

CHAPTER 10

Prairie Legacies—Birds

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To many naturalists, native birds of prairie landscapes are the drabest, most boring, and ecologically least significant of the North American avifauna. The generally small, mostly nondescript species forage in hidden places of nearly featureless landscapes much as small mammals do, rather than as their colorful brethren that flit through lush forests or display decorative plumes as they stride erectly through shallow wetlands. Yet the sun rises on calm spring mornings and males burst from their herbaceous hidings in a flight that exposes brightly colored underparts and melodious songs, often with accentuated wing movements that more resemble insects than birds. And off on a barren rise, chickenlike fowl of browns-with-barring puff gigantic orange-red neck sacks to boom an antediluvian drumming across still grasses. Wind muffles sounds on the prairie. But when wind stills, birds provide the sounds of the prairie. The consonance of bird songs speaks to the health of the grasslands that once stretched, unbroken, to every horizon.

The Endemic Prairie Avifauna

Prairie, or steppe, landscapes cover $7 \text{ ha} \times 10^9 \text{ ha}$ of the world—over half of its terrestrial surface (Imboden 1988). Almost $1.5 \text{ ha} \times 10^9 \text{ ha}$ of prairie occur in North America, representing about 17 percent of the continent. Despite the extensiveness of North American prairies, however, they have not resulted in the radiation of a diverse avifauna. Only 5.3 percent of North American bird species

evolved on prairies (Udvardy 1958; Mengel 1970). Excluding wetland and sagebrush associates, nine species are what might be considered narrow endemics (Bidley et al. 1992) of the Great Plains, and an additional twenty species are more widespread but have strong affinities to the Great Plains. These avian representatives of the native prairie vertebrates are equally divided between passerine and nonpasserine forms (see table 10.1).

Avian assemblages on grasslands are locally simplistic, often dominated by only a few species. Four species (common yellowthroat, red-winged blackbird, common grackle, and eastern meadowlark) collectively accounted for 63 percent of all individuals recorded during surveys from 1991 to 1994 on the Goose Lake Prairie area in Illinois (J. R. Herkert, personal communication). Another four species (horned lark, western meadowlark, lark bunting, and chestnut-collared longspur) accounted for 69 percent of all individuals recorded at many sites across the northern Great Plains (Kantrud and Kologiski 1982). Only three species (horned lark, McCown's longspur, and lark bunting) accounted for 913 of 1,047 (87 percent) of all birds that I recorded on 112 point surveys of the

Table 10.1
North American prairie avifauna of the Great Plains

Nonpasserines	Passerines
<i>Primary (Endemic) Species</i>	
Ferruginous hawk	Sprague's pipit
Mountain plover	Cassin's sparrow
Long-billed curlew	Baird's sparrow
	Lark bunting
	McCown's longspur
	Chestnut-collared longspur
<i>Secondary (More Widespread) Species</i>	
Mississippi kite	Horned lark
Swainson's hawk	Eastern meadowlark
Northern harrier	Western meadowlark
Prairie falcon	Dickcissel
Greater prairie chicken	Savannah sparrow
Lesser prairie chicken	Grasshopper sparrow
Sharp-tailed grouse	Henslow's sparrow
Upland sandpiper	Vesper sparrow
Burrowing owl	Lark sparrow
Short-eared owl	Clay-colored sparrow

Source: Modified from Mengel 1970.

Note: Excludes wetlands associates and species with stronger ecological associations with sagebrush (*Artemisia* spp.) landscapes of the Great Basin.

Pawnee National Grasslands, Weld County, Colorado in 1990. The total number of native species, excluding wetland associates and exotics, recorded in those three studies were 38, 29, and 14, respectively.

Distribution of Prairie Birds

As defined in earlier chapters, the North American prairie is usually viewed as comprising eastern tallgrass, central mixed-grass, and western shortgrass components. The mixed-grass and tallgrass components extend westward at more northerly latitudes. By definition, mixed-grass landscapes are ecotones between tallgrass and shortgrass associations, but do have specific floral elements (Risser 1985).

