest declining North American songbirds (Peterjohn et al. 1994). The Henslow's sparrow has more specialized habitat and management needs (Kahl et al. 1985; Zimmerman 1988; Smith and Smith 1992) than the other two species. The grasshopper sparrow, which is rarer and declining more rapidly than the dickcissel, seems to be the more sensitive of the two species to habitat changes and management methods (Skinner et al. 1984; Smith and Smith 1992; Zimmerman 1992).

Records indicate that these sparrows had declined considerably even before the Breeding Bird Survey began. Nineteenth-century sources summarized by Herkert (1994) reveal that Henslow's sparrow was at that time one of the most abundant birds in Illinois. Much of the Henslow's sparrow population losses actually occurred decades before Breeding Bird Survey monitoring began (Graber and Graber 1963; Herkert 1994), with a decline of 90% occurring between 1958 and 1979 in Illinois (Illinois Natural History Survey 1983). These three sparrow species have all undergone long-term range reductions in the eastern parts of their breeding ranges (Fretwell 1973; Smith and Smith 1992). The range of Henslow's sparrow is also contracting from the north (McNicholl 1988), and numerous local populations have disappeared in recent decades (Hands et al. 1989; Illinois Natural History Survey 1983).

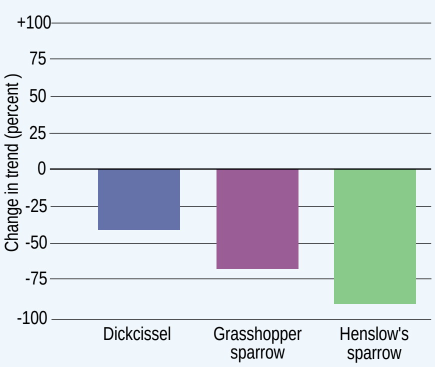


**Fig. 1.** Percent decline of three grassland sparrows in the U.S. Geological Survey Breeding Bird Survey between 1966 and 1993 (Peterjohn et al. 1994).

## Prairie Butterflies

No long-term monitoring program comparable to the Breeding Bird Survey is available for butterflies, and population dynamics are not as well documented for prairie butterflies as for birds. However, butterflies requiring prairie habitat have clearly experienced long-term declines, both along the fringes of their core ranges in the central United States and within the prairie province. The extinction wave of the regal fritillary (Fig. 2) from east to west and the species' increasingly localized occurrence within the prairie region are well documented (Swengel 1993). The Dakota skipper and the Poweshiek skipperling (Fig. 3) have also become more localized and restricted to prairie fragments (Opler and Krizek 1984; Johnson 1986).

Although declining grassland birds and prairie-specialist butterflies share the same habitats, their abundances are not necessarily correlated, in part due to differences in the geographic scales of their habitat use. For example, Henslow's sparrows and grasshopper sparrows are short-distance migrants, wintering primarily in the southern United States, while dickcissels winter mostly in northern South America (Fretwell 1973). Prairie-specialist butterflies are year-round residents on particular prairie patches, with relatively little dispersal among patches (Opler 1981; Opler and Krizek 1984; Moffat and McPhillips 1993). Although birds depend upon suitable habitat and resources being available at seasonally appropriate times in widely distributed regions, butterflies need resources and conditions to be consistently available within a particular habitat patch.

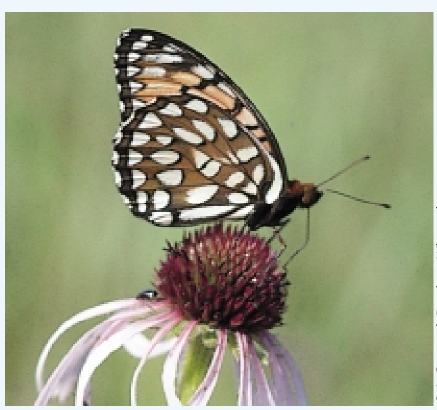

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**Fig. 2.** Regal fritillary on a purple coneflower.

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**Fig. 3.** Poweshiek skipperling.

Key habitat features and required resources differ between birds and butterflies. Both butterflies and birds show preferences for either wet lowlands or dry upland habitats; however, vegetational structure is particularly important only to birds (Hopkins 1991). Henslow's sparrow prefers large grassland expanses with consistent patches of dense cover provided by dead vegetation, whereas grasshopper sparrows favor shorter, more open vegetation with sparse cover (Kahl et al. 1985). Butterflies often have specific associations with plant species, especially in the larval life stage (for example, larval food plants), and as adults they show some degree of preference for certain nectar flowers (Opler 1981; Opler and Krizek 1984).

It may be difficult to census butterfly and bird populations in the same survey because of their differing daily and seasonal activity patterns. Songbirds are active early and late in the day, a pattern that is weak or lacking in most grassland birds (Kantrud 1981).

Butterflies tend to be more active in the warmer and sunnier parts of the day (Opler and Krizek 1984). Songbirds are more detectable during the breeding season in late spring to early summer, when they vocalize more. Butterflies are easier to see during their adult life stage, the timing of which varies considerably by species (Opler and Krizek 1984).

## Population Trends

Despite the difficulties associated with simultaneous surveys of grassland birds and butterflies, some covariances are apparent between populations of the two groups (Fig. 4). In our study, prairie-specialist butterfly species were more strongly correlated with grassland sparrows than with butterflies less restricted in habitat. The regal fritillary, the most widely occurring prairie-specialist butterfly, showed the most consistent co-occurrence with grassland sparrows.

Prairie birds and butterflies present both conservation concerns and opportunities for preservation. Though their populations have been much reduced through habitat loss, no known species of prairie-specialist butterfly or North American grassland sparrow has yet become extinct. Conservation activities that are effective at maintaining one prairie species may confer benefits to others. For example, in southwestern Missouri, prairie conservation management rotates midsummer haying (annually to triennially, though usually biennially) to benefit the greater prairie-chicken (Solecki and Toney 1986). This rotated haying also supports large populations of prairie-specialist butterflies (Swengel 1996) and grassland sparrows (Skinner et al. 1984). Grassland birds and butterflies also benefit from nonintensive grazing and hay-cutting regimes (Skinner 1975; Kantrud 1981; Smith and Smith 1992; Swengel 1996), and birds particularly benefit from idling of croplands, as in the United States Conservation Reserve Program, which rewards farmers for tilling a smaller percentage of their land (Johnson and Schwartz 1993).

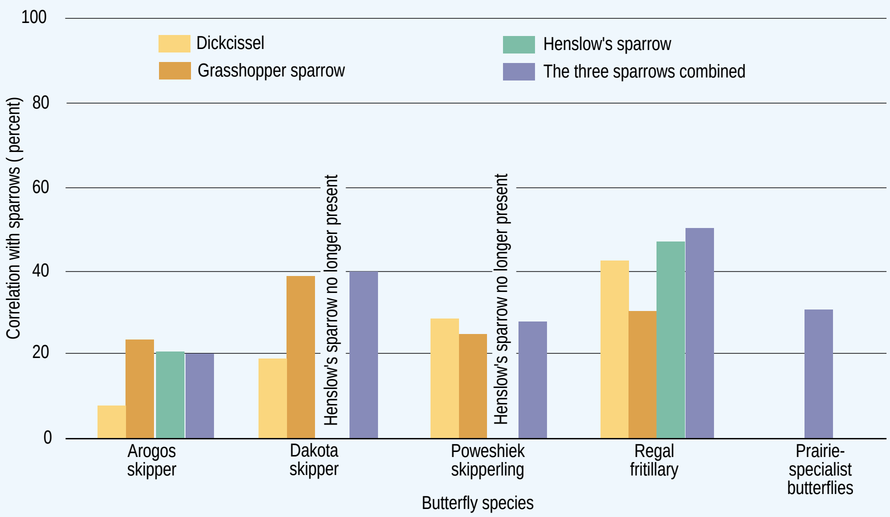


**Fig. 4.** Percent correlation in abundance between species pairs. A 100% correlation indicates a total correspondence in abundance patterns; 0% correlation indicates a complete noncorrespondence in abundance patterns. Percentages are based on Pearson's product-moment correlations of log-transformed observations of each species per hour per survey, in surveys from mid-June to 31 July 1988–1995 at 104 prairie sites in Illinois, Iowa, Minnesota, Missouri, and Wisconsin (methods described in Swengel 1996). Although Henslow's sparrows historically occurred at sites in the range of the Dakota skipper and the Poweshiek skipperling, they do not occur at these sites today.

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maculated manfreda skipper—and two moths—the rattlesnake-master borer moth and phlox moth—are federal species of concern. An additional six insects—the persius duskywing, poweshiek skipperling, ottoe skipper, byssus skipper, silver-bordered fritillary, and Ozark emerald—are considered species of concern by The Nature Conservancy, and another six are endemic to the prairie (Royer 1992).

Adequate inventory and distribution information is unavailable for predicting status and trends for most invertebrates. Ranges of a number of grasshopper species seem focused specifically on short-grass, a combination of short-grass and mixed-grass, and tall-grass prairies (Otte 1981). Ranges of many other grasshopper species center on grasslands but extend into adjacent forested and scrub habitats. The prairie mole cricket, a strikingly large insect (Fig. 12), and the superb spharagemon grasshopper are federal species of concern. Additional species of concern are the Ozark snaketail dragonfly, a true bug, a fly, six amphipods, nine cave spiders, two cave beetles, a cave amphipod, a cave shrimp, and a number of beetles, including the widely distributed sixbanded longhorn beetle.

Leafhoppers are among the most diverse and well-studied terrestrial insects on the grasslands (Whitcomb et al. 1994). The ranges of some species span considerable distances across the

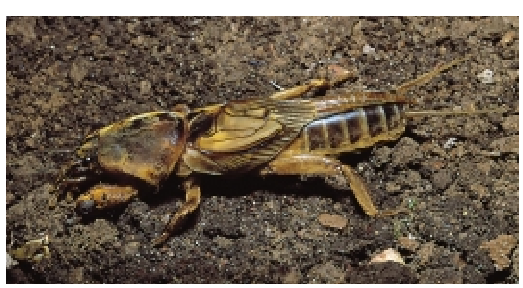

**Fig. 12.** The prairie mole cricket, an unusual and rare prairie species.

prairie, whereas other species are more restricted in distribution. Most are highly specialized, often endemic, and good indicators of grassland condition. On the short-grass prairie, 20 leafhopper species may colonize a single host, such as blue grama, which indicates a long record of coevolution. There is, however, a rather spectacular partitioning of resources: no more than 10 leafhopper species occur on the blue grama host at a given site. The "invisible wall" partitioning resources is climate, with each taxon showing singular limits to humidity, cold, and heat. Understanding any single assemblage of leafhoppers (and perhaps most other insects) requires knowledge of the communities in which they and their relatives reside and of the past structure and conditions of these communities.

Around 1889 abundant mussel populations of the Great Plains were recognized as an economic resource, particularly as the materials for button production. One example of the abundancy of this resource was a single mussel bed that covered an area of 2.4 kilometers by 288 meters in the Mississippi River near New Boston, Illinois (Carlander et al. 1986). The mussel bed was depleted by 1898, and large-scale propagation to restore the resource failed. No federal regulations restrict the harvest of mussels unless they are federally listed as endangered or threatened. Many states (Illinois, Iowa, Kansas, Minnesota, Missouri, Montana, Nebraska, North Dakota, Oklahoma, South Dakota, and Texas), however, have instituted harvest regulations.

Along with siltation and contamination, dams, with their altered flow regimes and accompanying reservoirs, are believed to have caused declines of mussels and other aquatic organisms. Four pearlymussels—the elktoe, spectacle-case, snuffbox, and scaleshell—are federal species of concern. The American Fisheries Society has identified 213 of 297 (71.7%) mussels found in the United States and Canada as threatened, endangered, or of special concern (Williams et al. 1993). Many of these species are endemic; for example, all three endangered and six threatened species, and about one-third (two of seven) of the mussels of special concern recently added by the American Fisheries Society list for Texas are species with restricted ranges. Several nonindigenous species, particularly the Asian clam and the zebra mussel, pose potential threats to the native mussel fauna on the Great Plains.

Across the grasslands, a number of snails, including both land and aquatic species, are federal species of concern: 10 are found in Texas, at least 8 in the upper Midwest (Illinois, Iowa, Minnesota), 5 in the central plains (Missouri and Oklahoma), and 3 in the West (Wyoming and the Dakotas). One snail, the Iowa Pleistocene snail, is listed as endangered. The same factors negatively affecting other species—habitat loss, drainage, water pollution, stream desiccation accompanying the lowering of water tables for agriculture and municipalities, and competition with and predation by introduced species—are thought to threaten freshwater native snails, crayfishes, and other aquatic invertebrates.

## Fishes

In general, drainages east of the Rocky Mountains have a richer fish fauna than those to the west (Brooks and McLennan 1993). The western Mississippi basin occupies much of the grasslands, including the basins of the Missouri, Arkansas, and Red rivers. Geological and pre-settlement history and current information depict changing fish distributions and abundances across this vast region (Cross et al. 1986). Geological information provides insights into how glacial advances fragmented fish populations into smaller, subregional distributions and transported species to distant and distinct drainages. Government surveys seeking routes for human immigrants to the Southwest and Pacific coast provide important historical information. Recent concern for prairie (and other) fishes has encouraged the continuation of many ongoing surveys.

