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The Great Plains

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Overview

The Great Plains of North America are grasslands or former grasslands that occupy more than 200 million ha (500 million acres) of land from central Alberta, Canada, to the Texas Panhandle and eastern New Mexico and from the front range of the Rocky Mountains to the forest edge in Minnesota, Missouri, and Oklahoma. The natural plant communities dominating this landscape are known as grasslands or prairie (French for meadow) and they are composed of a rich complex of grasses and forbs. The climate, soils, and topography of the eastern Great Plains are suitable for agriculture, and consequently most of the original prairie has been converted to row crops or pasture. In the western Great Plains, large areas of intact grassland are used as rangeland. Researchers estimate that less than 1% of the original grasslands remains undisturbed by human activities (Klopatek et al. 1979).

Articles in this section focus on the effects of more than 100 years of postsettlement manipulation of the Great Plains ecosystem. For example, fire was undoubtedly an important ecological force in maintaining historical grassland landscapes and species distributions. Following fire suppression, woody plants have invaded grasslands from adjacent forest and wooded stream valleys. In addition, water management practices and the planting of farm and ranch shelterbelts have resulted in the encroachment of trees into grassland habitat. In many parts of the Great Plains today, far more woody plants exist than before agricultural development. As endemic grassland birds have declined, they have been replaced by eastern forest species moving into newly wooded habitats (Knopf; Igl and Johnson, both this section).

Native prairie fishes also have experienced significant losses in their historical distributions. Impoundments constructed on many rivers and streams of the Great Plains have fragmented populations and eliminated colonization of vacant habitat. Several prairie fishes, including the Arkansas River shiner (*Notropis girardi*) and the Arkansas River speckled chub (*Macrhybopsis aestivalis tetranemus*), have shown significant declines in their distributions and abundances (Echelle et al., this section).

The fragmentation of native grassland due to agricultural encroachment as well as the elimination of keystone species, such as bison (*Bison bison*) and the white-tailed prairie dog (*Cynomys leucurus*), have led to a general decline in prairie wildlife, although some species have adapted to human-induced changes and some have even increased in

numbers. For example, native grassland birds have shown steeper, more consistent, and more geographically widespread declines than any other avian group, including Neotropical migrants (Knopf, this section). Species such as mallard (*Anas platyrhynchos*), blue-winged teal (*A. discors*), and northern pintail *(A. acuta*) are now at or near the lowest numbers ever recorded (Shaffer and Newton, this section). The primary reason for these declines in numbers is low nest success due to predation by common species such as red fox (*Vulpes vulpes;* Shaffer and Newton, this section). In other species, such as American coot (*Fulica americana*), drainage of wetlands compounded by severe drought may have played a role in depressing populations (Igl and Johnson, this section). In contrast to waterfowl, the coyote (*Canis latrans*) is increasing its range. Historical and recent trends in coyote populations and diet may reflect a response to land-use changes, especially agricultural changes and shifts in human populations on the Great Plains (Gipson and Brillhart, this section).

The Great Plains are becoming increasingly rural because of emigration of people and a shift of human populations away from farms to urban centers. Although the Great Plains encompass about 20% of the land mass of the lower 48 states, the population is only about 2% of the U.S. total. Federal agricultural land-retirement programs, such as the Soil Bank Program and the Conservation Reserve Program (CRP), devised to mediate fluctuations in the farm economy, may also help slow or reverse the declines of some grassland species. For example, recent field surveys have shown that several grassland birds that had declined in the Great Plains are much more common on CRP habitat than in cropland (Johnson and Koford, this section). In recent years numerous small to medium tracts of native grassland have been designated as preserves. These areas plus changes in agricultural practices that promote natural resource conservation (e.g., CRP) are important to protect the remaining biodiversity of the Great Plains.

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Declining Grassland Birds

by
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Native grasslands represent the largest vegetative province of North America. Almost 1.5 million km^2 (0.6 million mi^2) of grasslands historically occurred on the Great Plains. Although the Great Plains played a major role in the evolution of North American forest birds (Mengel 1970), the grassland avifauna itself is relatively poor with only 5% of all North American bird species believed to have evolved within the Great Plains. That group includes 12 species of birds that are considered endemic (i.e., evolved specifically within) to the grasslands, along with 20 others that have centers of evolution on the grasslands but range more widely into contiguous vegetative provinces.

The landscape of the Great Plains has undergone significant alteration from descriptions provided in early accounts. The influences have been varied with many (e.g., urbanization, mineral exploration, and defense installations) having primarily local effects on the native birds. Activities with more universal effects on the landscape have included transformation of the native grazing community, cultivation of grains and tame grasses, draining of wetlands, and woody development in the form of tree plantings in the dry central and western Great Plains (Knopf and Samson, in press). Also, ecological invasions following fire suppression in the eastern and central plains and water developments in the western plains have drastically altered historical landscapes.

Of the 435 bird species breeding in the United States, 330 have been recorded on the Great Plains. Current 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 (Table) while simultaneously (and rather independently) alien species have expanded their ranges (Knopf 1994).

Methods

Information on the annual status of endemic grassland birds was obtained through the Breeding Bird Surveys (1966-91), which are conducted annually during the bird breeding season at numerous sites across the nation.

Status and Trends

During the last 25 years, grassland species have shown steeper, more consistent, and more geographically widespread declines than any other behavioral or ecological guild of North American birds, including Neotropical migrants. Continental population trends of many individual species of grassland birds also declined. Excluding the wetland-associated marbled godwit (*Limosa fedoa*) and Wilson's phalarope (*Phalaropus tricolor*), 7 of the 10 endemic grassland species showed population

declines during the last 26 years. Population declines of four species (mountain plover [*Charadrius montanus*], Franklin's gull [*Larus pipixcan*], Cassin's sparrow [*Aimophila cassinii*], and lark bunting [*Calamospiza melanocorys*]) are statistically significant.

Similarly, 14 of the 20 more widespread species that evolved primarily on the Great Plains declined during this period, with the declines in the eastern meadowlark (*Sturnella magna*) and 5 sparrows (grasshopper [*Ammodramus savannarum*], Henslow's [*A. henslowii*], lark [*Chondestes grammacus*], Brewer's [*Spizella breweri*], and clay-colored [*S. pallida*]) being statistically significant. Across all grassland species, populations of only the upland sandpiper (*Bartramia longicauda*) and McCown's longspur (*Calcarius mccownii*) have increased significantly since 1966.

Patterns of Bird Declines

Reasons for population declines among species within the grassland avifauna are difficult to assess. Through examining trends for those species where declines are supported statistically, the declines appear to be localized for Franklin's gull, dickcissel, Henslow's and grasshopper sparrows, lark bunting, and eastern meadowlark; these species show a significant difference in the proportion of surveys with increasing versus 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. The seasonal distributions and ecology of these sparrows are poorly understood. The plover is now rare on its former wintering areas in southern Texas and has a fragmented wintering distribution in California. Ongoing research on plovers indicates that declines of these species may be attributable to decline or degradation in the quality of habitats available for wintering.

