Studies in Avian Biology No. 15:247–257, 1994.

# AVIAN ASSEMBLAGES ON ALTERED GRASSLANDS

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*Abstract.* Grasslands comprise 17% of the North American landscape but provide primary habitat for only 5% of native bird species. On the Great Plains, grasslands include an eastern component of tall grasses and a western component of short grasses, both of which have been regionally altered by removing native grazers, plowing sod, draining wetlands, and encouraging woody vegetation. As a group, populations of endemic bird species of the grasslands have declined more than others (including neotropical migrants) in the last quarter century. Individually, populations of the Upland Sandpiper and McCown's Longspur have increased; the wetlands-associated Marbled Godwit and Wilson's Phalarope appear stable; breeding ranges are shifting for the Ferruginous Hawk, Mississippi Kite, Short-eared Owl, Upland Sandpiper, Horned Lark, Vesper, Savannah, and Henslow's sparrows, and Western Meadowlark; breeding habitats are disappearing locally for Franklin's Gull, Dickcissel, Henslow's and Grasshopper sparrows, Lark Bunting, and Eastern Meadowlark; and populations are declining throughout the breeding ranges for Mountain Plover, and Cassin's and Clay-colored sparrows. Declines of these latter three species, and also the Franklin's Gull, presumably are due to ecological phenomena on their respective wintering areas. Unlike forest species that winter in the neotropics, most birds that breed in the North American grasslands also winter on the continent and problems driving declines in grassland species are associated almost entirely with North American processes. Contemporary programs and initiatives hold promise for the conservation of breeding habitats for these birds. Ecological ignorance of wintering habits and habitats clouds the future of the endemic birds of grasslands, especially those currently experiencing widespread declines across breeding locales.

*Key Words:* Grasslands; Great Plains; biological diversity; *Larus pipixcan*; *Charadrius montanus*; *Aimophila cassinii*; *Calamospiza melanocorys.*

Native grasslands represent the largest vegetative province of North America. Almost $1.5 \times 10^6$ km$^2$ of grasslands historically covered the continent on the Great Plains from south central Saskatchewan to central Texas, plus in the Central Valley of California and Palouse region of eastern Washington and Oregon (Knopf 1988). The continental grasslands of the Great Plains evolved in the rainshadow of the Rocky Mountains; seasonal precipitation falls mostly in spring or summer. These grasslands are characterized by warm-season grasses of the shortgrass prairie on the west and fire-maintained, cool- and warm-season grasses that grow much taller on the east. The mediterranean grasslands of the west coast states evolved with fall/winter precipitation and the historical composition of especially the California grasses is uncertain. This paper focuses specifically on the Great Plains landscape and major patterns of avifaunal metamorphosis over the last 100 years.

## THE NATIVE GRASSLAND LANDSCAPE

Inferences about the historical landscapes of the Great Plains are available in the writings of nineteenth century adventurers as Irving (1835), explorers as Frémont (1845) and Stansbury (1852), and civilian travelers along the Platte River Road (Mattes 1988). Read collectively, one envisions the short and taller grass prairies intergrading just east of an irregular line from El Reno, Oklahoma, through Fort Hays, Kansas, and North Platte, Nebraska, northwestward into the west-central Dakotas. The landscapes of eastern Oklahoma, Kansas, and Nebraska were heavily wooded stream bottoms in uplands of fire-maintained grasses of a meter or more in height. Wapiti (*Cervus canadensis*) and white-tailed deer (*Odocoileus virginiana*) were abundant. The grasses, however, do not cure well (i.e., lose their nutritive value when dried) and these ungulates survived the season of vegetative dormancy by

grazing or browsing within the wooded stream bottoms. Native Americans of this region, such as the Pawnee, hunted these species, but generally raised vegetables in relatively permanent villages along eastern prairie streams then journeyed west into the shortgrass province semiannually to hunt plains bison (*Bison bison bison*), for meat (Hyde 1974).

The shortgrass prairie landscape was one of relatively treeless stream bottoms and uplands dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), two warm-season grasses that flourish under intensive grazing pressure by reproducing both sexually and by tillering. Unlike the more eastern species, short grass species remain highly digestible and retain their protein content when dormant. This character supported the evolution of a major herbivore assemblage dominated by bison, pronghorn (*Antilocapra americana*) and prairie dogs (*Cynomys* spp.). Native Americans, including the Sioux and Cheyenne of shortgrass landscapes, tended to be seminomadic, following the massive bison herds upon which their lifestyle was specifically dependent in the late 1870s.