Native birds of prairies can be viewed relative to their distribution across the grassland associations of the Great Plains. Of the endemic prairie birds, short-grass and short-mixed-grass associates include six of the nine species, two species appear to be primarily mixed-grass associates, and one species, the Cassin's sparrow, occurs along the prairie-shrub ecotone of the southwestern United States (see fig. 10.1). Evolutionarily, these species radiated from the short-mixed-grass prairies of north-central Montana (see fig. 10.2). None of the endemic birds of North American grasslands are associates of tallgrass prairies.

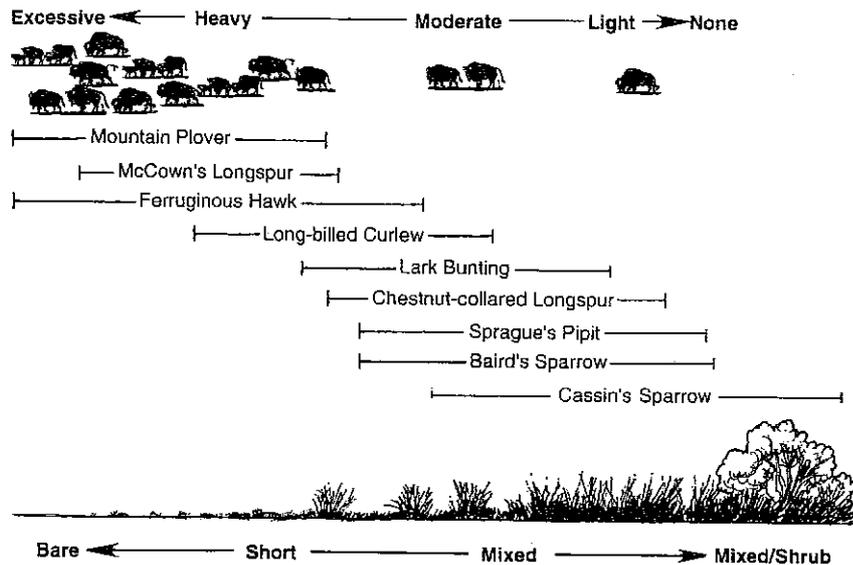


Fig. 10.1 Distributions of endemic birds of prairie uplands relative to grassland type and historical grazing pressure across the western landscapes of the Great Plains.

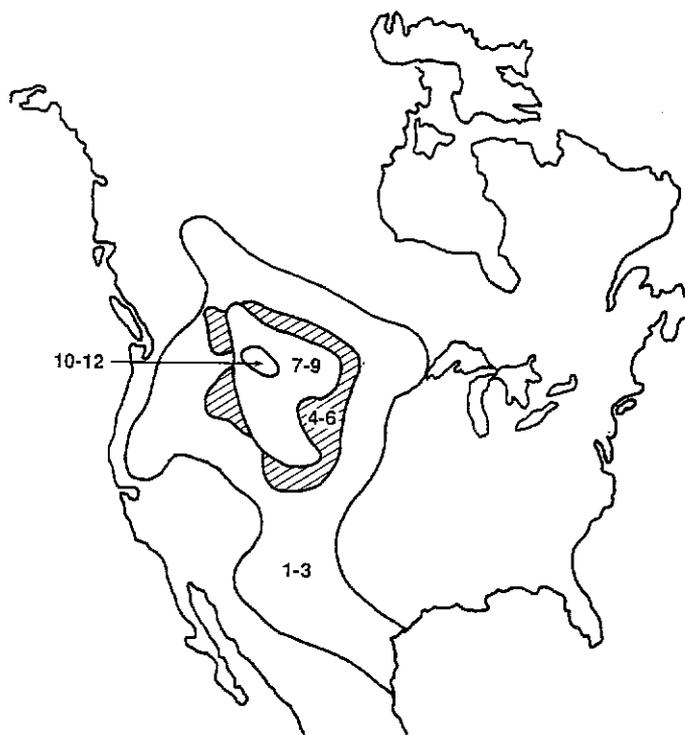


Fig. 10.2 Collective distributions of endemic birds of North American prairie (including three wetland species) illustrating the importance of shortgrass prairie as the biogeographic region from which these species radiated. Isoclines delineate the number of species nesting within a geographic area (after Mengel 1970). The center of radiation is approximately north-central Montana.