Population trends for a third group of grassland species (ferruginous hawk [*Buteo regalis*]; Mississippi kite [*Ictinia mississippiensis*]; upland sandpiper; short-eared owl [*Asio flammeus*]; horned lark [*Eremophila alpestris*]; western meadowlark [*Sturnella neglecta*]; and vesper [*Pooecetes gramineus*], savannah [*Passerculus sandwichensis*], 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.

Species	No. of routes	Percentage[a]		Population[b]
		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
More widespread species				
Mississippi kite	163	58.9	40.5*	+ 0.4
Swainson's hawk	607	48.8	46.6	+ 1.2
Northern harrier	1,075	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	1,708	40.6	56.8*	- 0.7
Sage thrasher	230	53.0	44.8	+ 1.4
Eastern meadowlark	1,714	30.5	68.6*	- 2.2*
Western meadowlark	1,304	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	1,418	42.9	54.4*	- 0.6
Grasshopper sparrow	1,446	37.6	58.8*	- 4.6*
Henslow's sparrow	249	30.9	61.8*	- 4.2*
Vesper sparrow	1,473	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*

[a]Percentages totaling <100% include some routes with no change in numbers of birds detected. Asterisk indicates significant differences ($P < 0.05$) between number of surveys with increasing versus decreasing species populations.
[b]Annual rate (expressed as a percentage) of change in population numbers. Asterisk indicates a statistically significant ($P < 0.05$) rate of population change.

Table. Annual rates of change in continental populations of endemic grassland bird species, 1966-91 (Breeding Bird Survey data).

Although species associated with wetlands have certainly declined since settlement of the grasslands in the mid-1800's, Breeding Bird Survey 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 two species.

Are There Fewer Birds on the Great Plains?

Many species of forest birds historically occurred west of their eastern deciduous forest habitats in streamside vegetation of the eastern Great Plains. As most endemic grassland birds have declined, they have been replaced locally by eastern species moving into windbreaks and developing riparian forests along streambeds of the short-grass prairie. The streamside forests evolved with water management practices in the west and have favored the movement of many species farther onto and across the grasslands.

At one location, Crook, Colorado, 83 species of birds in the vicinity included only 6 representatives of the Great Plains avifauna, of which only 3 species bred locally (Knopf 1986). None of those three species bred in the riparian vegetation. That riparian forest developed since 1900, and almost 90% of the native birds currently breeding in northeastern Colorado have colonized in recent times.

Causes of Declines Unknown

Ecological processes driving population trends of North American grassland birds are 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. 1989), declines in grassland species are occurring at a continental scale. For example, the decline in numbers of the mountain plover, Cassin's sparrow, and lark bunting are occurring across their ranges. The lack of understanding of the wintering ecology of grassland birds precludes optimistic projections, especially for these species experiencing widespread, geographic declines.

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Migratory Bird Population Changes in North Dakota

by
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The status of migratory bird populations in North America has received increased attention in recent years. Much of this consideration has been on Neotropical migrants, especially those associated with eastern forests. The status of migratory bird populations in the Great Plains has received far less attention. During the past quarter-century, populations of many species of birds that breed in the northern Great Plains have increased or declined, as indicated by trends from the North American Breeding Bird Survey.

In 1967 Stewart and Kantrud (1972) conducted a survey of breeding bird populations throughout North Dakota. This study offered a rare glimpse of bird populations breeding in the northern Great Plains as well as important baseline data on breeding bird populations. These data help us evaluate relationships between birds and habitat conditions. We repeated the survey to compare bird populations in North Dakota during 1967 with those in 1992 and 1993.

Study Areas and Methods

To aid in a direct comparison, the same 130 legal quarter-sections (64.7 ha, 160 acres) surveyed in 1967 were visited again in 1992 and 1993 (Figure). Surveys of breeding birds were conducted as similarly as possible to the methods used by Stewart and Kantrud (1972).

Each bird species was classified into one of three groups according to its migratory strategy: permanent resident (present in North Dakota year-round), short-distance migrant (winters north of the U.S.-Mexico border), and long-distance migrant (winters south of the U.S.-Mexico border). In addition, each species was categorized to a preferred breeding habitat: wetland/wet meadow, grassland/open habitat, open habitat with scattered trees, woodland/woodland-edge, shrubland, residential/habitat generalist, and other. Within each group, a mean population size was calculated and expressed as the number of indicated pairs per 100 ha (247 acres).

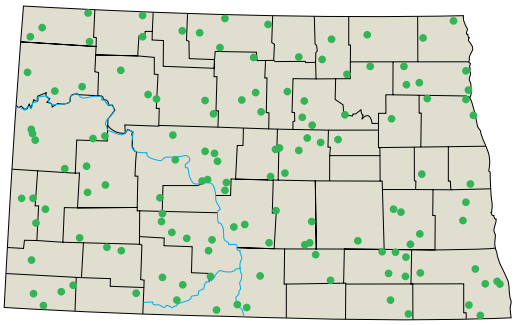

Figure. Distribution of the original 130 quarter-sections in North Dakota.

Status and Trends

Data were obtained on 160 breeding bird species within the 128 quarter-sections that we received permission to survey in all 3 years (Table 1), including 129 species in 1967, 144 in 1992, and 152 in 1993. Thus, about 72% of the known breeding avifauna of North Dakota (Faanes and Stewart 1982) were identified. Songbirds were the most common group,

Table 1. Distribution of species observed on 128 randomly selected quarter-sections in North Dakota in 1967, 1992, and 1993 by breeding habitat and migratory strategy.

Breeding habitat	Permanent resident	Short-distance migrant	Long-distance migrant	Total
Wetland/wet meadow	0	41	13	54
Grassland/open habitat	3	16	15	34
Open habitat with trees	1	4	3	8
Shrubland	0	4	5	9
Woodland/woodland-edge	8	15	24	47
Residential/ habitat generalist	4	1	2	7
Other	0	1	0	1
Total	16	82	62	160

accounting for about 80% of the total number of indicated pairs in each year.

Of the total number of breeding pairs of the 50 most common species in the 3 years (Table 2), the five most commonly encountered species, in order of abundance, were horned lark (*Eremophila alpestris*), chestnut-collared longspur (*Calcarius ornatus*), red-winged blackbird (*Agelaius phoeniceus*), western meadowlark (*Sturnella neglecta*), and brown-headed cowbird (*Molothrus ater*). The horned lark, the most common breeding bird species recorded each year, is a species that is most characteristic of cropland or heavily grazed prairie and which favors open areas with low sparse vegetation (Stewart 1975). The overall frequency and abundance of the brown-headed cowbird are of concern because this brood parasite has been implicated in the decline of some Neotropical migrants.