The western Mississippi basin contains at least 266 species of fishes from the United States, which is slightly more than one-third of the fish species in the United States and Canada (Cross et al. 1986). Thirty-one species were introduced to North America or now exist beyond their past ranges. Two species are diadromous (and thus reside at some time in their life cycles in marine waters), and 34 are endemic to one or more drainages in the vast basin.

Cross et al. (1986) described two physiographic regions that encompass the habitat of most fishes on the grasslands: the Great Plains, from eastern Montana south to western Texas, and the Central Lowlands, from North Dakota south to eastern Texas. Thirteen fishes are endemic to the two physiographic regions: 2 to the Central Lowlands, and 11 to the Great Plains. The Great Plains province has 77 fish species (86 including introduced species), that, with the exception of 5 species, are a subset of the Central Lowlands fish assemblage. The Central Lowlands has 139 native species with over 24 species introduced into the region, most intentionally as sport fish or forage for sport fish. Eleven grassland fishes are large-river species that have centers of origin in one or two adjacent physiographic regions but are shared among the Central Lowlands and Great Plains physiographic regions. Overall, the species inhabiting small streams and rivers outnumber those in large rivers about ten to one.

Decades of intensive agricultural development and modified flow regimes are held responsible for declines in the fishes endemic to the small streams and turbid rivers of the Great Plains (Cross and Moss 1987). Nevertheless, the first declines noted in regional endemic fishes were in those species in small, clear, spring-fed streams, particularly streams that were home to the Topeka shiner and Arkansas darter. Although agriculture and altered flow regimes may explain declines, patterns in decline differ among species, with colonization of suitable habitat of restricted stream and river reaches exceptionally rare. Several fish species of shifting-sand bottom streams in the Great Plains are considered federal species of concern, including the sicklefin chub, the sturgeon chub, the Arkansas River speckled chub (a subspecies of the speckled chub), and the Arkansas River shiner. The Topeka shiner, the plains topminnow, and the Arkansas darter, which occur in clear streams fed by springs and seeps, and the lake sturgeon are also candidates for species of concern (Echelle et al. 1995).

Overall, 9 of 10 species and subspecies of broad, shallow, and sandy-bottom streams seem to be in serious decline. Two additional species, the plains minnow and flathead chub, seem to be drastically declining (V. M. Tabor, U.S. Fish and Wildlife Service, Manhattan, Kansas, unpublished manuscript) and are candidates for federal listing. Marked increases are known in some fishes in the natural prairie community. Clear-water fishes, particularly sunfish, perch, and introduced species such as carps, replace species native to turbid conditions and tend to be increasing. Within the Missouri River drainage, the upper Missouri and Yellowstone rivers provide the best remaining habitat for the large-river natives. About 20% of the native large-river fish species are declining.

## Reptiles and Amphibians

Most grassland reptiles and amphibians are widely distributed. Half of the species (6 of 12) found in Alberta also occur several hundred kilometers to the south in northern Mexico (N. J. Scott, Jr., U.S. Geological Survey, San Simeon, California, unpublished manuscript). More than 40 reptiles and amphibians are characteristic of prairie habitat (Table 2). The number of local species is influenced by the presence of water (which amphibians need to complete their life cycle), complex habitats, and sandy or loose soils needed for concealment by some species.

**Table 2.** Reptiles and amphibians of the North American prairie by habitat association (N. J. Scott, Jr., U.S. Geological Survey, San Simeon, California, unpublished manuscript).

| Habitat | Species |
|---|---|
| Grassland | Ornate box turtle |
| | Great Plains skink |
| | Prairie skink |
| | Western slender glass lizard |
| | Racer |
| | Western rattlesnake |
| | Night snake |
| | Prairie kingsnake |
| | Texas slender blind snake |
| | Massasauga (rattlesnake) |
| | Lined snake |
| Temporary water | Wyoming toad |
| | Great Plains narrow-mouthed red toad |
| | Spotted chorus frog |
| | Plains leopard frog |
| | Yellow mud turtle |
| | Plains garter snake |
| | Common garter snake |
| | Checkered garter snake |
| Bare ground | Lesser earless lizard |
| | Texas horned lizard |
| | Coachwhip |
| | Six-lined racerunner |
| Bare ground and water | Great Plains toad |
| | Green toad |
| | Plains spadefoot toad |
| | Black-spotted newt |
| Sandy soils | Glossy snake |
| | Western hog-nosed snake |
| Sandy soils and water | Woodhouse's toad |
| Trees or rocks | Reticulate collared lizard |
| | Spot-tailed earless lizard |
| | Collared lizard |
| | Eastern fence lizard |
| | Great Plains rat snake |
| | Plains black-headed snake |
| | Milk snake |
| Rocky canyons and water | Red-spotted toad |
| | Spiny softshell |
| | Plain-bellied water snake |
| | Diamondback water snake |
| | Slider |

Loss of small water areas, nonindigenous terrestrial and aquatic predators, grazing, exotic plantings, and prairie dog control are believed to contribute to reptile and amphibian declines. Most reptiles and amphibians rely on temporary ponds rather than streams or rivers. Permanent water provides habitat for the especially predatory bullfrog, catfish, and sunfish. Woody vegetation near permanent water favors mammalian predators such as the Virginia opossum, raccoon, and skunk (Schwalbe and Rosen 1989). Moderate grazing increases habitat structure and patchiness important to reptile and amphibian abundance, but overgrazing reduces needed habitats, as does planting of nonindigenous species such as buffel grass (Scott 1997). Prairie dog burrows provide winter retreats and summer nesting sites for reptiles and amphibians, thus their destruction may cause local reptile and amphibian declines.

Most grassland reptiles and amphibians seem widespread and secure. Several, however, particularly those with very restricted ranges, are thought to be declining. Habitat for the

# Amphibians of the Northern Grasslands

## What Do We Know?

No cry of alarm has been sounded over the fate of amphibian populations in the northern grasslands of North America, yet huge percentages of prairie wetland habitat have been lost, and the destruction continues. Scarcely 30% of the original mixed-grass prairie remains in Nebraska, South Dakota, and North Dakota (See Table 1 in this chapter). If amphibian populations haven't declined, why haven't they? Or, have we simply failed to notice?

Amphibians in the northern grasslands evolved in a boom-or-bust environment: species that were unable to survive droughts lasting for years died out long before humans were around to count them. Species we find today are expert at seizing the rare, wet moment to rebuild their populations in preparation for the next dry season. When numbers can change so rapidly, who can say if a species is rare or common? A lot depends on when you look.

Some changes brought upon the northern Great Plains by human enterprise mimic this climatically induced variability. Frogs, toads, and salamanders that find themselves in a rare remaining wetland will thrive. Progeny will issue forth from the wetland in comfortingly large numbers, and those that return to breed the next year will be rewarded with a reasonable likelihood of success. Those that strike out for new breeding territory, as some percentage must, will likely be less fortunate but also less conspicuous: who searches wheat fields for the frog that didn't make it?

Other changes have no precedent. Aquaculture—which involves modifying the water regime in a previously semipermanent wetland so that it can support stocked fish populations—brings vulnerable larval amphibians into contact with predators against which they have no defense. In addition to supporting stocked fish, these modified wetlands provide new habitat for predatory bullfrog larvae that require two years of stable water to mature. As predatory species take hold, native amphibians die out (Hayes and Jennings 1986).

One way to decide if amphibian populations are changing is to conduct surveys in areas that were studied long ago. Often past data were collected as an offshoot of a detailed study of a particular species. The danger here is that the past data were probably collected at the very best sites investigators could find; populations at these sites are far more likely to decline than to increase, simply as a result of natural fluctuations (Johnson and Larson 1994). Nonetheless, it is possible to find past surveys (as opposed to ancillary species lists), and comparisons between current and former occurrences are, at the least, instructive.

Another method of assessing the stability of amphibian populations is to enlist volunteers in broad-scale monitoring programs, similar to the well-known U.S. Geological Survey Breeding Bird Survey. The North American Amphibian Monitoring Program, administered through the U.S. Geological Survey Biological Resources Division's Inventory and Monitoring Program, aims to do just that. Volunteers are being mobilized to conduct surveys of calling frogs and toads on carefully selected routes that will stand up to statistical scrutiny. Such a program could prove especially valuable for the northern Great Plains, where relatively few species are silent (tiger salamanders, skinks, and mudpuppies) and thus uncountable. After a reasonable number of years, such surveys will yield valuable information to help us distinguish between natural year-to-year fluctuation and real changes in population sizes.

## Two Case Studies

### Amphibians at the Cottonwood Lake Study Area

The Cottonwood Lake Study Area is a 49-hectare complex of 17 wetlands in the mixed-grass prairie of central North Dakota. We have monitored adult and larval amphibians there by using drift fences, pitfall traps, and aquatic funnel traps since the spring of 1992. Several noteworthy changes have occurred.

We have observed only four amphibian species at Cottonwood Lake: the gray tiger salamander, the striped chorus frog, the wood frog, and the northern leopard frog. Only tiger salamanders and chorus frogs have been common. Toads have been noticeably absent in our study. Although four species of toads are known to occur in the region (the American toad, the Canadian toad, the Great Plains toad, and Woodhouse's toad), we have not captured or observed a single individual of any toad species since monitoring began in 1992.

The dynamic nature of the Great Plains is well illustrated at Cottonwood Lake. In 1992, water levels were the lowest since record-keeping began in 1967, then record precipitation in 1993 and 1994 resulted in the highest water levels ever recorded at the study area. Tiger salamanders have responded accordingly: in 1992, we captured only 32 individuals; with the progressive return of water to wetlands, the number of captures jumped to 567 in 1993, 1,270 in 1994, and 2,862 in 1995. As water levels in wetlands have become more stable, tiger salamander larvae have begun to successfully overwinter. Throughout all of 1992, 1993, and 1994, only two overwintered salamander larvae were captured during our spring sampling (both in 1994); in 1995, we captured 50.

Striped chorus frog numbers also increased at Cottonwood Lake, but not until 1994. We captured only eight chorus frogs in our funnel traps in 1993. Captures increased to more than 300 in both 1994 and 1995.

Although leopard frogs are reported as abundant throughout the prairie pothole region, we have captured only 13 in our funnel traps (3 in 1993 and 10 in 1995). All 13 were adults, and all were captured in late summer, suggesting that they were newly metamorphosed individuals dispersing into the study area from surrounding wetlands. To date, we have observed no evidence of the reestablishment of a resident leopard frog population at Cottonwood Lake.

Wood frogs have been, and continue to be, captured in very small numbers at Cottonwood Lake. We captured three individuals in our funnel traps in 1992, two in 1993, three in 1994, and only one in 1995. The absence of an increase in wood frog numbers during this period of increasing water levels suggests that drought is not a key factor limiting wood frog populations.

### Prairie Pothole Amphibians: Changes Since the 1920's

In the summer of 1920, Frank Blanchard visited the Iowa Lakeside Laboratory in Dickinson County in northwestern Iowa, where he conducted what may have been the earliest study of prairie pothole amphibian populations. His expressed purpose was to provide baseline data for future herpetological surveys: "It is highly important that faunistic studies be undertaken here, and throughout our country, at as early a date as possible if we are to have any record of the composition and distribution of our native fauna, and if we are to deal intelligently with its preservation" (Blanchard 1923).

We repeated Blanchard's survey (Lannoo et al. 1994) and recorded the current amphibian diversity and relative abundance in Dickinson County. In addition to Blanchard's results, we relied on two locally written natural history accounts to determine the changes in amphibian populations. The first account (Anonymous 1907) estimated the number of northern leopard frogs taken from the region by commercial hunters. The second account (Barrett 1964) is a reminiscence about this early 1900's "frogging" industry in Dickinson County. These two accounts, while anecdotal, provide independent observations of the same hunting events and corroborate each other.

Five species reported by Blanchard persist: eastern tiger salamander, American toad, striped chorus frog, gray treefrog, and northern leopard frog. Two species reported by Blanchard were not found: mudpuppy and Blanchard's cricket frog. We collected two species not found by Blanchard: Great Plains toad and bullfrog. Great Plains toads may have migrated into Dickinson County from the west. Bailey and Bailey (1941) found Great Plains toads only west of Dickinson County; by 1984, Reeves (1984) found them east of Dickinson County. Together, these results suggest that between the early 1940's and the early 1980's, the Great Plains toad may have expanded its range eastward and entered Dickinson County. The bullfrog was introduced by state fisheries biologists.

Several changes have occurred in the relative abundances of amphibian species since 1920. American toads and striped chorus frogs now rank higher in relative abundance; tiger salamanders now rank lower. Blanchard (1923) stated that nearly every wetland he sampled had tiger salamander larvae. Today, only 13 out of 32 wetlands contain tiger salamanders. One cause for concern over this decline is that Dickinson County tiger salamanders, unlike any other known population of the eastern tiger salamander, have larvae that are polymorphic (that is, they exist in different forms), exhibiting typical, cannibal, and intermediate physical forms.

From descriptions of the commercial frogging industry in Dickinson County at the turn of the century, we estimate that the number of leopard frogs has declined by at least two—and probably three—orders of magnitude. This decline may be due more to the loss of wetland habitat than to past hunting pressure. In our opinion, the most immediate threat to the existing populations of native amphibians in northwestern Iowa comes from the introduced bullfrog, although aquacultural practices have been important in eliminating and isolating amphibian habitat in other portions of the eastern prairie pothole region.