## THE NATIVE GRASSLAND BIRDS

As is the case for most biogeographic provinces, pre-settlement information on native bird assemblages of Great Plains grasslands is limited. Ornithological study on the Great Plains commenced in 1832 when John Kirk Townsend (1839, the first trained zoologist to cross the continent) accompanied by the prominent naturalist Thomas Nuttall traveled with the Wyeth expedition along the Rocky Mountain Road to the Columbia River. Later, the surveys by Hayden (1862), Allen (1871, 1874), Coues (1878) and others provided additional insights into the regional avifauna. Generally, however, these earlier works were all exploratory, tended to emphasize avifaunas along stream courses (Allen 1874), and provided few perspectives of avian species densities or assemblages relative to local geographic features or vegetative associations.

Although the Great Plains played a major role in the evolution of the North American avifauna (Mengel 1970), the grassland avifauna itself is relatively depauperate. Only 5% of all North American bird species are believed to have evolved within the Great Plains (Udvardy 1958, Mengel 1970). Mengel (ibid.) listed 12 species of birds endemic to the grasslands along with 25 others that he considered to be secondarily evolved to grasslands (Table 1). Two of the endemics frequent wetland habitats within the grasslands, with the others being upland species. Species that are secondarily evolved to the grasslands typically occur in more widespread geographic areas and are found primarily in landscapes where brush or trees have invaded grasslands on the periphery of the Great Plains. None of the secondary species are wetland associates, although the breeding biology of the White Pelican (*Pelecanus erythrorhynchos*) suggests that it also is a member of this more widespread group (Knopf 1975). Five of the secondary species (Sage Grouse, Sage Thrasher, Green-tailed Towhee, Sage Sparrow, and Brewer's Sparrow) are really species of the Great Basin shrubsteppe.

The endemic birds evolved with specific ecological niches within the grasslands. Wetland species obviously occur locally at moist-soil sites. Species of taller grasses as the Greater Prairie-chicken and Dickcissel nest in habitats of standing residual vegetation from a preceding growing season and are dependent upon stand rejuvenation by periodic fires (e.g., Kirsch 1974). Many of the endemic species of shortgrass and mixed grass landscapes such as the Baird's Sparrow, McCown's and Chestnut-collared longspurs coevolved with grazing ungulates, whereas others such as the Ferruginous Hawk, Prairie Falcon, and Burrowing Owl are strongly associated with prairie-dog towns. Evolutionarily, drought tolerance appears to be the principal ecological process influencing grassland-bird assemblages

locally (Wiens 1974), with grazing (Hobbs and Huenneke 1992) and wildfire (Zimmerman 1992) having major, secondary roles.

## THE CONTEMPORARY LANDSCAPE

The landscape of the Great Plains has undergone significant alteration from descriptions provided in early accounts. The impacts have been varied, with many (e.g., urbanization, mineral exploration, defense installations) having primarily local impacts on the native avifauna. Activities with more universal impacts on the landscape have included 1) transformation of the native grazing community, 2) cultivation of grains and tame grasses, 3) draining of wetlands, and 4) woody development in the form of tree plantings and ecological invasions.

### *Removal of native grazers*

An estimated historical population of 30 million plains bison was systematically reduced to 281 by 1889 (Hornaday 1887, Roe 1951), with most of this reduction coming in the Great Slaughters of 1870–1873 south of the Platte River and 1880–1883 north of the Platte River. Beginning in the 1860s, cattle were quickly moved into locales as soon as bison were removed, but probably had little immediate impact as they were grazed over broad expanses. Homesteading of the grasslands commenced with the Homestead Act of 1862 and progressively resulted in grasslands being fenced into smaller parcels. The great blizzards of 1885 and 1886 killed 85% of the cattle in Colorado (Badaracco 1971) and blizzards of 1886 and 1887 locally killed 30–80% of the cattle in the northern plains states (Fedkiw 1989). The evolving cattle industry then began fencing also and switched from "open-range" grazing to a ranching industry to grow supplemental winter feeds. Subsequent homesteading acts of the early 20th century increased parcel size from 0.65 km$^2$ to 2.6 km$^2$ and resulted in the remaining (arably more marginal) public lands on the western plains becoming fragmented also. Cattle numbers on the western range in 1890 were estimated at 45 million, plus about that many domestic sheep (Fedkiw 1989). The ultimate consequence of fencing that many animals was to reduce the natural variability in grazing behavior of herding ungulates and, ultimately, to standardize grazing in-