Ninety percent of the 160 species observed in the 3 years are migrants (Table 1). Moreover, migrants constitute over 95% of the indicated pairs detected in the sample units in each year. The remaining (10%) species are year-round residents in North Dakota. Of the species that migrate, 82 (51%) are short-distance migrants and 62 (39%) are long-distance (Neotropical) migrants.

The data indicate that breeding bird populations show considerable short- and long-term variability. The patterns of population change for many grassland and wetland species are remarkably similar and consistent among taxonomic groups (e.g., mallard [*Anas platyrhynchos*] versus American coot [*Fulica americana*] versus savannah sparrow [*Passerculus sandwichensis*]) and migration strategies (long-distance versus short-distance migrant; Tables 2 and 3). A common feature of these species is their dependence on grassland and wetland habitats on the breeding grounds; most breed in the northern Great Plains but winter elsewhere. Severe drought conditions in the Great Plains may have played a major role in the depressed populations (Tables 2 and 3) of some wetland and grassland species in 1992 (an extremely dry year) compared with 1967 (a near-average year) and 1993 (an extremely wet year).

Several species associated with grassland and wetland habitats (e.g., savannah sparrow and American coot) were relatively common in 1967, showed major declines in 1992, and recovered slightly in 1993 (Table 2). The fact that populations of some species (e.g., black tern [*Chlidonias niger*], Wilson's phalarope [*Phalaropus tricolor*]) remain below their 1967 levels suggests that precipitation alone may not explain all of the changes in the populations of grassland and wetland species. Drainage of wetlands, agriculture encroachment, and increased fragmentation of native prairie are also suspected in the declines of some wetland and grassland species.

Table 2. Number of indicated pairs of the 50 most common bird species observed on 128 randomly selected quarter-sections in North Dakota in 1967, 1992, and 1993.

Species	Migration strategy*	Breeding habitat**	No. indicated pairs 1967	1992	1993
Horned lark (*Eremophila alpestris*)	SDM	G/O	1,253	1,093	1,661
Chestnut-collared longspur (*Calcarius ornatus*)	SDM	G/O	1,129	602	755
Red-winged blackbird (*Agelaius phoeniceus*)	SDM	WET	945	597	710
Western meadowlark (*Sturnella neglecta*)	SDM	G/O	926	487	646
Brown-headed cowbird (*Molothrus ater*)	SDM	W/E	460	643	610
Lark bunting (*Calamospiza melanocorys*)	LDM	G/O	604	679	298
Grasshopper sparrow (*Ammodramus savannarum*)	LDM	G/O	301	402	449
Mourning dove (*Zenaida macroura*)	SDM	W/E	292	339	337
Savannah sparrow (*Passerculus sandwichensis*)	SDM	G/O	516	134	276
Clay-colored sparrow (*Spizella pallida*)	LDM	SHR	364	261	289
Vesper sparrow (*Pooecetes gramineus*)	SDM	G/O	195	224	393
Common grackle (*Quiscalus quiscula*)	SDM	O/T	140	300	299
Eastern kingbird (*Tyrannus tyrannus*)	LDM	O/T	167	321	245
Cliff swallow (*Hirundo pyrrhonota*)	LDM	G/O	152	343	226
American coot (*Fulica americana*)	SDM	WET	348	76	124
Bobolink (*Dolichonyx oryzivorus*)	LDM	G/O	216	186	172
Blue-winged teal (*Anas discors*)	LDM	WET	286	99	145
Mallard (*Anas platyrhynchos*)	SDM	WET	212	113	200
House wren (*Troglodytes aedon*)	LDM	W/E	52	219	209
Barn swallow (*Hirundo rustica*)	LDM	G/O	96	187	194
Western kingbird (*Tyrannus verticalis*)	LDM	O/T	103	194	177
House sparrow (*Passer domesticus*)	RES	RES	96	181	174
Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)	LDM	WET	89	155	175
Common yellowthroat (*Geothlypis trichas*)	LDM	WET	134	91	175
American goldfinch (*Carduelis tristis*)	SDM	W/E	106	146	132
Baird's sparrow (*Ammodramus bairdii*)	LDM	G/O	170	77	125
Killdeer (*Charadrius vociferus*)	SDM	WET	105	112	142
Gadwall (*Anas strepera*)	SDM	WET	96	111	118
Marsh wren (*Cistothorus palustris*)	SDM	WET	51	113	153
American robin (*Turdus migratorius*)	SDM	GEN	67	117	123
Yellow warbler (*Dendroica petechia*)	LDM	GEN	102	90	105
Rufous-sided towhee (*Pipilo erythrophthalmus*)	SDM	W/E	94	83	118
Song sparrow (*Melospiza melodia*)	SDM	SHR	55	100	130
Upland sandpiper (*Bartramia longicauda*)	LDM	G/O	63	106	89
Northern pintail (*Anas acuta*)	SDM	WET	171	23	58
Bank swallow (*Riparia riparia*)	LDM	G/O	77	112	61
Brown thrasher (*Toxostoma rufum*)	SDM	SHR	42	85	104
Black tern (*Chlidonias niger*)	LDM	WET	118	39	39
Cedar waxwing (*Bombycilla cedrorum*)	SDM	W/E	23	149	43
Field sparrow (*Spizella pusilla*)	SDM	SHR	49	61	74
Northern shoveler (*Anas clypeata*)	SDM	WET	87	25	52
Franklin's gull (*Larus pipixcan*)	LDM	WET	22	79	56
Least flycatcher (*Empidonax minimus*)	LDM	W/E	23	52	81
Brewer's blackbird (*Euphagus cyanocephalus*)	LDM	SHR	19	47	83
Sora (*Porzana carolina*)	SDM	WET	32	41	78
Chipping sparrow (*Spizella passerina*)	LDM	W/E	22	51	70
Wilson's phalarope (*Phalaropus tricolor*)	LDM	WET	73	30	36
Lark sparrow (*Chondestes grammacus*)	LDM	G/O	40	52	40
Gray catbird (*Dumetella carolinensis*)	LDM	SHR	48	44	38
Ruddy duck (*Oxyura jamaicensis*)	SDM	WET	36	56	23

*SDM—short-distance migrant; LDM—long-distance migrant; RES—resident.
**G/O—grassland-open habitat; WET—wetland-wet meadow; W/E—woodland-woodland-edge; SHR—shrubland; O/T—open habitat with trees: GEN—residential-habitat generalist.

Table 3. Mean number of indicated breeding pairs in 128 randomly selected quarter-sections in North Dakota by year, migration strategy, and preferred breeding habitat.