***See end of chapter for references***

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reticulate collared lizard and spot-tailed earless lizard, species restricted to south Texas, is threatened by exotic buffelgrass (Scott 1997). Agriculture in the Lower Rio Grande valley in Texas has reduced the number of temporary ponds, which are needed by the black-spotted newt. Pesticides may negatively affect the Wyoming toad, an endangered species, but conclusive evidence is lacking. Across its range, the yellow mud turtle, a federal species of concern, is restricted to a few widely distributed ponds (Dodd 1983).

## Birds

Of the 435 bird species that breed in the United States, 330 breed on the Great Plains (Knopf and Samson 1995). Nevertheless, few North American bird species are believed to have evolved within the Great Plains. Mengel (1970) suggested that only 12 bird species are endemic to the grasslands. An additional 25 species are believed to have evolved on the grassland, though they range widely into adjoining vegetation provinces. Five of these 25 species are specifically associates of sagebrush landscapes of the Great Basin (Knopf and Samson 1995).

As a group, the endemic grassland bird species have shown more consistent, widespread, and steeper declines (Table 3) than any other guild of North American bird species

**Table 3.** Birds of the North American grassland with annual rates of change in populations. U.S. Geological Survey (Breeding Bird Survey data 1966–1993; Knopf 1986).

| Species | Rate of change |
|---|---|
| **Endemic species** | |
| Ferruginous hawk | +1.6% |
| Mountain plover | -3.7% |
| Long-billed curlew | -1.7% |
| Marbled godwit | +0.8% |
| Wilson's phalarope | -0.1% |
| Franklin's gull | -0.9% |
| Sprague's pipit | -3.6% |
| Lark bunting | -2.1% |
| Baird's sparrow | -1.8% |
| Cassin's sparrow | -2.5% |
| McCown's longspur | +7.3% |
| Chestnut-collared longspur | +0.4% |
| **Secondary species** | |
| Mississippi kite | +0.9% |
| Swainson's hawk | +1.4% |
| Northern harrier | -0.4% |
| Prairie falcon | +0.3% |
| Greater prairie-chicken | -6.9% |
| Lesser prairie-chicken | N/A[a] |
| Sharp-tailed grouse | +1.1% |
| Upland sandpiper | +2.7% |
| Burrowing owl | -0.2% |
| Short-eared owl | -0.6% |
| Horned lark | -0.7% |
| Eastern meadowlark | -2.3% |
| Western meadowlark | -0.5% |
| Dickcissel | -1.6% |
| Savannah sparrow | -0.5% |
| Grasshopper sparrow | -4.1% |
| Henslow's sparrow | -5.0% |
| Vesper sparrow | -0.3% |
| Lark sparrow | -3.5% |
| Clay-colored sparrow | -1.2% |

[a] N/A means sampling effort was inadequate.


Courtesy F. L. Knopf, USGS

**Fig. 13.** A mountain plover, an endemic bird species of the short-grass prairie that evolved with intensive grazing pressure from bison, pronghorn, and prairie dogs in Colorado.

(Knopf 1992, 1996). Individually, populations of the mountain plover (Figs. 13 and 14a), Cassin's sparrow (Fig. 14b), and clay-colored sparrow (Fig. 14c) are declining throughout their breeding ranges. Breeding habitats are disappearing locally for the Franklin's gull (Fig. 14d), the dickcissel (Fig. 14e), the Henslow's sparrow (Fig. 14f), the grasshopper sparrow (Fig. 14g), and the western meadowlark (Fig. 14h). Breeding ranges are shifting for the ferruginous hawk (Fig. 14i), the Mississippi kite (Fig. 14j), the upland sandpiper (Fig. 14k), the horned lark, the vesper sparrow, the savannah

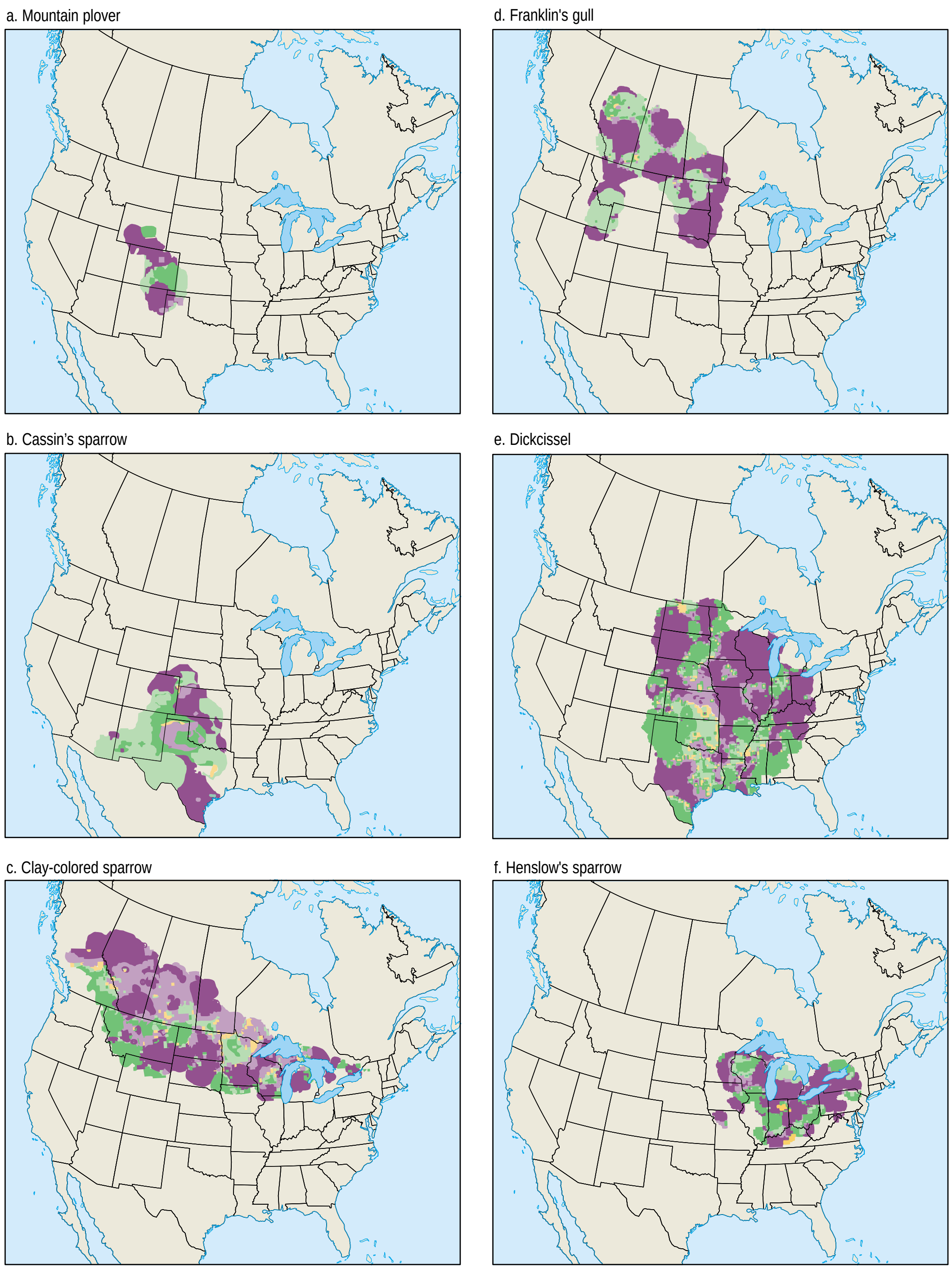


**Fig. 14.** Distribution and trends of selected grassland bird species in the United States and Canada.

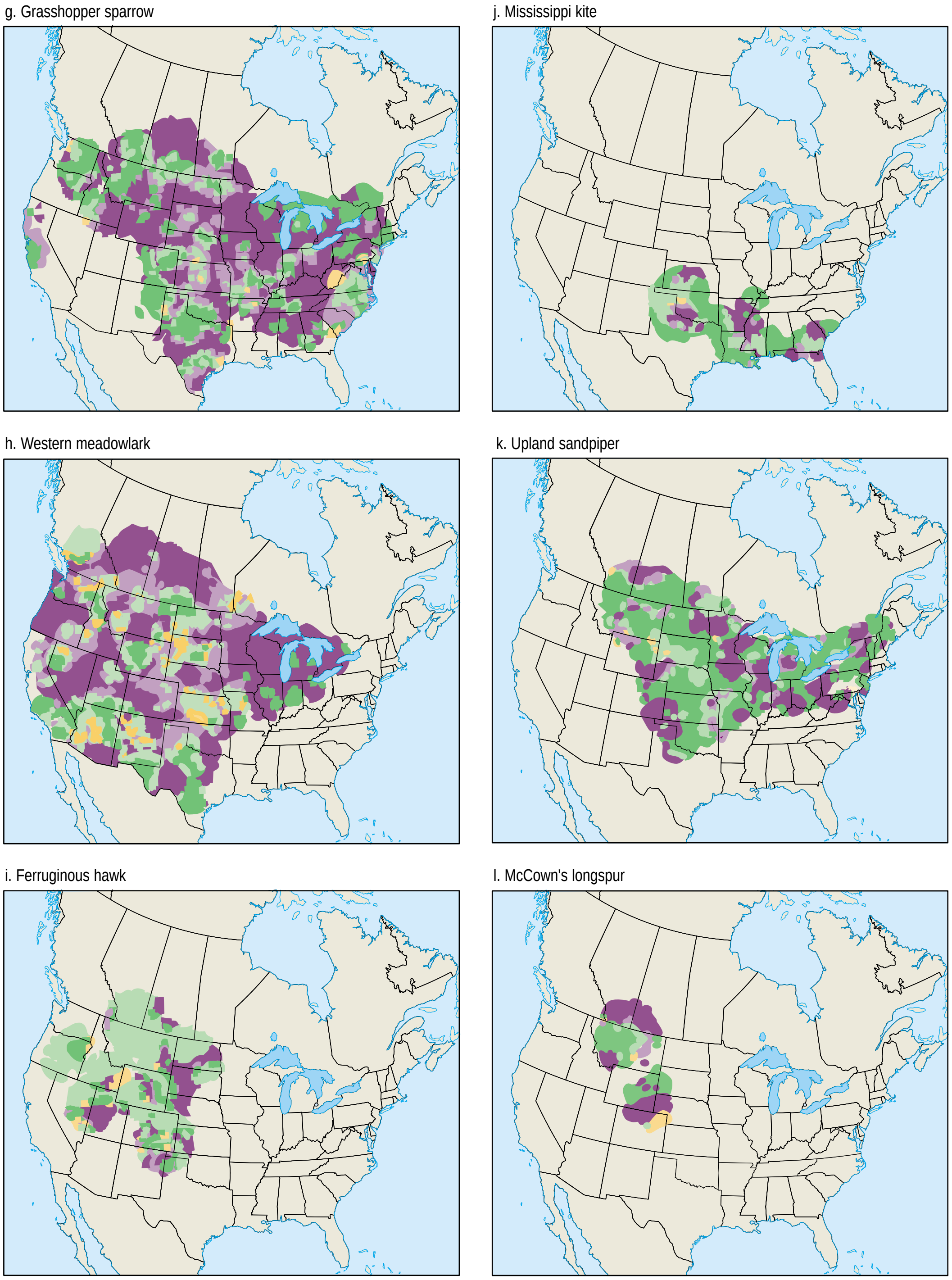


**Fig. 14.** continued.

sparrow, and the Henslow's sparrow. Populations of the wetland-associated marbled godwit and Wilson's phalarope seem stable, and populations of the upland sandpiper and McCown's longspur (Fig. 14l) have increased markedly.

Most of the endemic bird species of the short-grass and mixed-grass prairies are associated with large grazing animals (Fig. 15); others, such as the ferruginous hawk, prairie falcon, and burrowing owl, are either somewhat or strongly associated with prairie dog colonies.

Courtesy F. L. Knopf, USGS

**Fig. 15.** A bison herd in southwestern South Dakota.

# Wetland Birds in the Northern Great Plains

When the Wisconsin glacier retreated about 10,000 years ago, it left innumerable depressions scattered throughout the northern Great Plains. These depressional wetlands, called *prairie potholes*, contain water for various lengths of time in most years (Kantrud et al. 1989). Their size, permanence, hydrology, water chemistry, plant associations, and invertebrate communities vary widely among wetlands and, within a basin, through time (Cowardin et al. 1979).

These diverse wetlands support a breeding avifauna as rich and varied as the wetlands themselves. Johnsgard (1979) listed 72 breeding bird species associated with freshwater pond environments in the Great Plains. Other species, such as the northern harrier, marbled godwit, Le Conte's sparrow, and Nelson's sharp-tailed sparrow, are associated with grasslands but extensively use these prairie wetlands. Stewart (1975) identified 63 breeding bird species as wetland associates in North Dakota alone. Since 1975, several species could be added to Stewart's list (Faanes and Stewart 1982), including the reintroduced Canada goose (Lee et al. 1989) and several herons, egrets, and ibises that have expanded their breeding range into the state (Lokemoen 1979). Most wetland birds are short-distance migrants, wintering primarily north of the United States–Mexico border (Igl and Johnson 1995).