TABLE 1. THE NORTH AMERICAN GRASSLANDS AVIFAUNA (AFTER MENGEL 1970).

| Non-passerines | Passerines |
|---|---|
| I. Primary species (endemic) | |
| 1. *Buteo regalis* Ferruginous Hawk | 1. *Anthus spragueii* Sprague's Pipit |
| 2. *Charadrius montanus* Mountain Plover | 2. *Aimophila cassinii* Cassin's Sparrow |
| 3. *Numenius americanus* Long-billed Curlew | 3. *Ammodramus bairdii* Baird's Sparrow |
| 4. *Limosa fedoa* Marbled Godwit | 4. *Calamospiza melanocorys* Lark Bunting |
| 5. *Phalaropus tricolor* Wilson's Phalarope | 5. *Calcarius mccownii* McCown's Longspur |
| 6. *Larus pipixcan* Franklin's Gull | 6. *C. ornatus* Chestnut-collared Longspur |
| II. Secondary species (more widespread) | |
| 1. *Ictinia mississippiensis* Mississippi Kite | 1. *Eremophila alpestris* Horned Lark |
| 2. *Buteo swainsoni* Swainson's Hawk | 2. *Oreoscoptes montanus* Sage Thrasher |
| 3. *Circus cyaneus* Northern Harrier | 3. *Sturnella magna* Eastern Meadowlark |
| 4. *Falco mexicanus* Prairie Falcon | 4. *S. neglecta* Western Meadowlark |
| 5. *Tympanuchus cupido* Greater Prairie-chicken | 5. *Spiza americana* Dickcissel |
| 6. *T. pallidicinctus* Lesser Prairie-chicken | 6. *Pipilo chlorura* Green-tailed Towhee |
| 7. *T. phasianellus* Sharp-tailed Grouse | 7. *Passerculus sandwichensis* Savannah Sparrow |
| 8. *Centrocercus urophasianus* Sage Grouse | 8. *Ammodramus savannarum* Grasshopper Sparrow |
| 9. *Bartramia longicauda* Upland Sandpiper | 9. *A. henslowii* Henslow's Sparrow |
| 10. *Athene cunicularia* Burrowing Owl | 10. *Pooecetes gramineus* Vesper Sparrow |
| 11. *Asio flammeus* Short-eared Owl | 11. *Chondestes grammacus* Lark Sparrow |
| | 12. *Amphispiza belli* Sage Sparrow |
| | 13. *Spizella breweri* Brewer's Sparrow |
| | 14. *S. pallida* Clay-colored Sparrow |

tensities across broad landscapes (Knopf 1993).

The well known destruction of the bison on the shortgrass prairie was immediately followed by an equally intensive effort to eradicate the other major herbivore, the prairie-dog. Prairie-dogs historically occupied an estimated 404,858 km$^2$, compared to only 6073 km$^2$ in 1980 (Summers and Linder 1978). This 98% reduction has been attributed to the potential competition between prairie dogs and cattle for grass forage, claims which are neither supported by data (O'Meilia et al. 1982) nor by indications that ungulates and prairie dogs are actually symbiotic foragers (Krueger 1986). Most significantly, prairie-dogs are ecological "keystone" species (Gilbert 1980, Terborgh 1986). Keystone species are those that (by their presence) provide appropriate habitat conditions or prey for the continued existence of other species. In the case of prairie dogs and birds, such species include the endemics Ferruginous Hawk and Mountain Plover, and more widespread species as the Burrowing Owl.

