

POPULATION STATUS OF NORTH AMERICAN GRASSLAND BIRDS FROM THE NORTH AMERICAN BREEDING BIRD SURVEY, 1966–1996

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Abstract. We summarize population trends for grassland birds from 1966 to 1996 using data from the North American Breeding Bird Survey. Collectively, grassland birds showed the smallest percentage of species that increased of any Breeding Bird Survey bird group, and population declines prevailed throughout most of North America. Although 3 grassland bird species experienced significant population increases between 1966 and 1996, 13 species declined significantly and 9 exhibited non-significant trend estimates. We summarize the temporal and geographic patterns of the trends for grassland bird species and discuss factors that have contributed to these trends.

LA CONDICIÓN DE LA POBLACIÓN DE AVES DE PASTIZAL EN AMÉRICA DEL NORTE UTILIZANDO EL BREEDING BIRD SURVEY DE NORTEAMÉRICA, 1966–1996

Sinopsis. Resumimos las tendencias poblacionales para las aves de pastizal desde 1966 hasta 1996 utilizando datos del Breeding Bird Survey de Norteamérica. Colectivamente, las aves de pastizal tuvieron el menor porcentaje de especies que aumentaron entre todos los grupos de aves en el Breeding Bird Survey. Prevalcieron las disminuciones de poblaciones de estas aves en la mayoría de Norteamérica. Aunque 3 especies de aves de pastizal experimentaron importantes aumentos poblacionales entre 1966 y 1996, 13 especies disminuyeron significativamente y 9 manifestaron estimaciones de tendencias no significativas. Resumimos los patrones temporales y geográficos de las tendencias para especies de aves de pastizal y analizamos los elementos que han contribuido a estas tendencias.

Key Words: bird populations; Breeding Bird Survey; grassland birds.

The status and distribution of grassland birds in North America have apparently undergone dramatic changes in the past 200 yr. Settlement of the continent by Europeans had both positive and negative effects on grassland bird communities. In eastern North America, the conversion from a forested to a largely agricultural landscape enabled grassland species to increase populations and expand their distributions, primarily during the nineteenth century (Andrle and Carroll 1988, Brewer et al. 1991, Peterjohn and Rice 1991). In contrast, the native grasslands of central and western North America suffered from settlement activities, particularly where the conversion to cultivated crops or overgrazing eliminated or severely altered these habitats (Bock and Bock 1988, Knopf 1988).

Anecdotal evidence suggests that populations of most grassland birds have declined in North America during the twentieth century. Although a variety of factors have contributed to these declines, the continued degradation and destruction of native grassland habitats remain the most prominent factors across the continent (McNicholl 1988, Askins 1993, Knopf 1994). Changing agricultural land-use practices have also been detrimental, contributing to declines in species occupying non-native pastures and hay-fields (Bollinger et al. 1990, Askins 1993).

In this paper, we use data from the North

American Breeding Bird Survey (BBS; Robbins et al. 1986, Peterjohn and Sauer 1996) to describe the geographic and temporal patterns in trends of grassland bird populations during the breeding seasons between 1966 and 1996. We evaluate regional patterns of observed species richness and mean trends for all grassland birds, document the percentage of grassland species with increasing trends, and compare this percentage to other species groups of management and ecological interest.

METHODS

The BBS is a roadside survey of approximately 4,000 randomly located survey routes established along secondary roads in the continental United States and Canada (see Peterjohn 1994). Although route coverage varies temporally and geographically, more than 2,800 routes have been surveyed annually since 1980. Each route is 39.4 km long with 50 stops spaced at 0.8-km intervals and is surveyed once annually by a single observer during the peak of the breeding season, primarily in June. The observer records all birds heard or seen within 0.4 km of each stop during a 3-min period.

The BBS was started in 1966 in eastern North America, and by 1968 routes were established across the continental United States and southern Canada. Additional information on the history and methodology of the survey is provided by Robbins et al. 1986.

STATISTICAL ANALYSES

We used the total number of individuals of a species counted over the entire BBS route as a population in-

dex. Most of our analyses of BBS data used the time series of population indices from the routes to estimate trend (a measure of population change over a prescribed interval, usually presented as percent change/year) and relative abundance (mean count). We also summarized this information for regions. Because the sites were georeferenced by route starting points, we were able to map information such as trends, relative abundance, and species richness.

Species richness maps

We calculated the number of grassland species recorded on each BBS route in 1966–1996. We then developed contour maps of species richness, using the route species totals as input to smoothing procedures (Isaaks and Srivastava 1989, Cressie 1992).

We used inverse distancing (Isaaks and Srivastava 1989) to smooth these data. In this procedure, abundance was estimated at a location as a distance-weighted average of counts from nearby sites. We used inverse distancing to estimate abundances for uniformly spaced locations on a 21.4-km grid across the continental United States and southern Canada and then used the Arc/Info Geographic Information System program to make a contour map from the estimated abundances (Environmental Systems Research Institute 1991). See Sauer et al. 1995 and 1997 for applications and discussions regarding mapping of survey data.