**Table 2.** Breeding bird populations in North Dakota: numbers in 128 randomly selected quarter-sections and statewide population estimates, 1967 and 1992–1993.

| Species | Number of breeding pairs | | | Population estimate | |
|---|---|---|---|---|---|
| | 1967 | 1992 | 1993 | 1967 | 1992–1993 |
| Pied-billed grebe | 11 | 4 | 7 | 24,000 | 12,000 |
| Horned grebe | 2 | 1 | 0 | 4,000 | 1,000 |
| Red-necked grebe | 0 | 1 | 1 | 0 | 2,000 |
| Eared grebe | 40 | 48 | 22 | 90,000 | 78,000 |
| Western grebe | 0 | 2 | 1 | 0 | 3,000 |
| American white pelican | 0 | 0 | 2 | 0 | 2,000 |
| Double-crested cormorant | 0 | 1 | 10 | 0 | 12,000 |
| American bittern | 9 | 2 | 8 | 19,000 | 10,000 |
| Great blue heron | 2 | 1 | 3 | 4,000 | 4,000 |
| Black-crowned night-heron | 17 | 5 | 5 | 37,000 | 11,000 |
| Northern harrier | 15 | 21 | 34 | 33,000 | 60,000 |
| Yellow rail | 0 | 1 | 0 | 0 | 1,000 |
| Virginia rail | 3 | 5 | 2 | 7,000 | 8,000 |
| Sora | 32 | 41 | 78 | 68,000 | 128,000 |
| American coot | 348 | 76 | 124 | 761,000 | 220,000 |
| Piping plover | 5 | 2 | 1 | 11,000 | 3,000 |
| Killdeer | 105 | 112 | 142 | 227,000 | 280,000 |
| American avocet | 14 | 6 | 13 | 31,000 | 21,000 |
| Willet | 18 | 16 | 27 | 39,000 | 48,000 |
| Spotted sandpiper | 12 | 12 | 9 | 26,000 | 22,000 |
| Marbled godwit | 17 | 8 | 14 | 37,000 | 24,000 |
| Common snipe | 0 | 2 | 7 | 0 | 10,000 |
| Wilson's phalarope | 73 | 30 | 36 | 157,000 | 72,000 |
| Franklin's gull | 22 | 79 | 56 | 48,000 | 148,000 |
| Ring-billed gull | 1 | 49 | 11 | 2,000 | 65,000 |
| California gull | 0 | 0 | 2 | 0 | 2,000 |
| Forster's tern | 3 | 6 | 4 | 6,000 | 11,000 |
| Common tern | 6 | 6 | 3 | 13,000 | 10,000 |
| Black tern | 118 | 39 | 39 | 254,000 | 84,000 |
| Belted kingfisher | 0 | 1 | 1 | 0 | 2,000 |
| Sedge wren | 10 | 20 | 37 | 22,000 | 62,000 |
| Marsh wren | 51 | 113 | 153 | 112,000 | 293,000 |
| Common yellowthroat | 134 | 91 | 175 | 285,000 | 286,000 |
| Le Conte's sparrow | 6 | 2 | 14 | 12,000 | 16,000 |
| Nelson's sharp-tailed sparrow | 3 | 3 | 13 | 7,000 | 34,000 |
| Red-winged blackbird | 945 | 597 | 710 | 2,038,000 | 1,421,000 |
| Yellow-headed blackbird | 89 | 155 | 175 | 193,000 | 356,000 |

**Table 1.** Densities (breeding pairs per square kilometer) of breeding birds by wetland class in North Dakota (Kantrud and Stewart 1984).

| Species | Wetland class | | | | | |
|---|---|---|---|---|---|---|
| | Temporary | Seasonal | Semipermanent | Permanent | Alkali | Fen |
| Pied-billed grebe | | 5.4 | 11.9 | 1.3 | | 12.2 |
| Horned grebe | | 1.4 | 0.6 | 0.3 | | |
| Eared grebe | | 3.9 | 1.9 | 1.6 | | |
| Western grebe | | | 0.2 | 2.8 | | |
| American bittern | 5.8 | 3.3 | 5.8 | 0.1 | | 8.4 |
| Black-crowned night-heron | | 0.4 | 4.2 | 1.0 | | 17.2 |
| Northern harrier | | 0.6 | 1.5 | | | 7.5 |
| Virginia rail | | 0.4 | 1.8 | | | 7.5 |
| Sora | 10.1 | 12.9 | 12.6 | | 0.2 | 25.1 |
| American coot | 25.2 | 73.8 | 180.5 | 8.9 | | 52.8 |
| Piping plover | | | 0.2 | | 2.2 | |
| Killdeer | 20.6 | 7.2 | 5.3 | 1.2 | 2.0 | |
| American avocet | | 3.2 | 3.2 | | 19.5 | |
| Willet | 10.1 | 12.3 | 7.0 | 1.0 | 1.3 | 2.5 |
| Marbled godwit | 10.1 | 6.9 | 3.6 | 0.1 | 2.7 | 5.0 |
| Wilson's phalarope | 45.4 | 28.9 | 11.5 | 0.1 | 4.3 | 5.0 |
| Black tern | 5.8 | 19.0 | 44.9 | 3.3 | | 17.2 |
| Marsh wren | | 4.9 | 43.8 | | | 52.6 |
| Common yellowthroat | | 7.9 | 7.8 | | | 55.4 |
| Savannah sparrow | 188.9 | 21.5 | 15.4 | | 5.0 | 8.6 |
| Red-winged blackbird | 300.0 | 99.8 | 106.8 | 16.9 | 14.9 | 125.5 |
| Yellow-headed blackbird | 11.1 | 18.1 | 253.3 | | | 271.0 |
| Total | 633.1 | 331.8 | 723.8 | 38.6 | 52.1 | 673.5 |

Wetland birds are not easily monitored by standard census techniques (Bibby et al. 1992). Dense vegetation reduces the visibility of some species. Many species lack territorial songs or rarely call; others that make diagnostic sounds do so primarily or only at night. Some species, such as rails, are notoriously elusive, even within a few meters of an observer (Burt 1994). Others are colonial, resulting in tremendous spatial variability in their numbers. Thus, no single technique works well for censusing all wetland species. Accurate censusing of wetland birds requires a variety of techniques, including nocturnal surveys, nest counts, intensive efforts involving walking or canoeing through marshes, and the use of recorded calls to elicit responses (Weller 1986). Recently, an informal group that monitors marsh birds has formed to address such issues.

Kantrud and Stewart (1984) surveyed breeding populations of wetland bird species other than waterfowl on 1,321

**Table 3.** Trends from the U.S. Geological Survey Breeding Bird Survey for the central region, 1966–1994, 1966–1979, and 1980–1994. Also given is average number recorded per route (R.A.) for the entire period.

| Species | 1966–1994 | | 1966–1979 | 1980–1994 |
|---|---|---|---|---|
| | R.A. | Trend[a] | Trend[a] | Trend[a] |
| Pied-billed grebe | 0.39 | 0.5 | 1.2 | 5.8 |
| Eared grebe | 0.67 | 5.2 | 24.0 ↑ | –16.2 ↓ |
| American white pelican | 1.22 | 3.5 ↑ | 0 | 1.1 |
| Double-crested cormorant | 0.56 | 26.6 ↑ | 6.7 ↑ | 11.1 ↑ |
| American bittern | 0.50 | –3.1 | –4.9 | 0.1 |
| Great blue heron | 0.89 | 3.0 ↑ | 6.4 ↑ | 0.6 |
| Black-crowned night-heron | 0.37 | 3.3 | –10.3 ↓ | 2.2 |
| Yellow-crowned night-heron | 0.53 | 0.7 | 19.6 | – 2.9 |
| Great egret | 2.84 | 3.8 | 4.2 | 4.4 ↑ |
| Snowy egret | 1.66 | 27.5 | 87.2 | 15.7 ↑ |
| Little blue heron | 2.98 | – 1.8 | – 0.9 | – 3.9 ↓ |
| Tricolored heron | 1.20 | 10.4 | 88.0 | – 4.1 |
| Cattle egret | 21.67 | 2.2 | 5.2 | – 2.8 ↓ |
| Green heron | 1.00 | 0.6 | 1.2 | – 3.4 ↓ |
| White ibis | 6.10 | 22.3 ↑ | 80.0 | 17.4 ↑ |
| White-faced ibis | 5.90 | 8.5 | 9.1 | – 9.9 |
| Northern harrier | 0.61 | – 2.1 ↓ | – 1.9 | – 0.3 |
| King rail | 0.82 | – 1.4 | 5.0 | – 2.0 |
| Sora | 0.94 | – 2.6 | – 8.5 ↓ | 11.0 ↑ |
| Common moorhen | 1.79 | 6.1 | 22.4 ↑ | 0.6 |
| American coot | 2.14 | – 0.8 | – 1.5 | 3.6 |
| Killdeer | 8.88 | – 0.3 | 3.0 ↑ | – 2.0 ↓ |
| American avocet | 0.63 | – 0.2 | 11.2 ↑ | – 1.8 |
| Willet | 1.03 | – 1.8 | 4.7 ↑ | – 0.4 |
| Spotted sandpiper | 0.08 | 2.1 | 9.4 | – 2.2 |
| Marbled godwit | 1.36 | 0.7 | 7.9 ↑ | — |
| Common snipe | 1.22 | 0.7 | 6.7 ↑ | – 1.0 |
| Wilson's phalarope | 1.24 | – 3.2 | – 5.7 ↓ | 6.7 |
| Franklin's gull | 7.55 | – 7.6 ↓ | – 17.0 ↓ | 42.3 ↑ |
| Ring-billed gull | 2.47 | 6.4 ↑ | – 5.6 ↓ | 10.3 ↑ |
| California gull | 0.95 | 17.6 ↑ | – 9.3 | 11.3 ↑ |
| Laughing gull | 12.95 | 5.4 ↑ | 7.5 | – 3.2 |
| Forster's tern | 0.54 | 0.7 | 12.1 ↑ | – 0.9 |
| Black tern | 2.70 | – 5.0 ↓ | – 13.0 ↓ | 2.7 |
| Belted kingfisher | 0.16 | – 1.6 | – 1.4 | 0.8 |
| Sedge wren | 1.25 | 1.3 | – 4.1 ↓ | 5.7 ↑ |
| Marsh wren | 1.34 | 3.6 | – 4.9 ↓ | 6.7 ↑ |
| Common yellowthroat | 6.87 | – 0.9 ↓ | 1.8 ↑ | – 2.1 ↓ |
| Le Conte's sparrow | 0.84 | 0.7 | 6.5 | 7.3 |
| Nelson's sharp-tailed sparrow | 0.15 | 5.2 | 0 | 17.7 ↑ |
| Swamp sparrow | 0.25 | 1.3 | 6.3 ↑ | 2.5 |
| Red-winged blackbird | 85.09 | – 0.5 ↓ | 1.1 ↑ | – 1.3 ↓ |
| Yellow-headed blackbird | 15.77 | 0.5 | 3.3 | – 2.1 ↓ |

[a]Average percentage annual change between 1967 and 1993: ↓ indicates statistically significant population decline; ↑ indicates statistically significant population increase.

wetland basins in the prairie pothole region of North Dakota. Densities of each species were reported for six different classes of wetlands (as defined by Stewart and Kantrud 1971; Table 1). Four of the wetland classes (permanent, semipermanent, seasonal, and temporary) were distinguished by water permanence as indicated by the vegetative zone occupying the deepest part of the basin. Alkali wetlands were recognized by the occurrence of hypersaline surface water, and fens were identified by a characteristic zone of fen vegetation that develops where groundwater seeps saturate the soil. Most wetland species were found on semipermanent and seasonal wetlands, reflecting the variety of habitats within these wetland classes (Table 1). Although some species were found in all wetland classes, most species showed a preference for one or two classes.

Population estimates and trends of wetland bird species, exclusive of waterfowl, are limited. In 1967 Stewart and Kantrud (1972) conducted an extensive survey of breeding bird populations throughout North Dakota to obtain baseline estimates of statewide breeding bird abundance and frequency of occurrence. In 1992 and 1993 Igl and Johnson (1997) repeated the survey by using the same sample units and methods as the 1967 survey to examine changes in breeding bird populations. These data offer both overall population estimates and some indication of population changes from 1967 to now (Table 2). According to habitat affinities, wetland species composed the largest proportion (32%) of species and 22% of the observed breeding pairs during the three years covered in the two Igl and Johnson surveys. The species that declined in North Dakota were mostly grassland and wetland species, whereas increasing species were predominantly resident species and species associated with human structures and woody vegetation (Igl and Johnson 1995). Similarly, results from the U.S. Geological Survey Breeding Bird Survey for North Dakota showed that 23 of the 28 (82%) observed species with statistically significant decreasing trends in the state were associated with wetland or grassland habitats.

We obtained trends for abundance of 43 wetland birds from the Breeding Bird Survey (Robbins et al. 1986) for the central region (from the Rocky Mountains to the Mississippi River) during the entire survey period (1966–1994) and for two subperiods: early (1966–1979) and recent (1980–1994) (Table 3). Population increases outnumbered decreases for each of the three time intervals. The percentage of species with increasing trends was 67% during the early subperiod (1966–1979) and 55% during the recent subperiod (1980–1994). For the entire survey period (1966–1994), seven species increased significantly; these included mostly colonial-nesting species (American white pelican, double-crested cormorant, and three gull species). Five species decreased significantly; all of these frequently nest in emergent wetland vegetation (northern harrier, Franklin's gull, black tern, common yellowthroat, and red-winged blackbird).