*Cultivation*

The second major change in the Great Plains landscape has been the plowing of grasses, primarily for cereal grain production. The eastern plains have been virtually obliterated for grain (primarily corn) production, as evidenced by data available from Illinois and Iowa (Table 2). Only 10.4 km$^2$ of the original 103,600 km$^2$ of native prairie survives in the state of Illinois (Mlot 1990), although the structurally similar tame-grass hayfields provide acceptable habitats for some birds of the historic landscape. Where locally grown on the shortgrass and transition prairie zones, corn generally requires irrigation. These latter regions are sown mostly to dryland (winter) wheat. Unlike the eastern plains, however, the proportion of native grasslands on the western Great Plains (Colorado, Montana, Wyoming) that have remained in a grassland landscape is comparatively high. In addition, 15,436 km$^2$ remain in 19 National Grasslands (USDA 1990), with 17 of those on the Great Plains, predominantly in the shortgrass prairie. Compared to the eastern grassland landscape, the western is merely fragmented rather than obliterated.

TABLE 2. RELATIVE AREA (KM$^2$ × 10$^3$) OF PRIVATE LANDS IN CROPLAND, INTRODUCED PASTURE GRASSES, AND NATIVE GRASS RANGELANDS ON THE GREAT PLAINS OF THE UNITED STATES (ADAPTED FROM U.S.D.A. 1987)

| | Cropland | Pasture-land | Rangeland |
|---|---|---|---|
| Tallgrass prairie | | | |
| Illinois | 100.07 | 12.78 | 0.0 |
| Iowa | 107.00 | 18.36 | 0.0 |
| Total | 207.07 | 31.14 | 0.0 (0%) |
| Mixed prairies | | | |
| Kansas | 117.84 | 9.07 | 68.43 |
| Nebraska | 82.06 | 8.60 | 93.47 |
| North Dakota | 109.43 | 5.15 | 44.31 |
| Oklahoma | 46.82 | 28.89 | 60.95 |
| South Dakota | 68.58 | 10.94 | 92.02 |
| Total | 424.72 | 62.65 | 706.65 (59.2%) |
| Shortgrass prairie | | | |
| Colorado | 42.91 | 5.10 | 98.03 |
| Montana | 69.59 | 12.29 | 153.12 |
| Wyoming | 10.39 | 3.05 | 108.92 |
| Total | 122.89 | 20.44 | 360.07 (71.5%) |

The historical decline in native grasslands has slowed with additional losses of only 17.75 km$^2$ occurring from 1982 to 1987 (USDA 1989). The first four years of the Conservation Reserve Program prompted the reseeding of 21,697 km$^2$ to native grasses through 1989 (S. Brady, Soil Conserv. Serv., pers. comm.). The reseeding represented 5.3% of cropland in the three shortgrass prairie states and 3.4% of cropland in the transition prairie states. The program has had negligible impact on restoring taller grass sites to the east.

*Loss of wetlands*

The drainage of wetlands during cultivation practices has profoundly altered the phytogeography of grasslands locally (Dahl 1990). Losses in Illinois and Iowa have equalled 86.3% of an estimated 49,421 km$^2$ historical wetland area. Comparable values for Colorado, Wyoming, and Montana show

only a 40.0% loss of 20,838 km$^2$. Losses in the mixed-grass states have been an intermediate 56.6% of 70,478 km$^2$. These numbers support the intuitive relationship between the loss of wetlands and intensity of cultivation across the Great Plains.

### *Woody development*

The vertical structure of the grassland landscape is fragmented also. Fire control has enabled woody vegetation to encroach on the northern and southern grasslands (Bird 1961, Pulich 1976). In addition, almost 3% of the Great Plains is now forested by shelterbelts planted to reduce wind erosion (Baer 1989). Trees are currently being planted on the Great Plains at the rate of $20.7 \times 10^6$/year (Griffith 1976).

On the shortgrass prairie, woody vegetation has also increased through ecological processes. Shrub and small tree encroachment occur along the entire periphery of the Great Plains due to control of natural fires. Equally significant has been the ecological development of streamside forests of alien and exotic tree species across the western landscape. These forests appeared in response to 20th-century water-management practices that favor woody colonization and secondary succession (Knopf and Scott 1990, Johnson 1993).

## THE CONTEMPORARY AVIFAUNA

Of the 435 bird species breeding in the United States, 330 have been documented as breeding on the Great Plains (Johnsgard 1979). Whereas many species such as the Passenger Pigeon (Grinnell 1875) and Eskimo Curlew (Sutton 1967) historically appeared on the grasslands, a review of changes by species, genus, or even ecological guild is beyond the scope of this paper. Rather, I proffer that avian assemblages on the grasslands reflect two broad patterns of change that have occurred in the last century: native endemic species have declined in numbers while simultaneously (and rather independently) alien and exotic species have increased immeasureably.