The secondary prairie species are more widespread than the primary endemics (see table 10.2). Six are shortgrass or short-mixed-grass associates, three primarily mixed-grass, and six tallgrass or tall-mixed-grass. The horned lark is the only shortgrass-specific species, and the dickcissel and Henslow's sparrow are the only tallgrass-specific species. The dickcissel will use areas of shrub invasion into tallgrass (Zimmerman 1992), but primarily responds to the grass component locally (Zimmerman, personal communication).

Five additional widespread species characteristically use ecotonal areas of shrub incursion into prairie or forest savannah. These ecotone species include Mississippi kite and lesser prairie chicken on the south, and sharp-tailed grouse and clay-colored sparrow on the north and west. The lark sparrow occurs across prairie types and selects habitats based more on local brush associations than characteristics of the grasses.

Table 10.2

Relative ecological associations of grassland birds in North America

	Grass				
	Short	Short/Mixed	Mixed/tall	Tall	Ecotone ^a
<i>Primary (Endemic) Species</i>					
Mountain plover*	X				
Long-billed curlew	X				
McCown's longspur	X				
Ferruginous hawk	X	X			
Chestnut-collared longspur	X	X			
Lark bunting	X	X			
Baird's sparrow		X	X		
Sprague's pipit*			X		X
<i>Secondary (More Widespread) Species</i>					
Horned lark*	X				
Swainson's hawk	X	X			
Prairie falcon	X	X			
Burrowing owl	X	X			
Vesper sparrow	X	X			
Savannah sparrow		X	X		
Short-eared owl		X	X		
Western meadowlark		X	X		
Upland sandpiper			X	X	
Northern harrier			X	X	
Greater prairie chicken			X	X	
Grasshopper sparrow			X	X	
Eastern meadowlark*			X	X	
Henslow's sparrow*				X	
Dickcissel*					X
Mississippi kite					X
Lesser prairie chicken					X
Sharp-tailed grouse					X
Clay-colored sparrow*					X
Lark sparrow*					X

^aAreas of significant brush associations or forest savannas.

*Species declining at $P \leq 0.05$ (see Table 10.3).

Historical Ecology of Endemic Birds

The native landscape of the shortgrass prairie was a mosaic ranging from areas of excessive disturbance to areas of infrequent or no grazing. The primary herbivores included prairie dogs, pronghorn, and bison (see fig. 10.3). Bison and pronghorn preferentially graze on prairie dog towns (Coppock et al. 1983b; Krueger 1986), thus intensifying grazing and trampling pressure locally. In addition, areas at the headwaters of the Platte River held large herds of bison for prolonged periods. Large numbers of bison wallows are still discernable (see fig. 10.4), and many remain unvegetated in the 1990s even though bison were extirpated locally in 1867 (Hornaday 1889). Throughout the western Great Plains, prairie dog numbers have been reduced 98 percent (Summers and Linder 1978), and domestic cattle have been substituted for the bison.



Fig. 10.3 Historical distribution of bison in North America. The dashed line represents the approximate widest distribution (Hornaday 1889). The solid line identifies the shortgrass prairie where the large herds, and most animals, were located. The solid line also approximates the distribution of white-tailed and black-tailed prairie dogs.