These data are consistent with earlier reports showing that breeding bird populations in wetland ecosystems are as dynamic as they are rich. The divergent patterns observed among the species and studies reflect the species' disparate habitat requirements, geographic ranges, and unique responses to natural and anthropogenic changes in their environments. Determining the status and trends of wetland bird populations is a necessary first step toward the more daunting challenge of understanding the mechanisms that drive population changes.

***See end of chapter for references***

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# Waterfowl in the Prairie Pothole Region

The prairie pothole region of the northern Great Plains is one of the most important areas for duck reproduction in North America. The region produces, on average, 50% of the primary species of game ducks on the continent (Smith 1995), yet accounts for only 10% of the waterfowl breeding habitat in North America (Smith et al. 1964). Twelve of the 34 species of North American ducks are common breeders in the region. For seven species—mallard, gadwall, blue-winged teal, northern shoveler, northern pintail, redhead, and canvasback—the prairie pothole region accounts for more than 60% of the breeding population (Smith 1995). The region is also a major migration corridor during fall and spring for other ducks, geese, and other water birds.

Annual variations in the number and distribution of ducks are strongly influenced by dynamic water conditions in the prairie pothole region (Batt et al. 1989). Breeding duck population sizes and reproduction are positively related to the number of wetland basins holding water in May and July (Reynolds 1987; Johnson and Grier 1988; Batt et al. 1989). During periods of widespread drought in the grassland portion of the region, many ducks move into the parkland; when both regions are dry, ducks may be displaced to the boreal forest or tundra regions (Johnson and Grier 1988). Species such as pintail and blue-winged teal tend to be more affected by drought conditions because of their preference for temporary and seasonal wetlands, whereas canvasbacks and lesser scaup, which use more stable semipermanent and permanent wetlands, are less likely to be displaced unless drought is severe. For all species, however, productivity is generally reduced during drought conditions because of poorer nesting effort and success and low survival rates of young.

The U.S. Fish and Wildlife Service and Canadian Wildlife Service have conducted annual surveys of breeding waterfowl populations in the principal breeding areas of North America since 1955. The surveys provide data on habitat conditions (numbers of ponds), breeding population sizes, and production. The Waterfowl Breeding Population and Habitat Survey, conducted each May, uses east–west aerial transects spaced within 50 habitat strata (Smith 1995). Data from aerial counts in the region are adjusted for visibility based on results from selected ground survey areas to provide population estimates in each stratum. This annual survey is among the most extensive and comprehensive animal surveys conducted in the world, and it provides an important long-term data base for population and habitat trends and population management. I used these data (Smith 1995) for southern Alberta, southern Saskatchewan, southern Manitoba, eastern Montana, North Dakota, and South Dakota to assess the status and trends of 10 common duck species (mallard, gadwall, American wigeon, green-winged teal, blue-winged teal, northern shoveler, northern pintail, redhead, canvasback, and lesser scaup) over the last decade. Information on Canada geese breeding in the prairie pothole region is derived from May surveys and midwinter counts from the U.S. Fish and Wildlife Service. For information on trends in waterfowl populations before 1986, see Batt et al. (1989).

## Trends in Water Conditions Affect Duck Populations

During the last decade, spring water conditions in the prairie pothole region, as measured by the number of wetland basins holding water (ponds), ranged from good in 1986 (more than 5 million) to very poor during the 1988–1993 drought (3.6 million or less) to excellent by 1994–1995 (Table 1). In 1986 pond numbers were above the long-term averages (1974–1995) for both the U.S. and Canadian portions of the region. Conditions in both areas degraded markedly over the next 3 to 5 years with the onset of drought conditions. Severe drought conditions continued in the United States through 1992, then rebounded dramatically in 1994–1995. Water conditions across much of the region in early 1996 remained good to excellent.

## Trends in Breeding Duck Numbers

Over the past 10 years, the number of breeding ducks in the prairie pothole region averaged 15,195,000 (Table 1), 16% lower than the long-term average (1955–1995) of 18,166,000. Duck numbers were lowest during 1988–1993, when drought conditions were widespread. With the return of heavy precipitation and excellent water conditions in most areas in 1994–1995, duck numbers responded rapidly and exceeded the long-term average by 5% and 20%, respectively.

Numbers of mallards and blue-winged teal were relatively low during the drought but rebounded in 1994–1995 (Table 2). Although the gadwall is more closely associated with the prairie pothole region than other ducks (more than 90% of the continental surveyed gadwall population occurs in the region), gadwall numbers dropped only slightly below their long-term average during 1987–1988; by 1995 gadwall numbers were 111% above the long-term average (Table 2). Numbers of pintails in the region reached record lows during the drought as large portions of the population were displaced to northern areas, and their reproduction rate was low (Hestbeck 1995). Wigeon numbers in the region changed little over the past decade and remained below their long-term average despite some increase in 1994–1995.

The breeding population of northern shovelers in the prairie pothole region (Table 2) followed a pattern of decline and recovery similar to mallards and blue-winged teal. Green-winged teal populations did not decline markedly during drought years but did increase substantially in 1994–1995. Of diving ducks, lesser scaup showed the greatest response to the drought and the return of good water conditions. Numbers of redheads and canvasbacks were slightly depressed during drought years but, like scaup, responded to the return of good water conditions in 1994–1995. By 1995, redhead and canvasback numbers exceeded long-term averages.

## Status and Trends of Canada Geese

Three populations of migratory Canada geese occur in the Great Plains. The Highline population breeds in southeastern Alberta, southwestern Saskatchewan, eastern Montana, eastern Wyoming, and north-central Colorado. January surveys in Colorado and New Mexico indicated that the Highline population has grown an average of 10% per year over the past 10 years, from about 75,000 geese in 1985 to a record 174,400 geese in 1995 (U.S. Fish and Wildlife Service, unpublished data). The Western Prairie population nests in eastern Saskatchewan and western Manitoba, and the Great Plains population is a restored population breeding in Saskatchewan, North Dakota, Nebraska, Kansas, Oklahoma, and

**Table 1.** Breeding population estimates for all ducks in the prairie pothole region and estimates of numbers of ponds during May, 1986–1995.

| Year | Number of breeding ducks | Number of ponds | | |
|---|---|---|---|---|
| | | Total | United States | Canada |
| 1986 | 18,429,000 | 5,760,000 | 1,735,000 | 4,025,000 |
| 1987 | 16,521,000 | 3,872,000 | 1,348,000 | 2,524,000 |
| 1988 | 13,515,000 | 2,901,000 | 791,000 | 2,110,000 |
| 1989 | 12,725,000 | 2,983,000 | 1,290,000 | 1,693,000 |
| 1990 | 13,399,000 | 3,508,000 | 691,000 | 2,817,000 |
| 1991 | 11,944,000 | 3,200,000 | 706,000 | 2,494,000 |
| 1992 | 14,256,000 | 3,609,000 | 825,000 | 2,784,000 |
| 1993 | 12,180,000 | 3,611,000 | 1,350,000 | 2,261,000 |
| 1994 | 18,997,000 | 5,985,000 | 2,216,000 | 3,769,000 |
| 1995 | 21,892,000 | 6,336,000 | 2,443,000 | 3,893,000 |

**Table 2.** Breeding populations (in thousands) of 10 duck species in the prairie pothole region in 1986–1995 (Smith 1995). TYA = 10-year average; LTA = long-term average (1955–1995).

| Species | Year | | | | | | | | | | TYA | LTA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | | |
| Mallard | 3,900 | 3,678 | 2,726 | 2,957 | 2,800 | 2,863 | 3,326 | 3,188 | 4,516 | 5,352 | 3,531 | 4,678 |
| Blue-winged teal | 3,892 | 2,800 | 2,761 | 2,438 | 2,318 | 3,113 | 3,572 | 2,409 | 4,199 | 4,847 | 3,235 | 3,594 |
| Gadwall | 1,463 | 1,244 | 1,237 | 1,301 | 1,458 | 1,443 | 1,916 | 1,636 | 2,201 | 2,734 | 1,663 | 1,293 |
| Northern pintail | 1,655 | 1,398 | 674 | 1,002 | 966 | 524 | 905 | 1,075 | 2,066 | 1,805 | 1,207 | 3,112 |
| American wigeon | 544 | 440 | 440 | 398 | 508 | 510 | 685 | 504 | 763 | 852 | 564 | 1,021 |
| Northern shoveler | 1,609 | 1,349 | 930 | 930 | 1,080 | 1,078 | 1,195 | 1,290 | 2,187 | 2,177 | 1,382 | 1,444 |
| Lesser scaup | 1,311 | 856 | 1,023 | 621 | 741 | 822 | 919 | 738 | 1,020 | 1,253 | 930 | 1,107 |
| Redhead | 509 | 479 | 398 | 458 | 416 | 349 | 498 | 403 | 581 | 855 | 495 | 512 |
| Green-winged teal | 297 | 307 | 345 | 309 | 356 | 331 | 403 | 281 | 574 | 686 | 389 | 530 |
| Canvasback | 285 | 309 | 240 | 201 | 238 | 247 | 215 | 210 | 293 | 491 | 273 | 329 |

Texas. Because of the way the survey design relates to the breeding range boundaries, separate estimates for these two populations are not available. Estimates from May surveys for ducks suggest that the Western Prairie and Great Plains populations combined in the region have increased from 108,000 in 1986 to 228,000 in 1995 (U.S. Fish and Wildlife Service, unpublished data).

## Factors Affecting Recent Waterfowl Populations in the Prairie Pothole Region

The dynamics of water conditions and duck populations observed over the past decade are characteristic of the prairie pothole region (Lynch 1984). Widespread drought during 1988–1993 reduced wetland habitat available to waterfowl, causing a marked reduction in waterfowl production. Displacement of ducks, particularly pintails and mallards, to northern regions also reduced populations during the drought. Pintail populations also may have been depressed by intensification of agricultural activities (drainage, cropping, and grazing) in key breeding areas (Hestbeck 1995). The dramatic recovery of most duck species in the region in 1994–1995 resulted primarily from heavy precipitation patterns that began in late 1993 and replenished many wetlands, providing abundant food and habitat for breeding ducks.

Two other factors probably were significant in contributing to the large and rapid recovery by most species. First, changes in the predator community have altered predation pressures on nesting waterfowl in many areas (Greenwood and Sovada 1996). After the drought, red fox population sizes were low, favoring high nest success, and mink numbers were also low, enhancing duckling survival. Second, about 1 million hectares of cropland in the U. S. portion of the prairie pothole region were restored to perennial grassland through the Conservation Reserve Program. Fields in the Conservation Reserve Program provide attractive and often highly productive nesting cover for upland-nesting ducks (Kantrud 1993). The combination of good to excellent water conditions, reduced predator pressure, and improved availability of nesting habitat in the United States provided conditions for a dramatic rebound in duck numbers after the drought. However, these conditions are seldom synchronized for more than 2 or 3 years, and such high duck production is likely in only 2 or 3 years out of 10 where habitats are altered by agriculture (Lynch et al. 1963). High production of waterfowl, especially of early-nesting species such as mallards and pintails, has become more difficult to achieve during years of moderate water conditions (Lynch 1984; Batt et al. 1989).

The ability of duck populations to recover from naturally occurring droughts has been reduced by continued loss of nesting habitat to agricultural activities, primarily grain cropping and intensified grazing. These agricultural effects are likely to be greatest in the grassland portion of the prairie pothole region, which experiences the greatest variability in water conditions and has had the greatest expansion of agricultural activities (Bethke and Nudds 1995). Whereas parkland and boreal areas can sustain duck populations over time, it is the grasslands' capacity for high duck production during wet periods that is critical to the growth of waterfowl populations (Lynch 1984).

***See end of chapter for references***

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# Duck Plague: Emergence of a New Cause of Waterfowl Mortality

Disease-causing organisms are natural components of biological systems. Too often, however, the occurrence of disease in wildlife is directly associated with changes due to human actions. Duck plague is an example of an infectious disease of domestic waterfowl that has begun to infect migratory waterfowl populations. Our growing concern is that duck plague will soon become a major cause of death for North American waterfowl and that the threat may be heightened because actions necessary to combat duck plague appear to have become embroiled in controversy. The ensuing debate has affected both the response to outbreaks and disease prevention efforts, and it may be aiding the geographic spread of this disease.

Duck plague is an acute, contagious, and often fatal herpesvirus infection of ducks, geese, and swans (Leibovitz 1991). However, not all species of waterfowl are equally susceptible. For example, northern pintails are highly resistant, blue-winged teals are highly susceptible, and mallards are moderately susceptible. The amount of duck plague virus required to cause disease in these different species differs by orders of magnitude (Spieker 1977). Occurrence of disease is also complicated because different strains of duck plague virus vary greatly in their ability to cause disease and death (Jansen 1961; Spieker 1977).

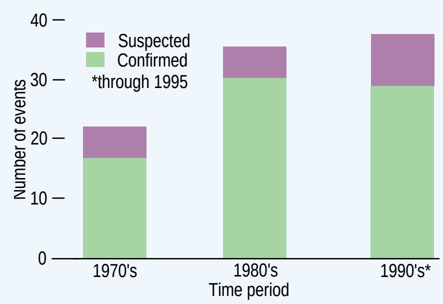
An outbreak of an acute hemorrhagic disease of domestic ducks in the early 1920's in the Netherlands is generally believed to be the first scientific documentation of this disease (Baudet 1923). However, identification of duck plague as a distinct disease of domestic waterfowl did not occur until 1942 (Bos 1942), despite numerous outbreaks in the Netherlands from 1923 to 1942 (Jansen 1964). The name "duck plague" was proposed by Jansen and Kunst (1949) and accepted as official terminology for this disease. "Duck virus enteritis" is the name based on the principal pathological features of the disease and is used to distinguish it from fowl plague in the United States (Leibovitz 1991).