TABLE 3. BIOME AND GUILD COMPARISONS OF CONTINENTAL TRENDS IN BIRD ASSEMBLAGES BASED ON BREEDING BIRD SURVEY DATA, 1966–1991 (ADAPTED FROM DROEGE AND SAUER 1993)

| Group | No. species | No. (%) increasing | P |
|---|---|---|---|
| Grassland Nesters[1] | 18 | 3 (17) | 0.008 |
| Wetland Nesters | 41 | 26 (63) | 0.117 |
| Waterfowl | 15 | 10 (67) | 0.302 |
| Woodland Nesters | 60 | 37 (62) | 0.092 |
| Deciduous Woodland Nesters | 15 | 9 (60) | 0.607 |
| Coniferous Woodland Nesters | 26 | 17 (65) | 0.169 |
| Scrub Nesters | 60 | 19 (32) | 0.006 |
| Urban Nesters | 12 | 4 (33) | 0.388 |
| Permanent Residents | 48 | 20 (42) | 0.312 |
| Neotropical Migrants | 90 | 53 (59) | 0.113 |
| Short-distance Migrants | 83 | 37 (45) | 0.380 |
| Primary Cavity Nesters | 11 | 6 (55) | 1.000 |
| Secondary Cavity Nesters | 27 | 17 (63) | 0.248 |
| Open-Cup Nesting Passerines | 103 | 50 (49) | 0.844 |
| Ground Nesters | 33 | 15 (46) | 0.728 |
| All birds | 302 | 153 (51) | 0.863 |

[1] Bird species defined at the Breeding Bird Survey include only upland, grass-nesting species that were recorded on ≥50 routes in 1966 and 1991. Of the endemics defined by Mengel, Long-billed Curlew, Sprague's Pipit, Lark, Baird's, Cassin's sparrows, and McCown's and Chestnut-collared longspurs met these criteria. Of the more widespread species, Greater Prairie-chicken, Upland Sandpiper, Horned Lark, Eastern and Western meadowlarks, Dickcissel, Savannah, Grasshopper, and Vesper sparrows met inclusion criteria. Two grassland-nesting species included in this guild that did not appear on Mengel's list include Ring-necked Pheasant (*Phasianus colchicus*) and Bobolink (*Dolichonyx oryzivorus*).

### *Declines in grassland endemic species*

During the last quarter of the century, grassland species have shown steeper, more consistent, and more geographically widespread declines than any other behavioral or ecological guild of North America species, including neotropical migrants (Table 3). Not surprising, the geographic pattern of these declines (Fig. 1) is polarized to the eastern and western provinces to which the grassland endemics are primarily adapted. More surprising, most of the species that breed on the grasslands also spend the winter on the continent (MacArthur 1959: Fig. 8-4). The problems of declines in grassland species is associated almost entirely with North American processes.

Population declines of individual species are often difficult to detect due to the in-