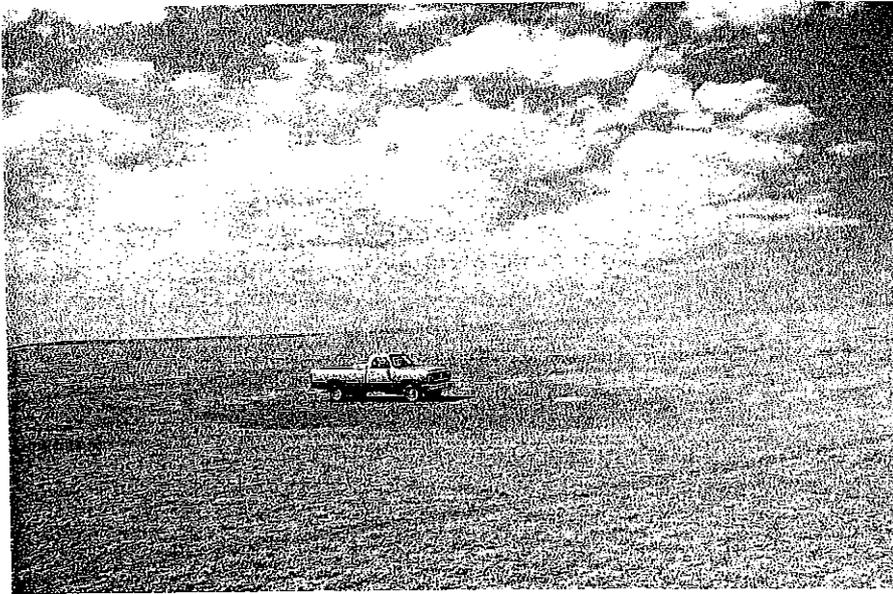


Fig. 10.4 A buffalo wallow on the Pawnee National Grassland. Wallows are readily discernible although the buffalo was extirpated locally over 125 years ago. Wallows are often up to 50 m in diameter and 3 m deep.

All of the endemic birds of prairies evolved within this grazed mosaic of the grassland landscape (see fig. 10.1). The mountain plover and McCown's longspur occur at sites of heavy grazing pressure to the point of excessive surface disturbance (Knopf and Miller 1994; Warner 1994). The plover will actually nest on plowed ground (Shackford 1991) and spends its winters in California's Central Valley, which was historically clipped by extensive kangaroo rat populations and grazed by an estimated six hundred thousand Tule elk (McCullough 1971). The ferruginous hawk also prefers moderate to heavily grazed sites as taller grasses reduce the detectability of their small-mammal prey (Wakeley 1978).

A second suite of species appear more adapted to moderate grazing intensities. The long-billed curlew, lark bunting, and Sprague's pipit prefer areas of taller grasses interspersed in a shortgrass landscape. All three species use the taller grass tufts to conceal nests (Bicak et al. 1982; Finch et al. 1987; Kantrud 1981), and the longspur may also sing from elevated perches.

The Baird's sparrow and chestnut-collared longspur appear at sites across a broad spectrum of grazing intensities (Kantrud 1981; Kantrud and Kologiski 1982). Both of these species also nest in hayfields of native grasses on the northern plains, that is, sites that are not grazed.

The Cassin's sparrow occurs in areas of at least 6 percent shrub cover that is generally lightly (Bock and Webb 1984) to moderately (W. H. Howe, personal

communication) grazed. Breeding habitats of this sparrow probably were outside the distribution of the historically large herds of bison on the plains. The shrub component of its habitat also implies that fire did not play as major a role in maintaining grass vigor as it did in other geographic regions of the Great Plains.

The universal use of grazed landscapes by endemic grassland birds points to the historical impact of grazing as an ecological force on the western Great Plains. Grazing played a significant role in breaking sod. Whereas the ferruginous hawk forages on small mammals, the remaining endemic grassland birds eat insects. Two primary food items, grasshoppers and beetles, require >10 percent of an area to be bare ground in order to lay eggs. Native mammals disturbed the grass sod locally, enabling these insectivorous herbivores to reproduce.

Recent Trends in Populations

Data on changes in bird populations are among the best available for any taxonomic group. The Breeding Bird Survey (BBS) is a coordinated annual inventory of birds in the United States and Canada (Robbins et al. 1986; Sauer and Geissler 1990). The survey presently includes >200,000 point counts at >4,000 locations (Sam Droege, personal communication). Survey results indicate that continental populations of many native birds of the North American prairies were changing rapidly from 1966 to 1991 (Knopf 1994). As a group, grassland birds in general (Askins 1993) and endemic grassland birds specifically (Knopf 1994) have shown steeper, more consistent, and more geographically widespread declines than any other behavioral or ecological guild of North American species.