Reports of duck plague in Europe and Asia have essentially been confined to domestic waterfowl, and outbreaks with severe economic effects have occurred in those countries. Therefore, the 1967 entry of duck plague into the Pekin duck industry of Long Island, New York, (Leibovitz and Hwang 1968) quickly resulted in aggressive actions by the U.S. Department of Agriculture to eradicate this foreign animal disease. Outbreaks also occurred in upstate New York during 1967. Duck plague reached Pennsylvania and Maryland in 1968, but in 1970 the U.S. Department of Agriculture declared success in its efforts to eradicate this disease from the United States. Secretary of Agriculture Clifford M. Harden issued certificates honoring New York State agencies and the Long Island Pekin duck industry for their part in the eradication effort. "The certificates officially proclaimed the eradication of duck virus enteritis (DVE) or duck plague from commercial waterfowl in the United States" (U.S. Department of Agriculture 1970). Unfortunately, this was not the end of duck plague.

No one knows how duck plague entered the western United States. The disease, however, appeared in San Francisco in 1972 after additional outbreaks in New York, Pennsylvania, and Maryland during 1970 and 1971. A city pond at the Palace of Fine Arts was the affected site in San Francisco (Snyder et al. 1973). The following year duck plague appeared in the Midwest and by 1975 had reached the Gulf of Mexico coast (Fig. 1) and Canada (Bernier and Filion 1975). Not only has there been a continual geographic expansion of duck plague (Fig. 2), but in some regions the number of outbreaks has also increased during each decade. Increased numbers of duck plague outbreaks and deaths have occurred within the eastern United States since 1970, but outbreaks in other regions have declined during the past decade (Friend 1995). The greatest number of outbreaks has occurred in Maryland (Fig. 1); New York, Virginia, and California also have relatively frequent occurrences of this disease (National Wildlife Health Center, Madison, Wisconsin, unpublished records).

In addition to domestic ducks, small numbers of wild waterfowl and wild species being maintained in avicultural collections or free as feral birds became infected during the 1967 Long Island duck plague outbreak. Collectively, more feral, captive, and wild waterfowl have become infected and

**Fig. 2.** Number of duck plague outbreaks in the United States by decade since 1970.



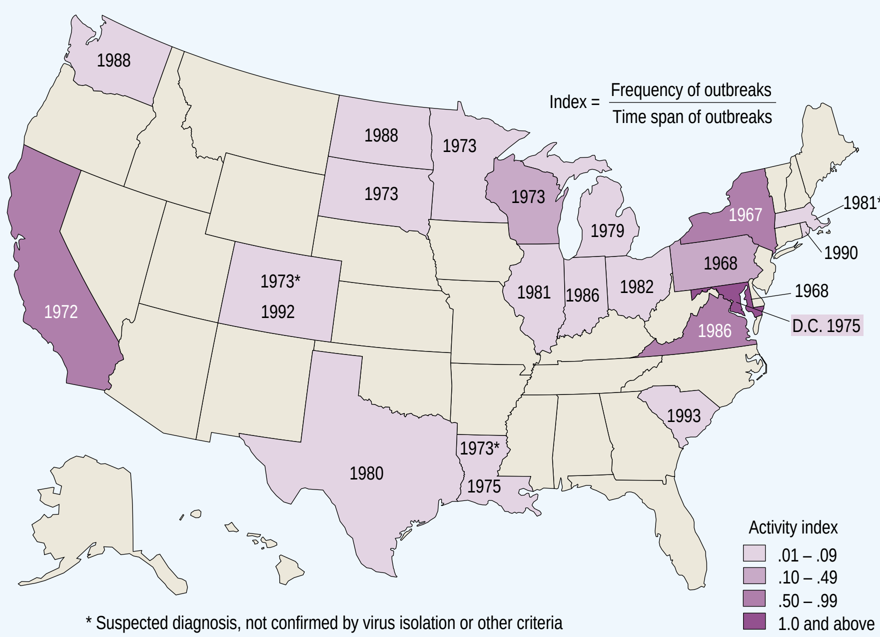




**Fig. 1.** Geographic distribution, spread, and relative activity of duck plague since its 1967 introduction into the United States. Years represent introduction into individual states.

survived subsequent outbreaks than have domestic ducks. The biological significance of those infections lies in the observation by Wobeser (1981) that birds surviving primary infection become carriers and potentially serve as future sources of additional duck plague outbreaks. To prevent the disease from spreading to other waterfowl populations, wildlife conservation agencies generally seek to destroy infected flocks. Infected waterfowl cannot be cured of the disease nor can disease carriers be readily detected by conventional technology.

Public opposition to the destruction of infected flocks is fueled by the fact that nearly all duck plague outbreaks occur in nonmigratory waterfowl in city parks and other public areas, or in captive flocks. Inherent human feelings for protecting animals, the beliefs that wild birds are the source for infection of urban and suburban waterfowl populations and that disease control is ineffective, and personal economic considerations are viewpoints often expressed by those opposing destruction of infected flocks. The objective of those opposing flock destruction is often to protect the individual birds surviving the outbreak. This is unfortunate since, as noted by Leibovitz (1991), the disease can best be controlled by eliminating entire infected populations.

The devastating 1973 duck plague outbreak in southeastern South Dakota at the Lake Andes National Wildlife Refuge demonstrated the negative effect that this disease can have on wild waterfowl (Fig. 3). Approximately 40,000 mallards and small numbers of other waterfowl species died. This was the first duck plague event involving a large-scale loss of wild waterfowl (Friend and Pearson 1973). Concern among the wildlife agencies responsible for managing the die-off resulted in the most aggressive actions ever taken to combat a disease outbreak in wild birds. Destruction of the large number of waterfowl that did not die from infection was considered but rejected because of arguments that methods were not available to prevent accidental dispersal of actively infected birds. It was feared that dispersed birds would initiate additional outbreaks as they relocated within other populations. Instead, the control effort focused on moving the birds from the confined area of Owens Bay at the refuge to the more open areas of the nearby Missouri River and then decontaminating the environment the birds had been removed from to kill any residual virus in the areas the birds had used. In a 6-month effort that involved approximately 90 people, researchers and refuge personnel decontaminated the environment by applying 7,000 pounds of chlorine gas, 2,000 pounds of calcium hypochlorite, and 64,000 pounds of soda ash. In addition, all dead birds that could be found were picked up daily and incinerated. Owens Bay was drained as much as possible and kept dry throughout the following summer months. The vegetation around the bay was burned, and all areas where disease-control activities took place on the refuge and other areas, including road surfaces and ice surfaces, were decontaminated. A sample of mallards was tested for exposure to duck plague and then color-marked before the birds dispersed from Owens Bay. The color marking was used to provide visible evidence of the location of birds that had dispersed so that researchers could survey their new sites for additional mortality and, if such mortality were detected, disease-control actions could begin quickly. Additionally, all workers in the area had to follow strict decontamination procedures to prevent disease spread. These unprecedented efforts are credited with minimizing the potential for additional outbreaks—there have been no occurrences of duck plague at Lake Andes since the 1973 event.

Courtesy M. Friend, USGS

**Fig. 3.** During the 1973 outbreak of duck plague at Lake Andes National Wildlife Refuge in South Dakota, more than 40,000 mallards died.

To date, the 1973 Lake Andes outbreak and a February 1994 outbreak that killed about 1,200 wild waterfowl in the Finger Lakes region of upstate New York (National Wildlife Health Center, unpublished records) are the only major outbreaks in wild waterfowl, although the pattern of duck plague outbreaks within the United States is one of an emerging disease (Figs. 1 and 2). The interface that often occurs between migratory and nonmigratory waterfowl provides opportunity for the transmission of disease between different populations (Tables 1 and 2). The international mobility of migratory waterfowl provides a means for widely disseminating duck plague; avian cholera has provided a precedent to support this concern. An important disease of domestic poultry within the United States since at least 1867 (Rhoades and Rimler 1991), avian cholera first appeared in wild waterfowl within the United States in 1944

**Table 1.** Classification of waterfowl involved in duck plague.

| | |
|---|---|
| Commercial | Birds raised for consumptive markets, such as white Pekin ducks |
| Captive collections | Zoological and other collections of birds for display and research |
| Game farms | Birds raised for release for sporting programs, such as mallards |
| Feral | Nonmigratory, nonconfined waterfowl of various species |
| Nonmigratory | Resident populations of native wild species such as mallards and Canada geese |
| Migratory | North American waterfowl that breed in one geographic area and winter in another before returning to breeding grounds |

**Table 2.** Status of duck plague in the United States.

| Waterfowl classification | Occurrence of disease | |
|---|---|---|
| | Mortality events | Trends, 1967–1995 |
| Commercial | Infrequent | Decreasing |
| Captive collections | Occasional | None; sporadic |
| Game farms | Occasional | None; sporadic |
| Feral | Common | Increasing |
| Nonmigratory | Occasional | None; sporadic |
| Migratory | Rare | None; rare |

(Quortrup et al. 1946; Rosen and Bischoff 1949). It wasn't until the mid-1970's, however, that avian cholera emerged as a major cause of death for migratory waterfowl across the nation (Friend 1995).

The recent emergence of new diseases and reemergence of old diseases have become a focus for increasing concerns involving human and domestic animal health. The subject of emerging diseases has captured the attention of filmmakers, as depicted by the movie *Outbreak*, and is the basis of popular books such as *The Coming Plague* (Garrett 1994). The subject has also earned extensive media coverage and has been the focus for scientific symposia, meetings, and publications. Duck plague is an emerging disease in the United States and must be addressed as such. The occurrence of this disease varies with different types of waterfowl populations. Migratory waterfowl have rarely been the primary species involved in outbreaks (Tables 1 and 2). It would be folly, when the opportunity exists to prevent it, to allow duck plague to join the ranks of avian botulism, avian cholera, and lead poisoning as another major cause of mortality for wild waterfowl.

Advances in molecular biology offer new potential for the detection of duck plague carriers, allow researchers to determine the origin of individual outbreaks, and aid in the search for answers to other important questions that will help resolve public and scientific debate involving this disease. Research is needed to develop required technology and to implement methodical epizootiological investigations. The resulting information will provide wildlife management agencies with the information necessary to develop strategies to make duck plague a matter of historical record rather than a major cause of death for migratory waterfowl.

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Locally, drought tolerance seems to be the principal ecological process influencing the composition of grassland bird communities (Wiens 1974), with grazing (Hobbs and Huenneke 1992) and wildfire (Zimmerman 1992) playing secondary roles. Unlike most forest birds that winter in the Neotropics, virtually all endemic grassland birds winter on the continent; thus influences on their status and trends occur within North America.

The prairie pothole region is a key breeding area for species such as the mallard, blue-winged teal, and northern pintail. Researchers believe that preserving native grassland and wetlands is essential for slowing declines in duck numbers, including the mallard, American widgeon, and northern pintail (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1994). Predation on eggs and hatchlings by red foxes, striped skunks, raccoons, and other species substantially reduces the abundances of ducks (Ball et al. 1994).

## Mammals

The grasslands have a fertile history of plant- and seed-eating mammals (Hall and Kelson 1959). A rich array of large herbivores, including camels, rhinoceroses, mammoths, mastodons, and bison, evolved on the North American grasslands only to disappear during the last Ice Age (Van Valkenburgh and Janis 1993). The surviving large grassland herbivore, the plains bison, evokes a mystique not shared by any other North American mammal and which is largely derived from Native American and frontier heritages (Meagher 1978). In the past, bison (Fig. 15) numbered from about 60 to 70 million and roamed in large herds that, in the 1860's, often required horseback riders several days to successfully penetrate and cross.

As many as 5 billion prairie dogs may have been in North America before European settlement. An estimated 98% decline in prairie dog numbers has occurred since European settlement (Summers and Linder 1978). The black-tailed prairie dog may occupy less than 0.5% of its original range, the short-grass and mixed-grass prairies. As a result, a variety of species closely associated with the prairie dog are either federally listed as endangered or are being considered for listing as threatened or endangered. These include the black-footed ferret, the swift fox, and the mountain plover.

The ranges of more than 100 native mammals extend into the prairie; nearly half of these occur in the forest–grassland ecotone and others in diverse habitat types (Risser et al. 1981). Nevertheless, surveys of eastern and western species whose ranges stop short of the Great Plains support the effectiveness of the grassland as an evolutionary barrier to dispersal (Hall and Kelson 1959). Estimates of Great Plains-restricted mammals range from as few as 10 (Risser et al. 1981) to as many as 18 (Jones et al. 1985). These species include one lagomorph (the white-tailed jack rabbit), eight rodents (thirteen-lined ground squirrel, Franklin's ground squirrel, black-tailed prairie dog, plains pocket gopher, olive-backed pocket mouse, plains pocket mouse, plains harvest mouse, and prairie vole), and two carnivores (swift fox and black-footed ferret).

One recent extinction, the Audubon bighorn sheep, was a subspecies found along the upper Missouri River, including North Dakota, South Dakota, Wyoming, and Nebraska. Populations of the caribou, a species once common across northern North Dakota but which is now extirpated, are still common in Canada. Similarly, the gray wolf and elk, once common on the grasslands, and the less common mountain lion and wolverine are found elsewhere.