Migration and habitat	Mean pairs/100 ha		
	1967	1992	1993
Migration strategy			
Permanent resident	2.6	5.7	6.1
Short-distance migrant	95.5	74.7	99.5
Long-distance migrant	43.2	52.3	45.4
Breeding habitat			
Wetland/wet meadow	37.5	24.7	32.6
Grassland/open habitat	71.7	59.3	68.3
Open habitat with trees	5.5	10.6	9.7
Shrubland	7.2	7.5	9.0
Woodland/woodland-edge	15.6	24.6	25.3
Residential/generalist	3.7	5.7	5.8
Other	0.1	0.3	0.3
Total	141.3	132.7	151.0

Federal land-retirement programs (such as the Soil Bank Program in 1967 and the Conservation Reserve Program in 1992-93) may help slow or reverse the declines of some grassland species. For example, between 1982 and 1991, the sedge wren (*Cistothorus platensis*) showed a significant decline on Breeding Bird Surveys in North Dakota. Over 50% of sedge wren breeding pairs found in all 3 years were found in these set-aside habitats.

In contrast, the populations of birds associated with woody vegetation may be less vulnerable to climatological factors such as drought. Species associated with woody vegetation have increased dramatically between 1967 and 1992-93 (Tables 2 and 3). In presettlement times, fire and grazing pressures played a major role in the formation and maintenance of the grassland landscape of the northern Great Plains. The relaxation and alteration of these pressures resulted in the encroachment of shrubs and trees into grassland habitats. Landscape fragmentation by tree plantings (e.g., farmstead windbreaks and field shelterbelts) is also suspected in the increase in species associated with woody vegetation. These conditions provided woodland and woodland-edge species with nesting opportunities that did not exist or were quite limited in presettlement times. In addition, maturation of the woody vegetation in these tree plantings may be attractive to certain species. For example, 14 of 15 species that nest in tree cavities showed increasing or stable populations in this survey.

Conservation Implications

Further analysis of habitat changes between 1967 and 1992-93 are needed to fully understand the changes in bird populations in North Dakota. Many species associated with the increasing amount of woody vegetation are common and have widespread distributions in North America (Johnson et al. 1994). On the other hand, many grassland and wetland species experienced declines and have few habitat alternatives to the Great Plains. The implication is that preservation of native grassland and wetland habitats is necessary to support breeding populations of migrants in the northern plains.

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Duck Nest Success in the Prairie Potholes

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Since the early 1970's, the numbers of some waterfowl species such as mallard (*Anas platyrhynchos*), blue-winged teal (*A. discors*), and northern pintail (*A. acuta*) have reached or nearly reached the lowest ever recorded. Low nest success (the proportion of nests in which one or more eggs hatch) in key breeding areas, including the U.S. Prairie Pothole region, is partly responsible for declines in duck numbers (Klett et al. 1988; Johnson et al. 1992).

Methods

We examined status and trends of duck nest success for mallard, blue-winged teal, gadwall (*A. strepera*), northern shoveler (*A. clypeata*), and northern pintail, for one to four time periods between 1966 and 1989, and for five regions in North and South Dakota and Minnesota (Fig. 1). Nest success data originated from numerous independent studies conducted throughout the region. Some data from 1966 to 1984 were previously analyzed by Klett et al. (1988). We followed the methods of Klett et al., except we considered one additional time period (1985-89) and one additional habitat (Conservation Reserve Program lands).

Nest Success

Mallard

Data for 4,093 mallard nests showed that their nest success ranged from 6% to 20% (Fig. 2). Only 3 of 14 nest success estimates reached or exceeded 15%, the level of nest success thought necessary to maintain mallard numbers at a stable level in central North Dakota (Cowardin et al. 1985). These three areas were central South Dakota (1966-74), eastern South Dakota (1985-89), and central North Dakota (1985-89).

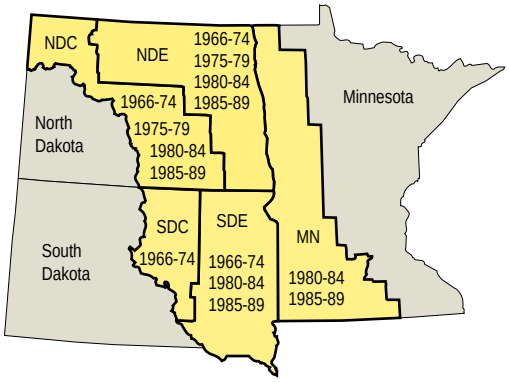

Fig. 1. Areas of the Prairie Pothole region and time periods for which estimates of duck nest success were made. See Fig. 2 for abbreviations.

Mallard nest success was relatively steady from 1966-74 to 1980-84, but increased from 1980-84 to 1985-89. In 1985-89, mallard nest success was still less than 15% in two of four regions where data were available. Predation was the major cause of nest failure, accounting for 85% of mallard nest failures in North Dakota.

Blue-winged Teal

Data for 9,819 blue-winged teal nests revealed that nest success of blue-winged teal ranged from 12% to 29% (Fig. 2). The level of nest success needed to maintain stable numbers of blue-winged teal is believed to be 20% (Klett et al. 1988). Nest success of blue-winged teal was generally below this level, except in South Dakota.

Nest success increased slightly from 1980-84 to 1985-89, but was still generally less than 20%. Predation, the principal cause of blue-winged teal nest failures, accounted for 92% of the failed nests in North Dakota.

Gadwall

Data on 3,782 gadwall nests showed that their average nest success ranged from 11% in western Minnesota (1980-84) to 26% in central South Dakota (1966-74; Fig. 2). Nest success was generally below 20%, the minimum level believed necessary to sustain populations (Klett et al. 1988).

Gadwall nest success increased from 1980-84 to 1985-89 and reached or exceeded 20% during 1985-89 in North and South Dakota. Predation was the primary cause of nest failure, accounting for 90% of failed gadwall nests in North Dakota.

Northern Shoveler

Nest success in 1,212 shoveler nests ranged from 5% in western Minnesota (1980-84) to 35% in central South Dakota (1966-74; Fig. 2). Nest success was generally below 20%, the minimum level believed necessary to sustain populations (Klett et al. 1988). In western Minnesota and eastern North Dakota, nest success was less than 10%, but it was greater than 20% in central North and South Dakota.

Shoveler nest success increased from 1980-84 to 1985-89, but was still much less than 20% in western Minnesota and eastern North Dakota. Predation was the primary cause of nest failure in all regions, and in North Dakota caused 88% of shoveler nest failures.

Northern Pintail

Data for 1,633 pintail nests revealed that their success ranged from 5% to 20% (Fig. 2). Fifteen percent is the minimum level of nest success believed necessary to sustain pintail numbers (Klett et al. 1988). Only 2 of 14 nest success estimates reached or exceeded 15%; these were for central South Dakota (1966-74) and central North Dakota (1985-89).