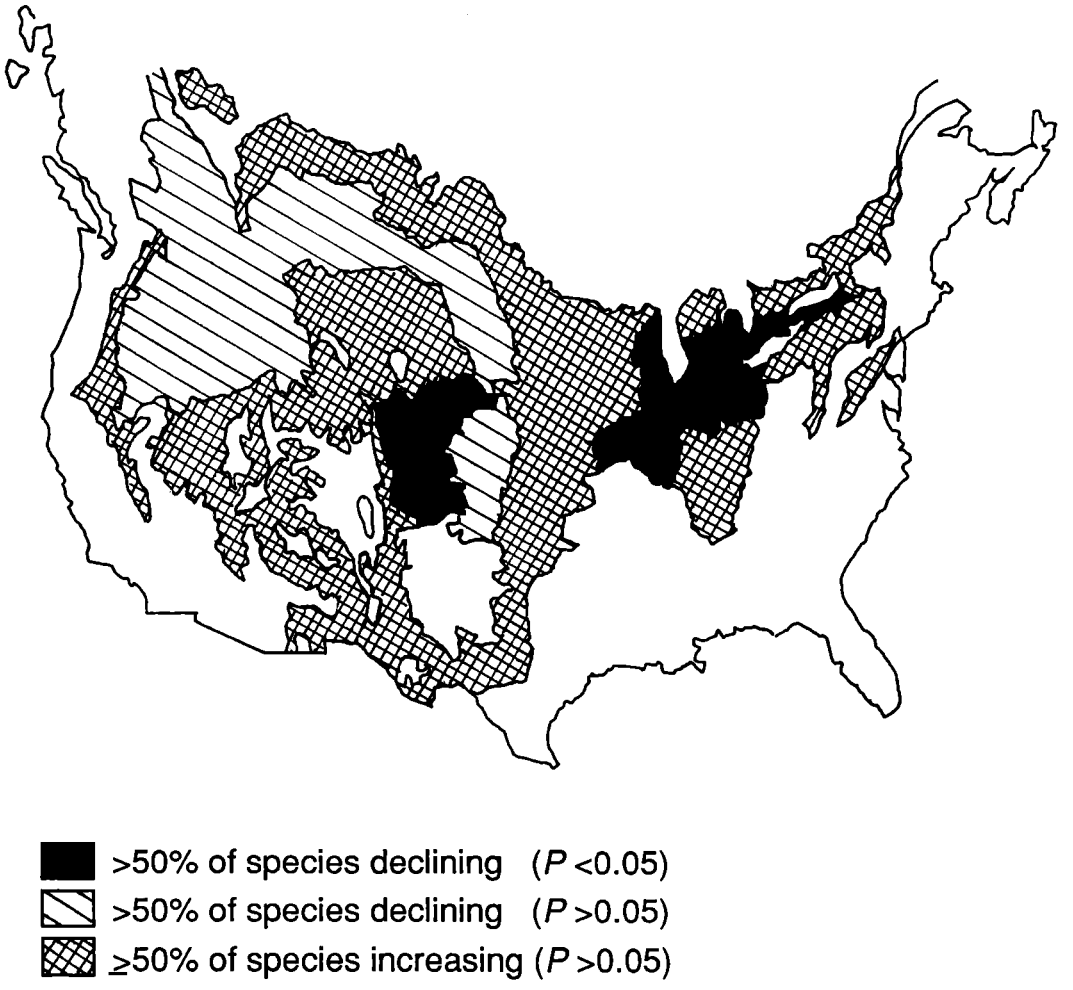


FIGURE 1. Geographical patterns of population changes for grasslands birds of North America based on analyses of Breeding Bird Survey data within physiographic strata. (Figure adapted from Droege and Sauer 1993).

herent variability in geographic distribution of a species population as illustrated for Dickcissel (Robbins and Van Velzen 1969, Fretwell 1986). However, continental population trends for individual species within the native grasslands avifauna (Table 4) generally support the decline seen for the grassland-nesting guild. Excluding the wetland-associated Marbled Godwit and Wilson's Phalarope, seven of the ten endemic species showed population declines during the last 26 years, with declines of four (Mountain Plover, Franklin's Gull, Cassin's Sparrow, Lark Bunting) being statistically significant. Similarly, 16 of the 25 more widespread species declined during this time period with six (Eastern Meadowlark, Grasshopper, Henslow's, Lark, Brewer's, and Clay-colored sparrows) being statistically significant. Across all grassland species, populations of only the Upland Sandpiper and McCown's Longspur have increased significantly since 1966.

Reasons for population declines among species within the grassland avifauna are difficult to assess. Examining trends for those species where declines are supported statistically, the declines appear to be localized

TABLE 4. ANNUAL RATES OF CHANGE IN CONTINENTAL POPULATIONS OF GRASSLAND BIRD SPECIES 1966–1991 (BREEDING BIRD SURVEY DATA)