# Population Trends for Prairie Pothole Carnivores

Since settlement of the prairie pothole region of the northern Great Plains by Europeans in the late 1800's, carnivore populations have changed considerably—mostly due to habitat alteration and human-inflicted mortality. At least 19 species of carnivorous mammals once occurred in the prairie pothole region (Jones et al. 1983). Presently, only eight are common throughout the region—coyote, red fox, raccoon, American badger, striped skunk, mink, ermine, and long-tailed weasel (Sargeant et al. 1993). Other species that occur locally or intermittently are mountain lion, lynx, bobcat, gray wolf, gray fox, swift fox, spotted skunk, and least weasel. Grizzly bears, wolverines, and river otters once occurred in the region but are now extirpated.

Competition among species affects the distribution of coyotes, wolves, and foxes (Carbyn 1982; Rudzinski et al. 1982; Sargeant et al. 1987; Bailey 1992). These larger canids are keystone species that suppress the distribution of smaller canids (Johnson and Sargeant 1977; Dekker 1989; Johnson et al. 1989).

**Fig. 1.** Coyote hunting in prairie grassland.
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**Fig. 2.** Red fox in prairie grassland.
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## Gray Wolf

Human influences on canid communities began in the late 1800's, first with the killing of wolves and later, coyotes, because the predators killed livestock (Johnson and Sargeant 1977; Andelt 1987). Treatment of wolves was especially harsh; consequently, they were essentially eliminated from the prairie pothole region.

## Coyote

Coyotes are most abundant in the northwestern prairie pothole region (Sargeant et al. 1993; Fig. 1). In spring, populations are composed of family groups, each generally a mated pair and one or more associated adults (Voigt and Berg 1987), which occupy relatively exclusive territories (Sargeant et al. 1987). In spring, recorded home ranges of family groups averaged 61 square kilometers in North Dakota (Allen et al. 1987) but only 12 square kilometers in Alberta, where coyote densities were higher (Roy and Dorrance 1985). Home ranges are smaller where coyotes are more abundant (Allen et al. 1987).

Coyotes increased in the prairie pothole region after European settlement and the extirpation of the gray wolf (Bailey 1926; Criddle 1929). Coyotes were numerous in the prairie pothole region in the early 1900's, but populations were noticeably lower by the 1950's and remained low through the 1970's. Population reduction by killing was greatest in farmed areas of the southeastern portion, especially after the 1940's, and some populations were completely eliminated. Survival of coyotes increased after government bans in 1972 of certain predator control methods (Johnson and Sargeant 1977) and with reduced harvest pressure in response to low pelt values in the 1980's. In 1985 and subsequent years, millions of hectares of cropland in the prairie pothole region were enrolled in the Conservation Reserve Program of the U.S. Department of Agriculture (Young and Osborn 1990). Security provided by these extensive grasslands likely enhanced coyote survival. In the early 1990's, coyotes were present throughout most of the prairie pothole region (Sargeant et al. 1993; Sovada et al. 1995). However, an outbreak of sarcoptic mange is now causing declines in coyote populations in North Dakota (Allen 1996) as well as in adjacent states and Canadian provinces. This outbreak may lead to notable population changes in coming years.

## Red Fox

Red foxes generally are more abundant in the central and southeastern portions of the prairie pothole region (Sargeant et al. 1993; Fig. 2). In spring, red fox populations are composed of family groups, usually mated pairs (Sargeant 1972). In North Dakota, documented family groups occupied exclusive territories that ranged from 3 to 21 square kilometers but that generally were smaller than 12 square kilometers (Sargeant 1972). Home ranges are smaller when red foxes are more abundant and are affected by nearness of resident coyotes (Sargeant et al. 1987).

In the prairie pothole region, red fox population trends are generally opposite those of coyotes (Fig. 3). Red fox populations expanded greatly in the prairie pothole region between the 1890's and 1930's, especially in the southern portion; expansion began in the 1950's in the northern portion, especially in the northeast (Bird 1961; Johnson and Sargeant 1977). Red foxes were abundant throughout the eastern part of the prairie pothole region between the 1940's and 1970's. In the late 1970's to mid-1980's, red fox populations declined in the prairie pothole region during periods of high fur prices (Sargeant 1982). More recently, red fox populations have declined in the southern portion, apparently in response to competition from increased coyote populations (Sovada et al. 1995). Mange is expected to affect red fox populations in coming years (Allen 1996).

## Striped Skunk

Striped skunk populations fluctuate erratically throughout the prairie pothole region (Rosatte 1987; Sargeant et al. 1993). Striped skunks are solitary, except in winter when they may occupy communal dens (Verts 1967). Recorded densities of adults in North Dakota in spring ranged from 1.2 to 1.5 animals per square kilometer, but densities were difficult to estimate because of the species' movements (Greenwood et al. 1985). During April in North Dakota, the minimum home range size averaged 242 hectares for females and 308 hectares for males (Greenwood et al. 1985). Striped skunks were less abundant in the presence of badgers and coyotes, both of which are predators (Sargeant et al. 1982; Johnson et

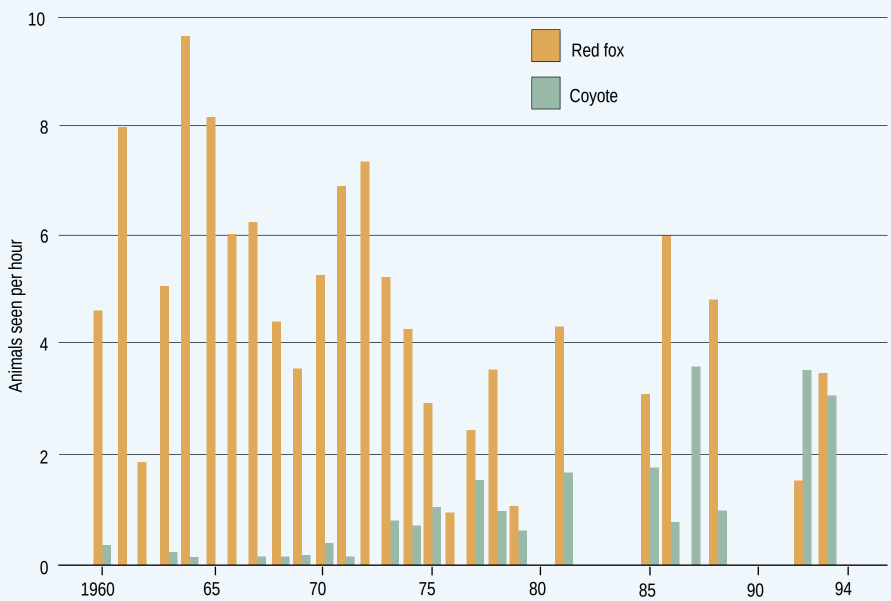


**Fig. 3.** Number of red foxes and coyotes seen per hour during winter aerial deer censuses in the Missouri Coteau of North Dakota (information from *North Dakota Outdoors*).

al. 1989). Striped skunks in the prairie pothole region die primarily because of diseases such as rabies, but they are also killed by humans, and some starve to death in the winter (Bjorge et al. 1981; Sargeant et al. 1982; Wade-Smith and Verts 1982). High reproduction (Greenwood and Sargeant 1994) and excellent dispersal (Sargeant et al. 1982) allow striped skunks to rapidly repopulate areas where populations are decimated.

## American Badger

Badgers are at the northern limit of their range in the prairie pothole region (Hall 1981). The presence of badgers is tied to extensive grasslands (Messick et al. 1981; Sargeant et al. 1993), and they avoid cultivated areas (Messick and Hornocker 1981). Burrowing rodents found in grasslands are important prey of badgers (Messick 1987). Badgers are solitary, and little is known of their home range size or density in the prairie pothole region. Their populations in this region seem to have declined significantly since European settlement and have remained relatively low, probably because of the large areas of grassland converted to cropland. Human-inflicted mortality (for example, trapping and shooting) also influences badger populations (Messick et al. 1981). Recently, badgers have extended their range to the east and north in the prairie pothole region, probably as a result of clearing of trees in parkland, draining of wetlands, and increases in rodent populations (Nugent and Choate 1970; Lintack and Voigt 1983; Long and Killingley 1983). Based on numbers of captures in the last 5–10 years, badger populations appear to have increased slightly in the region (U.S. Department of Agriculture, Animal Damage Control, Bismarck, North Dakota, unpublished data). The population increase may be related to extensive grassland habitat provided by the Conservation Reserve Program and to reduced hunting caused by low pelt value.

## Mink

Mink population sizes are erratic in the prairie pothole region, especially where shallow basin wetlands, their preferred habitat, predominate (Arnold and Fritzell 1987a; Eagle and Whitman 1987; Sargeant et al. 1993). In spring, populations are composed of territorial males that occupy large areas and females that occupy smaller areas (Eagle and Whitman 1987). In the prairie pothole region of Manitoba during May–July, home ranges of male mink averaged 646 hectares (Arnold and Fritzell 1987b) but were larger during the breeding season. Drought reduces mink reproduction (Eberhardt 1974) and has catastrophic effects on their populations (Sargeant et al. 1993). Widespread wetland drainage probably affects mink populations in ways similar to drought.

During the droughts of the 1980's, mink were undetected in many areas of the prairie pothole region (Sargeant et al. 1993). Population lows also probably occurred during the droughts of the 1910's, 1930's, and 1960's. During droughts, rivers and lakes harbor mink populations. The high reproductive potential of mink (Eagle and Whitman 1987) allows the rapid recovery of their populations when prairie wetlands recover from drought. Mink populations likely were extremely low in much of the prairie pothole region of North Dakota in the early 1990's, after the drought of the 1980's. Since 1993, however, populations have begun to recover with improved wetland conditions (M. A. Sovada, U.S. Geological Survey, Jamestown, North Dakota, personal observation).

## Weasels

Populations of weasels fluctuate greatly in response to availability of prey, primarily small mammals (Gamble 1981; Jones et al. 1983). Information on distribution and population trends of weasels is scant. Long-tailed weasel and ermine populations are believed to be fragmented and small throughout the prairie pothole region (Fagerstone 1987; Sargeant et al. 1993). Local occurrence is influenced by prey diversity and abundance, availability of water and den sites, and harvest pressure (Simms 1979; Jones et al. 1983; Fagerstone 1987). Extensive conversion of native uplands and wetlands to cropland probably has reduced the distribution and abundance of ermines and long-tailed weasels throughout the prairie pothole region.

Long-tailed weasel populations appear relatively stable, in contrast to ermine populations, which may fluctuate markedly. This stability reflects the long-tailed weasel's wide range of foods, which differs from the specialist ermine's narrow diet (Simms 1979; Gamble 1981; Fagerstone 1987). From the mid-1980's to early 1990's, the long-tailed weasel was considered threatened in the prairie provinces of Canada as a result of habitat loss and increased use of pesticides (Gamble 1982). However, based on a survey conducted in 1991, Proulx and Drescher (1993) reported the species was present throughout central and southern Alberta. Sargeant et al. (1993) observed large weasels (no distinction was made between long-tailed or ermines) in 20 of 33 study areas in Alberta, Manitoba, Saskatchewan, North Dakota, and South Dakota. The Conservation Reserve Program likely has enabled weasel populations to increase in the southern part of the prairie pothole region.

## Raccoon

Raccoons are most common in the southeast part of the region (Sargeant et al.

1993). In spring, density of adult raccoons in North Dakota was estimated at about one or less per square kilometer (Fritzell 1978). Raccoon populations in the prairie pothole region consist of territorial males with large home ranges; females, often attended by young from the previous year, have smaller home ranges (Fritzell 1978). In North Dakota, home ranges of males averaged 2,560 hectares, and those of pregnant females or females with young averaged 806 hectares. Females did not maintain exclusive home ranges.

Raccoons are semiaquatic omnivorous carnivores that have benefited from European settlement of the prairie pothole region. Agricultural crops (cereal grain, corn, and sunflowers) provide a stable food base that replaces mast (fallen nuts on the forest floor) consumed by raccoons in forested areas (Greenwood 1982). Raccoons probably occurred only in riparian and wooded areas in the southeastern portion of the region before European settlement (Bailey 1926). Raccoons were absent in Canada, except possibly in southern Manitoba (Houston and Houston 1973). After European settlement, raccoons became more widely distributed in the southern portion of the prairie pothole region, although populations were low. In the 1940's, raccoons were abundant throughout much of the southeastern portion of the prairie pothole region. In the 1950's, populations in Canada expanded (Lynch 1971; Houston and Houston 1973), and by the 1960's, raccoons were considered a major predator of nesting canvasbacks in southwestern Manitoba (Stoudt 1982). Principal causes of raccoon death in North Dakota are related to human activities (shooting, vehicle impact, and so forth). There is evidence of a negative relationship between coyotes and raccoons (Johnson et al. 1989), suggesting that coyotes may suppress raccoon populations. Suppression of coyotes in the 1950's may have contributed to the range extension of raccoons.

**Acknowledgments**

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***See end of chapter for references***

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# Prairie Integrity and Legacies

## Intercommunity Management: Prairie Integrity

Integrity here means maintaining species and ecological processes characteristic to a particular landscape (Samson and Knopf 1993); this is an emerging goal in resource conservation (Angermeier and Karr 1994). The human-caused breakdown of barriers to dispersal that has permitted invasion of nonindigenous species has caused the extinction of more grassland species than any factor except habitat loss (D'Antinio and Vitousek 1992). Nonindigenous species include exotics, which are transported beyond their natural range, and aliens, those that colonize an altered landscape. Introducing nonindigenous species may increase the number of local species, but it reduces integrity, above- and belowground, and also the number of native species, both aquatic and terrestrial.