Within each region, pintail nest success was generally lowest in 1966-74 and highest in 1985-89. Even in 1985-89, however, nest success was much less than 15% in all regions where data were available, except central North Dakota. Predation was the major cause of nest failure; for example, in North Dakota it accounted for 81% of pintail nest failures. In addition, because pintails nest more frequently in cropland than other species (Klett et al. 1988), farming operations were also an important cause of nest failure, accounting for 16% of pintail nest failures.

Trends

Our results suggest that nest success of the five species of ducks considered here was and probably still is too low to maintain stable numbers of breeding ducks in most areas of the Prairie Pothole region. For example, even though nest success increased from 1980-84 to 1985-89, it was still below the level needed to sustain populations for most species in most regions. Except for pintails, whose nest success generally increased, we observed no consistent increases or decreases in nest success across periods. In central South Dakota in the 1966-74 period nest success was much higher than in other regions, exceeding the level needed to sustain populations. This region likely contributed a "surplus" of ducks in 1966-74 that helped make up for the "shortage" of ducks produced in other regions. Unfortunately, no data for central South Dakota have been available since then.

Predation was the primary reason for the low nest success we observed. Predator species such

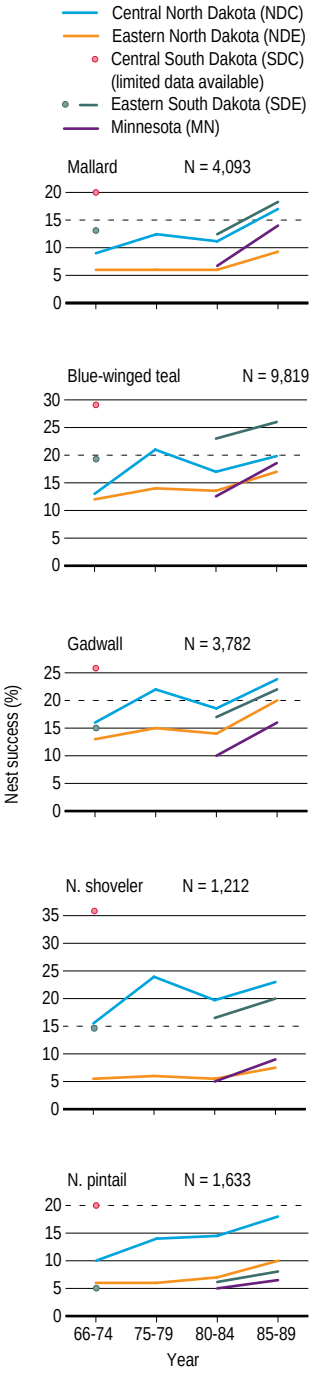

Fig. 2. Nest success (%) by period for five areas in the Prairie Pothole region for five duck species. Dashed line = level of nest success believed necessary for a stable population.

as red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*) are common or numerous throughout the region (Sargeant et al. 1993). Both red foxes and striped skunks are important predators of duck nests (Johnson et al. 1989), and red foxes also take many female ducks during the breeding season (Sargeant et al. 1984).

More than two-thirds of the Prairie Pothole region is in Canada. Greenwood et al. (1987) studied mallard nest success in that portion of the region from 1982 to 1985. Their findings were similar to ours: mallard nest success averaged 12% and only 7 of 31 estimates on individual areas reached or exceeded 15%. Predators caused most nest failures. The authors concluded that nest success in much of Prairie Canada in 1982-85 was too low to maintain stable numbers of breeding mallards.

The status of duck nest success in the recent past in the Prairie Pothole region seems clear. Nest success was too low for duck populations to sustain themselves. Unless steps are taken to improve duck nest success in the future, we will likely see further declines in numbers of these and possibly other waterfowl species.

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Conservation Reserve Program and Migratory Birds in the Northern Great Plains

by
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U.S. Department of Agriculture programs have mediated supply and demand of commodities and maintained the agricultural industry, but several programs have also offered various kinds of conservation benefits. The 1985 Food Security Act (Farm Bill) featured the Conservation Reserve Program (CRP), which paid farmers to plant perennial cover on highly erodible lands and to leave this land intact for a 10-year contract period. During that period we conducted two studies to determine the value of CRP fields to breeding birds in the northern Great Plains.

Methods

In one investigation, we censused breeding birds on about 400 fields in nine counties in eastern Montana, North Dakota, South Dakota, and western Minnesota (Johnson and Schwartz 1993). These four states have about 4 million ha (9.9 million acres) of CRP land, which is nearly 30% of all land included in the program. Most of these CRP fields were planted to mixtures of native and introduced grasses and legumes. We compared the average estimated density of breeding pairs in CRP fields in North Dakota with the density in croplands in a random sample of quarter-sections surveyed in the state (see Igl and Johnson, this section). We believe this is an appropriate comparison because nearly all CRP lands would have been in cropland without the program. In addition, North Dakota is the only state with comparable information about bird populations in cropland. Results are available for 1992 and 1993.

In a second investigation, we examined daily survival rates of nests (eggs and young), a key component of reproductive success, on 11 CRP fields in North Dakota and Minnesota in 1991-93. For comparison with CRP fields, we also studied an alternative habitat with a similar breeding-bird community. We studied 11 idle grassland fields on upland parts of federal Waterfowl Production Areas (WPAs); their vegetation typically is planted to mixtures of legumes and to grasses.

Bird Populations and Reproductive Success

Seventy-three different species were counted in the first study; most of these species were far more common in CRP fields than in cropland (Table 1). Differences were especially great for several grassland species that had declined markedly in the Breeding Bird Survey's Central Region of North America between 1966 (when the surveys began) and 1990. For example, lark buntings (*Calamospiza melanocorys*) and grasshopper sparrows (*Ammodramus savannarum*), whose numbers fell by about two-thirds during that period, were about 10 and 16 times more common in CRP habitat than in cropland.

The most recent Breeding Bird Surveys indicate that these grassland species, which had been declining for a long time, appear to be increasing (Reynolds et al. 1994).

Overall, daily survival rates of nests were similar in CRP fields and WPA fields (Table 2). In North Dakota there was some indication that nests of grasshopper sparrows and western meadowlarks (*Sturnella neglecta*) had higher daily survival rates in CRP fields than in WPA fields. Differences between states and among years, however, make generalizing difficult. Predation caused 80% of the nest failures.

Implications

These studies show that federal agricultural programs can have an enormous effect on wildlife resources over broad areas. In addition, with the restoration of suitable habitat, in this case mostly a mixture of introduced grasses and legumes rather than native prairie, populations of grassland birds can flourish. The similar daily survival rates of nests in CRP and WPA fields indicate that the habitat quality of CRP fields and WPA fields is roughly comparable.

More information is needed to provide a fuller picture of how the CRP is affecting trends in grassland birds. Information on temporal and spatial effects is especially useful. As CRP fields age, their attractiveness to certain species may change. Daily survival rates of nests also may change. Spatial effects are apparent in our censuses and undoubtedly exist on a wider scale. Finally, we need to integrate results from field studies with trend data from the Breeding Bird Survey.