| Species | No. of routes | Percentage[1] | | Population trend[2] |
|---|---|---|---|---|
| | | Increasing | Decreasing | |
| Endemics | | | | |
| Ferruginous Hawk | 242 | 51.7 | 42.6* | +0.4 |
| Mountain Plover | 40 | 45.0 | 50.0 | −3.6* |
| Long-billed Curlew | 222 | 45.5 | 50.0 | −0.6 |
| Marbled Godwit | 181 | 54.7 | 43.1 | +1.0 |
| Wilson's Phalarope | 339 | 41.3 | 54.6 | +0.8 |
| Franklin's Gull | 225 | 35.1 | 60.4* | −7.4* |
| Sprague's Pipit | 136 | 38.2 | 55.9 | −3.1 |
| Cassin's Sparrow | 169 | 49.7 | 48.5 | −3.4* |
| Baird's Sparrow | 132 | 39.4 | 56.8 | −1.6 |
| Lark Bunting | 344 | 39.8 | 57.6* | −3.3* |
| McCown's Longspur | 66 | 45.5 | 47.0 | +7.9* |
| Chestnut-colored Longspur | 151 | 42.4 | 54.3 | +0.6 |
| Secondary species | | | | |
| Mississippi Kite | 163 | 58.9 | 40.5* | +0.4 |
| Swainson's Hawk | 607 | 48.8 | 46.6 | +1.2 |
| Northern Harrier | 1075 | 43.7 | 52.5 | −1.0 |
| Prairie Falcon | 261 | 47.1 | 43.7* | +0.2 |
| Greater Prairie-chicken | 47 | 40.0 | 53.2 | −10.3 |
| Lesser Prairie-chicken | 8 | 25.0 | 62.5 | +8.1 |
| Sharp-tailed Grouse | 180 | 41.7 | 52.8 | +0.9 |
| Sage Grouse | 103 | 52.4 | 46.6 | +6.2 |
| Upland Sandpiper | 668 | 51.5 | 45.8* | +3.5* |
| Burrowing Owl | 349 | 43.3 | 51.6 | −0.2 |
| Short-eared Owl | 268 | 38.1 | 57.5* | −0.7 |
| Horned Lark | 1708 | 40.6 | 56.8* | −0.7 |
| Sage Thrasher | 230 | 53.0 | 44.8 | +1.4 |
| Eastern Meadowlark | 1714 | 30.5 | 68.6* | −2.2* |
| Western Meadowlark | 1304 | 38.0 | 59.7* | −0.6 |
| Dickcissel | 780 | 37.6 | 60.9* | −1.7* |
| Green-tailed Towhee | 207 | 43.0 | 51.2 | +0.3 |
| Savannah Sparrow | 1418 | 42.9 | 54.4* | −0.6 |
| Grasshopper Sparrow | 1446 | 37.6 | 58.8* | −4.6* |
| Henslow's Sparrow | 249 | 30.9 | 61.8* | −4.2* |
| Vesper Sparrow | 1473 | 38.5 | 58.2* | −0.6 |
| Lark Sparrow | 909 | 44.7 | 52.6 | −3.4* |
| Sage Sparrow | 205 | 38.0 | 58.5* | −2.4 |
| Brewer's Sparrow | 359 | 39.8 | 55.7* | −4.1* |
| Clay-colored Sparrow | 441 | 43.8 | 52.4 | −1.5* |

[1] Percentages totaling <100% include some routes with no change in numbers of birds detected. Asterisk indicates trend significantly ($P < 0.05$) different from no difference between number of surveys with increasing vs. decreasing species populations.
[2] Annual rate (expressed as a percentage) of change in population numbers. Asterisk indicates a statistically significant ($P < 0.05$) rate of population change.

for Franklin's Gull, Dickcissel, Henslow's and Grasshopper sparrows, Lark Bunting, and Eastern Meadowlark in that these species show a significant difference in the proportion of surveys with increasing vs. decreasing populations. This pattern of significant local declines for species that also are declining continentally reflects a pattern of loss of local breeding habitats.

Declines in populations of Mountain Plover, and Cassin's and Clay-colored sparrows were universal across their respective geographic ranges (not varying among surveys). The seasonal distributions and ecology of the sparrows are poorly understood. The plover is now rare on its former wintering areas in southern Texas and has a highly fragmented wintering distribution in California. Based upon the plover example, declines in this group of birds appear attributable to decline or degradation in the quality of habitats available for wintering.

Population trends for a third group of grassland species (Ferruginous Hawk, Mississippi Kite, Upland Sandpiper, Short-eared Owl, Horned Lark, Western Meadowlark, Vesper, Savannah, and Henslow's sparrows) show significant changes in relative abundance among surveys even though continental numbers are stable. The geographic distributions of these species appear to be changing at present.