A more subtle threat to integrity is loss of genetic diversity. Species hybridize along forested corridors that now fragment the Great Plains (Knopf 1986). Human activity, either accidental or deliberate, moves species from one place to another at ever-increasing rates (Knopf 1992). As a result, species that evolved in isolation from one another are forced into contact. In terms of conservation of biological diversity, the loss of six bird subspecies due to the hybridization arising from these forested stepping stones and artificial corridors (Knopf 1986) rivals the loss of three species attributed to fragmentation of the eastern deciduous forest.

These recent forest patches and woody corridors that border rivers on the Great Plains also favor movement of reptiles and mammals from east to west, which contributes to the degradation of the biological diversity and integrity of the Great Plains (Knopf and Scott 1990). In 1842, in eastern Colorado, the explorer John C. Frémont observed that "antelope were tolerably abundant, wolves were seen in great numbers, and buffalo absolutely covered the plains on both sides of the (South Platte) river" but reported no deer (*in* Nevins 1956). In recent years, deer abundance has increased markedly, particularly that of the eastern white-tailed deer, which may replace the mule deer, known to have occurred on the western plains since before European settlement (Kufeld and Bowden 1995). Hybridization between the two deer is known to occur (Stubblefield et al. 1986).

Nonindigenous species now account for 13% to 30% of prairie species (U.S. Congress, Office of Technology Assessment 1993; C. Freeman, Kansas Natural Heritage Program, Lawrence, personal communication). Increases in distribution and abundance are inevitable without action to prevent them, as evident in the naturalization of Russian-olive trees in the western United States (Olson and Knopf 1986). Russian-olives, which were introduced from Europe in colonial times, range across the Great Plains into the West. In agricultural areas, this species interferes with farming operations; it also hinders management activities on national wildlife refuges, increases degradation of river channels, contributes to declines in river levels, and supplants native riparian tree species. Its adaptability and resistance to control measures, two life-history traits shared with other nonindigenous species, will continue to add to the management concerns associated with the ever-growing number of other nonindigenous plant and animal species.

## Intracommunity Management: Prairie Legacies

The approximate action to take after intercommunity management is to identify and retain a set of species and natural processes that sustain communities characteristic of a particular landscape (Chaplin et al. 1996). The Nature Conservancy has identified significant concentrations—legacies—of prairie species that are rare or of declining abundance (Figs. 16–23). Principally these are species that are federally listed or are species of concern that occur within certain communities and ranges of environmental features, including those from prairie wetlands to cottonwood savannahs.

Recommending the restoration of ecological processes in conservation is not new (Leopold 1933). Understanding scale, spatial and temporal, in management is new (Gibson et al. 1993).

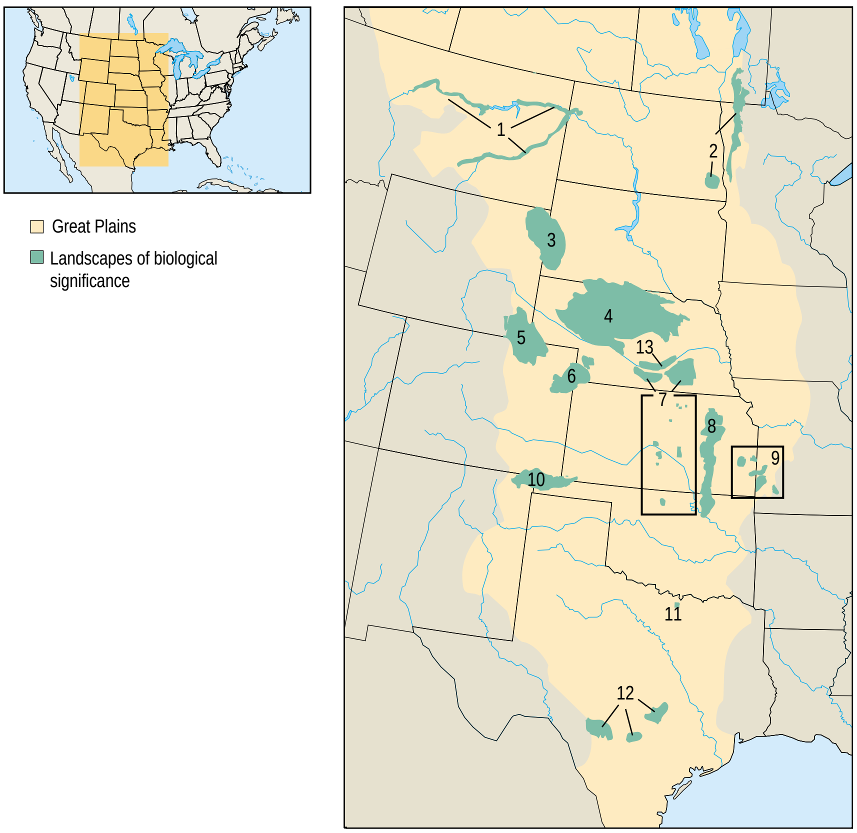


**Fig. 16.** Priority landscapes of biological significance in the Great Plains: 1) Upper Missouri and Yellowstone rivers and watersheds in Montana and North Dakota; this area is an example of a free-flowing Great Plains river and watershed (see Fig. 17) ; 2) Glacial Lake Agassiz Interbeach Area in North Dakota and Minnesota; this area has a number of large, intact expanses of tall-grass prairie; 3) Black Hills and grasslands in South Dakota and Wyoming; these are two of the largest publicly owned examples of short-grass and mixed-grass prairies (see Fig. 18); 4) Sandhills in Nebraska and South Dakota; this is the largest dune system and one of the largest expanses of native grassland left in North America; 5) Western high plains grassland in Colorado, Nebraska, and Wyoming, which includes the Pawnee National Grassland and other adjacent short-grass prairie habitat; 6) Arikaree Sandsage Prairie in Colorado, Kansas, and Nebraska, which includes sandsage and an example of the rare cottonwood–switchgrass savanna (see Fig. 19); 7) Central Plains Wetlands in Nebraska, Kansas, and Oklahoma (areas in box plus areas indicated above box); this area is a string of significant wetlands (see Fig. 20); 8) Flint Hills in Kansas and Oklahoma, which is the largest remaining area of native tall-grass prairie; 9) Osage Cuestas Tallgrass in Kansas (in box), which has rolling to level tall-grass prairie with examples of wet savanna and bottomland forest; 10) Upper Cimarron Mesas in Colorado, Kansas, New Mexico, and Oklahoma; within this area are extensive grasslands and mesas, along with the headwaters of the Cimarron River (see Fig. 21); 11) Fort Worth Prairie in Oklahoma and Texas, which is an unbroken tall-grass prairie; 12) Texas Hill Country in Texas, which has four differing landscapes, each significant to a unique assemblage of natural and rare communities (see Fig. 22); and 13) Central Platte River in Kansas; this is a shallow, braided river of immense wetland importance (see Fig. 23).

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**Fig. 17.** Confluence of turbid waters of the Yellowstone and clear waters of the Missouri as a result of the Ft. Peck Reservoir just upstream.

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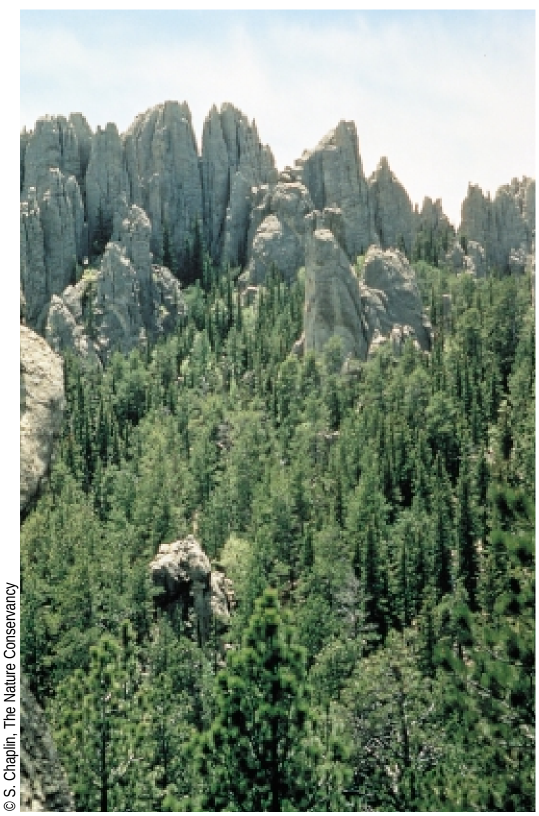

**Fig. 18.** Black Hills: Cathedral Spires, South Dakota.

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**Fig. 19.** Arikaree River, Colorado.

**Fig. 20.** Rainwater Basin, Nebraska.

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**Fig. 21.** Upper Cimarron Mesas: Lasa, Mesa de Maya, Colorado, Cobert Mesa.

© L. Williamson, Texas Parks and Wildlife Department

**Fig. 22.** Texas Hill Country: San Marcos River, Texas. The San Marcos runs through the Hill Country and is important to a large number of endemic salamanders.

**Fig. 23.** Platte River with sandhill cranes.

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## Resource and Research Needs

Solutions to the deterioration of grassland resources appear to revolve around a single emerging concept—*sustainability*—and conform to a proposed strategy. It is important to increase our understanding of the long-term sustainability both of populations of species and of the overall ecosystem. The strategy arises from the following conceptual principles:

- Support public, private, and governmental prairie conservation initiatives as a step toward the long-term goal of grassland sustainability.

The Western Governors' Association's Great Plains Program, the first broad-scale ecosystem management effort in the United States, seeks to demonstrate that economic and environmental interests are served by preventing declines in the numbers of prairie species and their host ecosystems (Clark 1996). The program is built on broad-based science (Johnson and Bouzaher 1996).

- Develop information that recognizes the biological and ecological significance of prairie communities.

The International Institute for Sustainable Development's Sustainable Development for the Great Plains Policy Analysis (Tyrchniewicz and Wilson 1994) links, at an ecosystem level, the well-being of grassland biological resources, particularly soil and water, and society in general. Increasing evidence suggests that dry ecosystems, whether in South America (Mares 1992) or North America (Samson and Knopf 1994), are unusually diverse compared with wet or rain-forest ecosystems. In the face of global warming, the health of planet Earth may depend on grasslands because they are superior carbon sinks compared to forests with similar environmental characteristics (Seastedt and Knapp 1993).

- Identify, inventory, and conserve prairie-limited animals and plants, particularly the large number of plant and invertebrate species.

Sustainability depends on biological diversity to keep all ecological systems, aquatic and terrestrial, functioning and healthy (Lubchenco et al. 1991). Sustainability and biodiversity are two sides of the same coin (Raven 1991). Information and appropriate actions are required to minimize any negative effects on prairie genetic stock and thus on biodiversity, because diverse natural ecosystems help maintain hydrological cycles, regulate climate, absorb and break down pollutants, and contribute to the process of soil formation (Tyrchniewicz and Wilson 1994).

- Evaluate the status of species of concern and other sensitive species, and encourage measures to reverse downward trends in population numbers of prairie species and rare communities.

Putting the maintenance of diversity as a top priority builds ecological knowledge accessible to the public and environmental decision makers (public and private) and provides opportunities to cooperate in conservation of rare species and communities (Chaplin et al. 1996). Sites for tourism and recreation are often identified in the process as well. The net payoff of understanding and displaying diversity is identification of areas of endemism as an essential aid in planning for the conservation of the nation's biodiversity. An urgent need exists to further develop and refine this process on a national and international basis (International Council for Bird Protection 1992).

- Prairie management should mimic the natural disturbance regime to take advantage of preselected traits of prairie species.

The importance of disturbance in shaping grassland communities (Figs. 3 and 10) and ecosystem dynamics is recognized, yet significant questions remain to be answered on the relationship between disturbance and species persistence (Bragg and Steuter 1996; Steinauer and Collins 1996; Weaver et al. 1996). The purpose of conservation is not to conserve species per se but to conserve interactions among species and processes that maintain the health and productivity of communities and ecosystems (Odum 1992).

The Conservation Reserve Program is one of the most popular and successful conservation programs ever implemented by the U.S. Department of Agriculture. By establishing needed grassland, the Conservation Reserve Program has improved game species habitat, prevented loss of topsoil, improved water quality by reducing pesticide and fertilizer runoff, and provided billions of dollars in environmental benefits over the life of the program. The act, however, needs refocusing to be of major conservation benefit to endemic grassland species (Allen 1993).

- Education programs should play an integral role in ensuring conservation of grasslands.

The premise in prairie conservation is that attitudes of individual landowners and the community as a whole play decisive roles in determining the eventual fate of grasslands (Mack 1996). Programs must foster a climate favorable to grassland conservation as an integral component of agricultural land management (Dyson 1996), to the development of covenant agreements to protect remnants (World Wildlife Fund Canada 1988), to cooperative conservation programs between private and neighboring government-managed lands (Bueseler 1996), and to the importance of science-based management (Johnson and Bouzaher 1996).

Almost a half-century has passed since Weaver (1954) noted that the disappearance of a major unit of vegetation—the North American prairie—is an event worth considering. Fortunately, to a growing segment of our society, prairie "looms as large as the universe, as intimate as a village" (Least Heat Moon 1991).

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