Table 1. Densities (pairs per 100 ha) of most common birds in Conservation Reserve Program fields and in cropland fields in North Dakota, 1992-93, and trends from the Breeding Bird Survey for the Central Region of North America, 1966-90.

Species	CRP fields		Cropland		Trend
	1992	1993	1992	1993	
Lark bunting (*Calamospiza melanocorys*)	24.54	9.14	2.01	1.28	-64.5
Red-winged blackbird (*Agelaius phoeniceus*)	21.50	10.90	1.86	0.90	-1.0
Grasshopper sparrow (*Ammodramus savannarum*)	21.14	10.21	1.33	0.58	-67.5
Savannah sparrow (*Passerculus sandwichensis*)	7.28	8.60	0.12	1.48	16.3
Brown-headed cowbird (*Molothrus ater*)	7.11	5.03	2.61	2.51	-6.1
Bobolink (*Dolichonyx oryzivorus*)	7.74	3.53	2.73	2.11	-48.7
Western meadowlark (*Sturnella neglecta*)	5.43	5.26	1.28	1.16	-7.8
Clay-colored sparrow (*Spizella pallida*)	5.07	3.63	0.02	0.02	-39.6
Common yellowthroat (*Geothlypis trichas*)	2.49	1.87	0.02	0.02	-7.4
Horned lark (*Eremophila alpestris*)	2.38	0.53	19.96	29.18	-3.5
Sedge wren (*Cistothorus platensis*)	0.73	1.13	0	0	-15.5
Dickcissel (*Spiza americana*)	1.37	0.03	0.19	0	-29.4
Baird's sparrow (*Ammodramus bairdii*)	0.26	0.68	0.34	0.02	-46.6
Upland sandpiper (*Bartramia longicauda*)	0.40	0.13	0.92	0.65	145.7
Chestnut-collared longspur (*Calcarius ornatus*)	0.02	0.03	11.38	2.08	-10.7

Table 2. Daily survival rates of nests in Conservation Reserve Program fields and on Waterfowl Production Areas, North Dakota and Minnesota. Numbers of nests are in parentheses.

Species	North Dakota		Minnesota	
	CRP	WPA	CRP	WPA
American coot (*Fulica americana*)	-	-	0.92 (14)	-
Blue-winged teal (*Anas discors*)	-	-	0.94 (19)	0.95 (34)
Bobolink (*Dolichonyx oryzivorus*)	-	-	0.92 (16)	0.93 (32)
Clay-colored sparrow (*Spizella pallida*)	-	0.93 (49)	-	0.97 (24)
Grasshopper sparrow (*Ammodramus savannarum*)	0.95 (39)	0.91 (14)	0.92 (13)	-
Mallard (*Anas platyrhynchos*)	0.96 (20)	-	-	0.97 (10)
Red-winged blackbird (*Agelaius phoeniceus*)	0.92 (70)	-	0.86 (25)	-
Savannah sparrow (*Passerculus sandwichensis*)	-	-	0.86 (13)	0.95 (30)
Upland sandpiper (*Bartramia longicauda*)	-	0.99 (19)	-	-
Western meadowlark (*Sturnella neglecta*)	0.95 (20)	0.87 (14)	-	-

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Decline of Native Prairie Fishes

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Several prairie fishes that were once widespread and abundant in riverine ecosystems of the south-central Great Plains have declined markedly in their distributions and abundances. Declines of such species likely reflect degradation of riverine ecosystems, particularly in the Arkansas River basin. At a 1994 interregional meeting, the U.S. Fish and Wildlife Service, representing various regions, considered eight riverine aquatic species in the Arkansas and Missouri river basins as Category 2 species (i.e., more data needed to determine appropriateness of listing as federally endangered or threatened species). Four of the eight species were small prairie fishes, including the Arkansas River shiner (*Notropis girardi*) and the Arkansas River speckled chub (*Macrhybopsis aestivalis tetranemus*).

We recently investigated distribution and reproductive status of the Arkansas River shiner and the Arkansas River speckled chub in relation to human alterations of river flows within the Arkansas River basin. Human impacts were identified that are detrimental to the long-term stability of native prairie fish assemblages.

Historical distributions of the Arkansas River shiner and the Arkansas River speckled chub were determined by reviewing collection records from appropriate museums. Current distributions of both species were assessed with intensive seine samples throughout historical ranges in Colorado, Kansas, New Mexico, Oklahoma, and Texas (153 collections at 116 localities for the shiner; 223 collections at 159 localities for the speckled chub). River discharges throughout the year were evaluated relative to the reproductive cycles of the fish.

Arkansas River Shiner

This shiner is endemic to the Arkansas River basin; it was widespread in the basin before

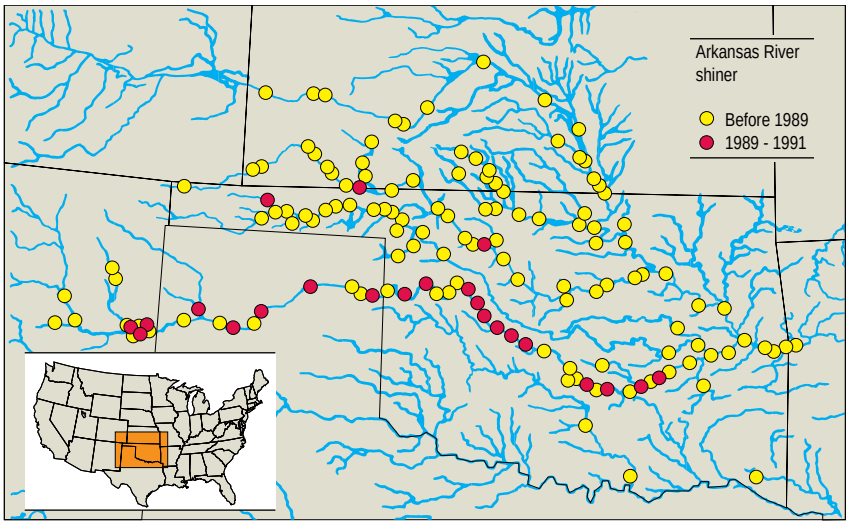

Fig. 1. Historical occurrences of the Arkansas River shiner from collections before 1989 and current occurrences from 1989 to 1991.

1985, but relative abundances varied widely. In three main tributaries of the Arkansas River (North Canadian River, Cimarron River, and Salt Fork of the Arkansas River), the shiner declined markedly between 1983 and 1985, and no specimens were collected after 1990. Our sampling between 1989 and 1991 indicated that native populations were common only in the South Canadian River in Oklahoma, Texas, and New Mexico. An introduced population (perhaps a result of bait transport) occurs in the Pecos River, New Mexico, southwest of the shiner's normal distribution (Bestgen et al. 1989). Overall, the shiner has been extirpated from about 75% of the river reaches in its historical range (Fig. 1). That, coupled with the speed with which populations became extinct in the mid-1980's, prompted action to list the shiner as threatened.