An update of the population trend information through the most recent analyses (1993) confirms the patterns of decline I reported earlier among the grassland species (see table 10.3). Six of the nine endemic species are declining, and half of those at a statistically significant ($P < 0.05$) rate. The major significant change from the earlier reporting is that the decline in the continental population of Sprague's pipit is now statistically supported.

BBS data are inadequate to determine trends in lesser prairie chickens, but fourteen of the nineteen remaining widespread species were declining, and again half at a significant rate. Only three of the collective twenty-eight species were increasing significantly: the ferruginous hawk, upland sandpiper, and McCown's longspur. Thus, two-thirds of native prairie birds are declining, and half of those declines are supported statistically.

A second major historical inventory of North American birds has been the annual Christmas Bird Count (CBC). Christmas Bird Counts are inventories of all species and numbers of birds recorded in a one-day period within a count area with a radius of 11.2 km. The survey routes tend to focus efforts on more diverse landscapes (wetlands, riparian areas, forest edges) along environmental gradients to maximize the total number of species seen in a day, and thereby probably do

Table 10.3

Annual rates of change in continental populations of grassland bird species 1966–1993

Species	No. of Routes	Birds/Route	Population Trend ^a
<i>Endemics</i>			
Ferruginous hawk	276	0.20	+1.64**
Mountain plover	46	0.39	-3.69***
Long-billed curlew	253	1.37	-1.67
Sprague's pipit	142	1.43	-3.63***
Cassin's sparrow	190	13.64	-2.54***
Baird's sparrow	138	1.62	-1.75
Lark bunting	390	27.31	-2.13*
McCown's longspur	72	4.68	+7.30***
Chestnut-collared longspur	151	9.87	+0.44
<i>Secondary (More Widespread) Species</i>			
Mississippi kite	188	0.71	+0.88
Swainson's hawk	678	0.82	+1.37*
Northern harrier	1,155	0.43	-0.36
Prairie falcon	296	0.10	+0.33
Greater prairie chicken	54	0.55	-6.85
Lesser prairie chicken	N/A ^b		
Sharp-tailed grouse	187	0.49	+1.05
Upland sandpiper	709	1.90	+2.67***
Burrowing owl	379	0.58	-0.18
Short-eared owl	285	0.12	-0.57
Horned lark	1,830	24.65	-0.70**
Eastern meadowlark	1,807	18.02	-2.25***
Western meadowlark	1,424	42.19	-0.52*
Dickcissel	817	12.44	-1.63***
Savannah sparrow	1,502	7.39	-0.53
Grasshopper sparrow	1,540	3.43	-4.11***
Henslow's sparrow	253	0.11	-4.96**
Vesper sparrow	1,548	7.18	-0.29
Lark sparrow	1,013	4.02	-3.45***
Clay-colored sparrow	464	6.61	-1.20***

Source: Breeding Bird Survey.

^aAnnual rate (expressed as a percent) of change in population numbers;

* = $P < 0.10$ ** = $P < 0.05$ *** = $P < 0.01$.

^bInadequate data.

not represent the true numbers of prairie birds as well as the BBS routes, which are more vegetation-specific, standardized in effort, and conducted when birds are actively displaying on territories. Nevertheless, the data are meaningful for those species for which a substantial proportion of the continental population winters in the United States. The Migratory Bird Management Office of the National Biological Service first entered CBC data from twenty-four hundred local counts for the years 1959 to 1988 into electronic form in 1994 (Sam Droege, personal communication).