Whereas wetlands-associated species have certainly declined since settlement of the grasslands in the mid 1800s, BBS data indicate that populations of the endemic Marbled Godwit and Wilson's Phalarope are stable. Wetland conservation actions to benefit waterfowl have apparently stabilized populations of these latter species.

*Increases in cosmopolitan species*

The negative consequences of landscape fragmentation to local and regional avian assemblages are well known (Robbins et al. 1989b) and have real implications to the conservation of grassland birds (Samson 1980, Johnson and Temple 1986). Fire control and woody plantings on the grasslands have had such an effect by favoring many species that can colonize the newly created forest patches. Regional responses of bird assemblages to a century of fire control are not available, but can be inferred from studies (e.g., Dixon 1989) of individual species populations.

A large percentage of breeding bird species on the central Great Plains appear restricted to sites of artificial woody plantings (Martin 1981). Most shelterbelt species are forest-edge inhabitants historically present in midwestern oak (*Quercus* spp.) savannas and eastern deciduous forests. Yahner (1983) reported that only three (Western Meadowlark, Savannah and Vesper sparrows) of the 47 most abundant species using shelterbelts on his study area were typical of the historic grasslands of western Minnesota.

Although forest-bird species historically occurred west of their general habitats and into streamside forests of the eastern grasslands (Coues 1874), the development of riparian forests along streambeds of the shortgrass prairie has effectively created linear forests that have favored the movement of many species farther onto (and even across) the grasslands. At one location, Crook, Colorado, 83 species of birds in the riparian vegetation during the early breeding season included only three representatives (Cassin's, Clay-colored, and Harris' sparrows) of the Great Plains avifauna, and none of those bred locally (Knopf 1986). That riparian forest developed since 1900, and >90% of the native birds currently at that site have colonized in recent times. The proportion is >95% if exotic species are included.

As a consequence of the riparian forest development on the western Great Plains, some of the invading species established secondary contact with closely related congeners. Such species include representatives of flickers, jays, buntings, grosbeaks, towhees, and orioles (Sibley and West 1959, West 1962, Sibley and Short 1959, 1964; Short 1965, Rising 1970, Williams and Wheat 1971, Emlen et al. 1975, Moore and Buchanan 1985); there are so many species, in fact, that the region has been ornithologically identified as the Great Plains Hybrid Zone (Rising 1983). Further north, western riparian species such as the Yellow-breasted Chat (*Icteria virens*) and American Goldfinch (*Carduelis tristis*) were historically hypothetical or accidental in Wyoming (Knight 1902), yet breed state-wide today. Enhanced deciduous forests on the grasslands have also favored movements of reptiles and mammals (Knopf and Scott 1990) and have, in part, been fundamental in defining faunal mixing as a conservation issue (Knopf 1992).

## CONSERVATION INTO THE NEXT CENTURY

Just as grasslands are avifaunistically simple, so too appear the challenges facing conservation of these birds. Unquestionably, faunal invasions of the central grasslands are wildlife enhancements. Such en-

hancements have positive public-awareness benefits for conservation issues in general and, thus, seem desirable except where aliens and exotics degrade habitats of endemic species. The U.S. Department of Agriculture's Conservation Reserve Program promises to reverse the decline in breeding habitats for some species, much as waterfowl conservation programs have had some secondary benefits for wetlands species. The Western Governor's Association is currently discussing a political template for regionalizing conservation action, which will be the first step towards aligning conservation action with biogeographic provinces (Knopf 1992). That international action, the Great Plains Initiative, holds great promise for a proactive and more cost-effective approach to conservation by focusing conservation on the floral and faunal integrity of the Great Plains (Knopf and Samson 1995).

Ecological processes driving population trends of North American grassland birds are currently undescribed. As a group, grassland birds have declined more than birds of other North American vegetative associations. Unlike neotropical migrants which have experienced declines primarily in the northeastern deciduous forests (Robbins et al. 1989a), however, declines in grassland species are occurring at a continental scale. The decline in the Mountain Plover, Cassin's Sparrow, and Lark Bunting are major conservation concerns. The lack of understanding of the wintering ecology of grassland birds precludes optimistic projections for especially these species experiencing widespread, geographic declines.

ACKNOWLEDGMENTS

I thank J. R. Jehl, Jr. and N. K. Johnson for the opportunity to develop this manuscript and S. Droege for his insights.

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