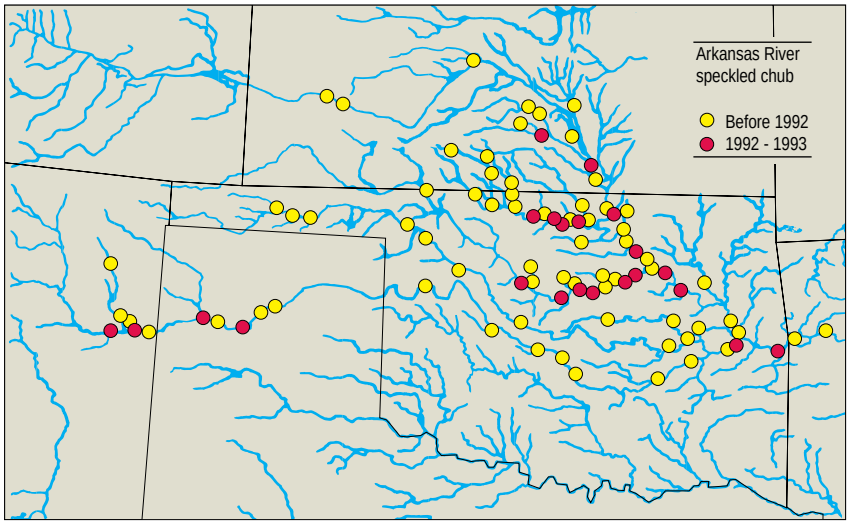

Fig. 2. Historical occurrences of the Arkansas River speckled chub from collections before 1992 and current occurrences from 1992 to 1993.

Arkansas River Speckled Chub

Historically, the speckled chub occurred throughout the Arkansas River, including the main tributaries in Arkansas, Colorado, Kansas, New Mexico, Oklahoma, and Texas. Our seining collections between 1991 and 1993, however, resulted in capture of speckled chubs at only 22 of the 159 sites sampled, indicating a marked reduction in distribution (Fig. 2). Only six stream reaches in Kansas, New Mexico, Oklahoma, and Texas support speckled chub. We believe that the species is extirpated from Arkansas and Colorado, the North Canadian and Deep Fork rivers in Oklahoma, the Salt Fork of the Arkansas River and Medicine Lodge River in Kansas, and parts of the South Canadian River. Its population in the Cimarron River in Oklahoma varied from very common in collections before 1950, absent from 1984 to 1991, and rare in 1992 and 1993.

River Flows and Reproduction

We examined duration curves of river flows from three time periods (before 1950, 1950-69, and 1970-88). Our analyses indicated that May-September river flows at most sampling sites were depressed from 1970 to 1988. Overall, 17 of 21 (81%) significant differences among river flows involved depressed flow levels from May to September.

Reproductive activity of the Arkansas River shiner extends from early May to August. The highest reproductive activity in shiners collected in 1989 occurred in June and was coincident with peak river flows. Reproductive activity in shiners in 1989 decreased as river flows declined throughout the summer. Although we do not have comparable reproductive data for the speckled chub, it is clear that it is as affected by river flows (Bottrell et al. 1964) as the shiner.

Both the shiner and the speckled chub have experienced sizeable losses (ca. 75%) in their historical distributions. Local abundances of the shiner have declined since at least the mid-1960's. The shiner and speckled chub now occur together only in the South Canadian River between two reservoirs in Texas and New Mexico and possibly in the Cimarron River in Oklahoma. Declines of these two species parallel similar declines in other native prairie fishes, such as the plains minnow (*Hybognathus placitus*; Cross and Moss 1987).

Reproduction in these two species appears dependent on periodic and intensive river flows during spring and summer when buoyant eggs are deposited directly into the current. Eggs drift in the current and hatch in 2-4 days (Moore

1944; Bottrell et al. 1964; Cross et al. 1985). In general, the south-central Great Plains is characterized by low but intense rainfall, high evaporation rates, and periodic drought (Zale et al. 1989). Such conditions likely cause great population changes year-to-year and may even cause local extinctions.

Extensive agricultural activities and resultant demands for irrigation water, coupled with the construction of numerous reservoirs in the Arkansas River basin, have degraded and restricted habitats of the shiner and speckled chub and likely other prairie fishes (Cross and Moss 1987). Successful reproduction or recruitment seems to have been impaired. Impoundments have fragmented once contiguous populations of the shiner and speckled chub to restricted river reaches with suitable habitat, effectively eliminating movements between populations and colonization of vacant habitat. Although altered flow regimes may be the ultimate explanation of the declines of these and other species, the actual pattern of decline differs between species. Overall, these declines indicate that human activities have degraded aquatic prairie ecosystems to the point of endangering parts of endemic fish assemblages.

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The Coyote: An Indicator Species of Environmental Change on the Great Plains

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Increases or declines in wildlife populations are often the first noted indicators of widespread environmental change. Behavioral changes such as diet shifts or habitat-use also may provide sensitive indicators of environmental change. The coyote (*Canis latrans*) is an example of an opportunistic wild animal that may show both numerical and behavioral responses to environmental change.

Recent trends in populations and diets of coyotes and other canids (e.g., wolves, foxes, dogs) may reflect changes in land use, especially agricultural changes, and shifts in human populations. This article reviews both published accounts and original research to summarize how coyotes appear to have responded to changes in human populations and land use on the Great Plains.

Methods

Data presented in this paper were taken from many published sources (Sperry 1941; Young and Jackson 1951; Fichter et al. 1955; Gier 1968; Johnson and Sargeant 1977; Socolofsky and Self 1988) and from original research on coyote diets (Brillhart 1993). Although most of these studies were conducted on specific biological or social issues, we compare them to help understand human and wildlife population changes through time.

Human Population Changes

Two large-scale movements of people into the central Great Plains, from Nebraska south through Kansas and Oklahoma, occurred during the 1800's. The first large influx took place during the late 1820's, 30's, and 40's, as displaced Native American tribes were moved to the region.

Information about wildlife before 1850 is limited, but accounts suggest that bison (*Bison bison*), other big game, and wild canids were abundant when eastern Native American tribes moved into the region (Allen 1874; Cragin 1885; Mead 1899; Choate and Fleharty 1975; Bee et al. 1981). Native Americans on the Great Plains lived a subsistence lifestyle dependent upon these game animals, but even when relatively large numbers of Native Americans were moved to the region, they generally left the prairies and wildlife populations intact.