For the endemic prairie birds, the CBC data corroborate the annual declines in lark bunting and increases in McCown's longspur populations as statistically valid (see table 10.4). The CBC further imparted some statistical significance to declines of the Baird's sparrow and increases of the ferruginous hawk. For the widespread species, declines of the eastern meadowlark and lark sparrow are corroborated, and the nonsignificant BBS trends for four other species (sharp-tailed grouse, short-eared owl, western meadowlark, and vesper sparrow) gained statistical support. These data all must be viewed with caution, however, pending knowledge of what proportion of each species population winters north of Mexico.

Conservation of Prairie Birds

The native prairie landscape was once viewed as home to a meager avifauna that only needed trees to attract birds and become a lavish showcase of color and song. Studies of avifaunas at forest edges (Kendeigh 1941) and within shelterbelts (Martin 1981; Yahner 1983) corroborate this potential. Three percent of the Great Plains is now forested (Knopf and Samson 1995), much of it with exotic tree species such as Siberian elm and Russian-olive. More generally, however, the number of bird species within a local assemblage increases with any human development of a landscape (Grinnell 1922; Knopf and Scott 1990). Such increases in the number of alien and exotic species in native landscapes often result in population declines, or extirpations, of narrow-endemic species going unnoticed (Knopf 1992).

Endangered Species, Endangered Ecosystem

The present proposal activity to list the mountain plover under the Endangered Species Act may be viewed as a precursor to similar action for other prairie bird species as continental populations of one-third of the species are currently declining at statistically significant rates. These declines support the view that the prairies of the Great Plains are the most endangered ecosystem in North America (Samson and Knopf 1994).

Table 10.4

Annual rates of change in continental populations of endemic grassland bird species

Species	BBS	CBC
<i>Endemics</i>		
Ferruginous hawk	+1.64***	+3.9***
Baird's sparrow	-1.75	-1.4***
Lark bunting	-2.13*	-3.7*
McCown's longspur	+7.30***	+2.13**
<i>Secondary Species</i>		
Sharp-tailed grouse	+1.05	+2.2**
Short-eared owl	-0.57	-1.8**
Eastern meadowlark	-2.25***	-2.6**
Western meadowlark	-0.52*	-1.4**
Vesper sparrow	-0.29	-1.7*
Lark sparrow	-3.45***	-2.0**

Note: Numbers in the CBC column reflect bird species that were adequately sampled on Christmas Bird Counts from 1959 to 1988. An adequate statistical sample does not equate to confirmed trends; the proportion of the continental population wintering in the United States is unknown for most of these species. Numbers in the BBS column are from the Breeding Bird Survey. Numbers are the annual rate (expressed as percent) of change in population numbers.

* = $P < 0.10$ ** = $P < 0.05$ *** = $P < 0.01$

Conservation Priorities for Prairie Birds

Densities of prairie bird populations are highly variable from one year to the next and between locales (Robbins and Van Velzen 1969; McNicholl 1988). Reproductive success also varies annually, with some years exhibiting very poor productivity (George et al. 1992; Knopf and Rupert 1996). Such variability is particularly obvious in seasonally unpredictable climates such as the Great Plains, where drought often affects food supplies over broad areas of landscape. Birds have been argued as relatively poor indicators of local environmental degradation (Morrison 1986). Annual fluctuations in populations led Temple and Wiens (1989) to conclude that the duration of a trend is more important than the magnitude of change. The availability of the BBS data (especially where it can be cross-validated with CBC data) far exceeds the scope and detail of information for any other taxonomic group.

Conservation of shortgrass and mixed-grass prairies appears most critical given that sizable areas of these associations remain intact. Declines of the two

shortgrass species, the mountain plover and horned lark, appear relatively universal across biogeographic provinces. The narrowly distributed mountain plover is declining in all regions where it occurs. The widely distributed horned lark is stable at many locations but areas of major decline include such widely separated regions as the Central Valley of California, southern Rocky Mountains, Pinon-Juniper Woodlands, Aspen Parklands, Ozark-Ouachita Region, Ohio Hills, Allegheny Plateau, and Southern Piedmont.

Whereas the endemic species evolved within a mosaic of grazed landscapes, the relatively standardized approach to rangeland management using allotments and applying the same grazing intensity across broad landscapes is contradictory to the historical ecology of these species (Knopf 1996). Alternatively, factors driving widespread declines of prairie birds may not even be in the breeding habitat of the species. Patterns of declines of Cassin's and clay-colored sparrows point to problems at nonbreeding locales (Knopf 1994).

Questions about Widespread Species

Targeting shortgrass and mixed-grass prairies for conservation priority is based on the habitats that they provide for the narrow-endemic species. Unlike the shortgrass prairie, which is still more than half intact, however, the tallgrass prairie is 98 percent tilled (Samson and Knopf 1994), and prairie remnants are isolated and often too small to support some species (Samson 1980; Herkert 1994a). Populations of tallgrass species such as the dickcissel and Henslow's sparrow have historically declined significantly due to the overwhelming fragmentation of the prairie. In contrast to land-management emphasis in the conservation of grassland endemics, conservation of tallgrass species is much more dependent on a series of prairie preserves throughout the region. Management of those preserves also needs to emphasize the wise use of fire, the major natural disturbance critical to maintaining the ecology of tallgrass prairie (Collins and Wallace 1990). Preserves alone may be inadequate, however, and conservation of tallgrass birds will need to address agricultural land-use in many areas.

Population changes among the more widespread species permit some generalizations that can ultimately be posed as hypotheses. For example, declines in eastern meadowlark populations are dominated by trends in eastern states with the species stable and actually increasing at locales on the southern Great Plains. Declines of this meadowlark represent a decline in agricultural pastures and hay meadows due to agricultural intensification in the Midwest (Warner 1994) and succession to forests in eastern states (Askins 1993). Simultaneously, the BBS data indicate that declines in Cassin's and lark sparrows are occurring especially in that region (the Edwards Plateau of Texas) where eastern meadowlark populations are increasing rapidly. Together, these trends point toward ecological phe-

nomena (perhaps brush control) as driving population changes of all three species. A similar ecological scenario may be driving clay-colored sparrow declines, which are primarily occurring in the aspen parklands of Canada.

Assuming that the more widespread species of prairie edges increased historically with fire control and subsequent woody invasion of native prairies, conservation focus for these species strongly depends on the historical reference time that one chooses for comparison. Population distributions of many species in the 1990s may be reverting more toward 1850 patterns. Further diagnostic inquiry into patterns of population change are required to define the long-term significance of declines among the prairie-edge species.

Summary

The endemic avifauna of the Great Plains prairies includes only nine species of upland birds. An additional twenty species apparently evolved on the prairies and currently range broadly into other biogeographic areas. The endemic species are primarily shortgrass or short-mixed-grass associates. Historically, they evolved with the large native herbivore assemblage of the western Great Plains. The landscape was a mosaic of differentially grazed sites. The individual species evolved to specific site characteristics based on local soils, drought cycles, and grazing pressure.

As a group, grassland birds have shown steeper, more consistent, and more geographically widespread declines than any other behavioral or ecological grouping of North American species. Six of the nine endemic and fourteen of nineteen widespread species are declining, and half of all declines are supported statistically. The mountain plover is currently listed as a C-1 candidate species under the Endangered Species Act. The rates of decline in continental populations of the endemic Sprague's pipit, Cassin's sparrow, and lark bunting are cause for immediate concern. Of the more widespread species, declines in the eastern meadowlark, dickcissel, grasshopper sparrow, Henslow's sparrow, lark sparrow, and clay-colored sparrow are also statistically valid. These collective declines point to major landscape-ecosystem changes that warrant immediate ecological inquiry.

Conservation priority for endemic grassland birds is on the historically grazed western Great Plains. In addition, a network of prairie preserves are critical to sustain core populations of tallgrass prairie birds due to the extent of fragmentation of the eastern Great Plains. Unlike other taxonomic groups addressed in this volume, native prairie birds are equally dependent on the quality of breeding, migration, and wintering habitats. Conservation actions require a more cosmopolitan view that extends well beyond the geographical boundaries of the Great Plains.

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Prairie Conservation

Preserving
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