The second major influx of people occurred from 1860 through the 1880's when thousands of settlers from eastern states and Europe came to homestead or to buy land from the railroads. Settlers and market hunters killed tens of thousands of bison yearly; several million bison hides were shipped from Dodge City and other railroad communities (Socolofsky and Self 1988). Before the turn of the century, bison and elk (*Cervus elaphus*) were extirpated from the region. European settlers converted the prairies into farms, ranches, and towns. They also

replaced big game with cattle, sheep, hogs, and poultry, and later waged poisoning campaigns against wolves (*Canis lupus*), coyotes, and other predators.

Since the late 1800's, a steady shift in human populations from farms to urban centers has occurred on the Great Plains. In some plains states, these changes have resulted in more people living in urban centers than in rural areas. For example, in 1880, about 90% of the Kansas population lived on farms, but by 1930, farm residents accounted for 60% of the total population (U.S. Department of Commerce 1993). Since that time, there have been further decreases in the proportion of the rural population; by 1990 about 30% lived on farms.

In addition, most farms have become larger and more highly mechanized than those 40-50 years ago. Changes also have occurred in production of domestic animals, with fewer farms today raising cattle, hogs, sheep, and chickens. Further, livestock and poultry are better cared for now and often are raised in confinement where they are unavailable to coyotes (Robel et al. 1981).

Canid Population Changes

Populations of wolves, coyotes, red foxes (*Vulpes vulpes*), swift foxes (*V. velox*), and dogs (*Canis familiaris*) on the Great Plains probably were relatively stable until settlers began arriving in the 1860's. Wolves dominated the canid social system except for the immediate area around villages, where village dogs probably dominated (Fig. 1). Because wolves are aggressive toward coyotes, coyote numbers probably were depressed (Young and Jackson 1951; Mech 1970). Mech (1994) and others have shown that the buffer zones that exist between adjacent wolf packs (about 6-7 km wide) provide refugia for deer and other animals. Coyotes may have occupied these buffer zones as well. Red and swift foxes were locally common during the 1800's, and there was probably little conflict between wolves and foxes. Because coyotes are aggressive toward foxes, fox numbers likely declined as coyote numbers increased (Johnson and Sargeant 1977).

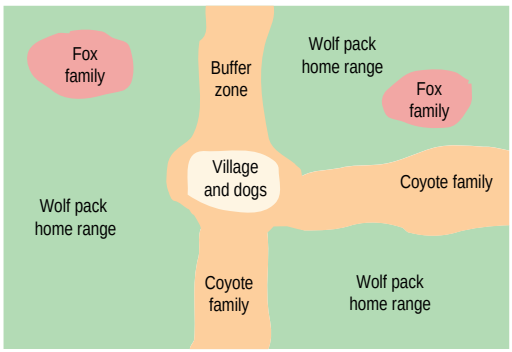

Fig. 1. Presettlement spatial relationships among home ranges of three packs of wolves, two families of coyotes, and two families of foxes near a Native American village with free-ranging dogs. Buffer zones and boundaries of wolf pack territories are dynamic, changing with availability of food and composition of wolf packs.

Coyotes increased during settlement and expanded their ranges as wolves were eliminated and bison were replaced with cattle and sheep. Coyotes may have reached their highest densities in North Dakota, and possibly other parts of the Great Plains, from about 1895 to 1915 (Johnson and Sargeant 1977).

Federal predator control started in 1915 when Congress appropriated $125,000 to organize and conduct control operations in partnership with states and local sponsors. The initial emphasis was on eliminating wolves from western and midwestern states. This wolf-control partnership was amazingly successful—almost all wolves were removed from western states by 1923 (Young and Goldman 1944). Coyotes generally increased in numbers as wolf populations declined.

Coyote populations fluctuated from 1915 to 1950, but bounty records suggest a general decline after 1915 (Gier 1968; Johnson and Sargeant 1977). In Kansas, low coyote populations were recorded from 1932 through 1940 (Cockrum 1952) and from 1954 through 1958 (Gier 1968). Compound 1080 (sodium fluoroacetate) was used to control coyotes in Kansas from 1950 through 1960; coyote numbers declined dramatically there.

Through the 1960's, coyote numbers continued to decline with increased use of Compound 1080 and other predator-control toxicants. Coyote numbers generally increased throughout the Great Plains after 1972 when the use of toxicants on federal lands was prohibited. Local fluctuations in coyote populations have occurred since 1970, largely in response to coyote fur prices and trapping and hunting.

Changing Coyote Diets

Coyote diets on the Great Plains today are markedly different than they were at the turn of the century, a likely reflection of changes in agricultural systems and human populations. Early in this century, most people on the Great Plains lived on mostly small farms and raised a variety of domestic animals. These farms usually were distributed fairly evenly across much of the region, making domestic animals widely available as prey for coyotes. Many farms suffered livestock and poultry losses from coyotes, which intensified predator-control efforts.

Studies of coyote diets on the Great Plains through the 1960's demonstrated that rabbits, rodents, and domestic animals were important food items (Sperry 1941; Fichter et al. 1955; Gier 1968). For example, in Kansas, almost 90% of the coyote diet was dominated by these three prey groups (Fig. 2), and more than half of all coyote stomachs sampled contained remains of either domestic livestock or poultry (Gier

1968). Similar patterns in consumption of rabbits, rodents, and domestic animals were evident in Nebraska, with livestock and poultry occurring in a third of all samples (Fichter et al. 1955).

Recent studies of coyote diets on the Great Plains also have shown the importance of rodents and rabbits as coyote prey (Brillhart 1993). In contrast to earlier studies, however, domestic livestock and chickens are eaten infrequently (Fig. 2); other common coyote foods today include certain insects, fruits, and wild birds.

Conclusions

Circumstantial evidence and prevailing professional opinion support our hypothesis that populations and diets of canids have changed in response to changing agricultural practices and shifts in human populations on the Great Plains. Because direct evidence is lacking to confirm these associations, research with specific testable hypotheses is needed.

Widespread changes in agricultural practices are inevitable and corresponding changes in wildlife populations should be expected. Recent changes in agricultural practices that are likely to result in changes in wildlife populations include a shift to dryland farming in formerly irrigated areas because of groundwater depletion, government regulations, and increasing energy prices. Agricultural set-aside programs authorized by the 1985 Food Security Act are positively influencing many wildlife populations, and future programs of a similar nature may benefit wildlife populations further.

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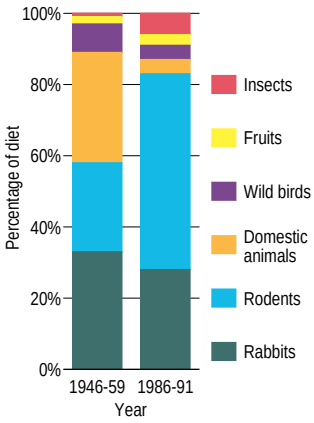

Fig. 2. Comparison of coyote diets in Kansas during the late 1940's and 1950's with diets from the late 1980's to 1991 (Gier 1968; Brillhart 1993).

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