Trend estimation

We estimated trends from each route using the estimating equation procedure in which a multiplicative trend is modeled (Link and Sauer 1994). As in earlier analyses, we incorporated observer effects in the model to minimize bias associated with improved observer quality over time (Sauer et al. 1994).

Maps of regional patterns of trend were also estimated using contouring. To accommodate the differences in quality of information among routes, however, trend estimates were weighted by estimates of variances of trends and relative abundances from individual routes. This weighting was similar to that used in the estimation of the regional mean trends (e.g., Geissler and Sauer 1990, Link and Sauer 1994).

We estimated regional trends as a weighted mean of the route-specific trends. Weights of abundance along routes, precision of trend estimates, and areas were used to accommodate inequities in data quality and regional variation in numbers of samples (Geissler and Sauer 1990). The areas of BBS physiographic strata in states and provinces were used in the weighting (see Butcher 1990 for a map of BBS physiographic strata). Bootstrapping was used to estimate variances of trends. Regional trends were estimated for the entire survey area of the BBS (hereafter called "continental"), BBS regions (Eastern, Central, and Western; Bystrak 1981), states, and provinces. Regional trends were estimated for three time periods: 1966–1996, 1966–1979, and 1980–1996. Subinterval trend estimates were based on smaller samples of routes and were sometimes much less precise than long-term estimates. Hence, long-term trends may not be accurately reflected in either or both of the subinterval estimates.

Annual indices

To evaluate nonlinear patterns of population change, we used the residual method for estimating annual indices of abundance (Sauer and Geissler 1990). In these analyses, a composite yearly index of abundance was estimated as a mean residual from the estimated regional trend. Nonlinear patterns in the indices were illustrated with LOESS smooths (James et al. 1990).

Composite analysis of grassland birds

Although several authors have developed lists of grassland bird species (Udvardy 1958, Mengel 1970), no consensus exists regarding the composition of this ecological grouping. In this paper we use the 25 species included in the grassland bird group of Peterjohn and Sauer 1993. This group is generally restricted to obligate grassland species, although the raptors occupy large territories that may include mixed grassland-shrubland communities, open areas, and other habitats. The group does not include species that regularly use nongrassland habitats during some seasons of the year or in sizable portions of their ranges, however. For each BBS route, we calculated the total number of grassland bird species and mean trend for the species group. Maps were made using inverse distancing to illustrate geographic patterns in distributions and trends.

We estimated percentages of increasing species for other groupings of birds to compare with composite trends in grassland birds. These groups are defined in Peterjohn and Sauer 1993 and include groups based on breeding habitat (wetland, scrub/successional, woodland, urban), migration form (short-distance migrant, neotropical migrant, permanent resident), nest type (cavity, open cup), and nest location (ground/low, midstory/canopy). For each group, we estimated trends for each species in the group over the surveyed area and determined the percentage of species with positive trend estimates using a procedure based on empirical-Bayes methods that incorporates the relative variances of the component trend estimates (Link and Sauer 1995). We used a z-test to evaluate the null hypothesis that the percentage of species with increasing trends did not differ from 50.

RESULTS

Grassland bird species richness in North America was greatest in the Great Plains, especially in portions of North Dakota, Montana, and the adjacent prairie provinces of Canada (Fig. 1). Species richness was noticeably reduced east and west of the Great Plains, becoming most depauperate in the southeastern states. Trends for the entire group showed declines prevailing throughout most of the United States and southern Canada (Fig. 2). Areas with increasing populations of grassland birds were small and locally distributed, although one of these areas (in northeastern Montana and northwestern North Dakota) corresponded with the northern Great Plains where species richness was greatest. Only 23% of grassland bird species—the smallest proportion of any BBS bird group—showed posi-

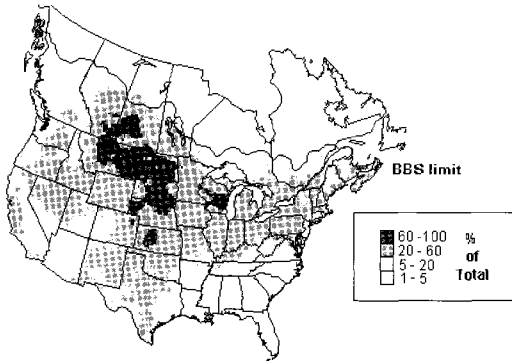


FIGURE 1. Species richness map for grassland bird group, 1966–1996, expressed as the percentage of the total group.

tive population trend estimates during 1966–1996 (Fig. 3).

The continental trend estimates for all grassland birds (25 species) are summarized in Table 1. Although the entire grassland bird group generally declined throughout North America between 1966 and 1996, individual species showed a variety of temporal and geographic patterns in population trends. These trends are discussed in greater detail below.

SPECIES WITH INCREASING POPULATION TRENDS

BBS data indicate that only three grassland bird species experienced significant increases in their continental populations between 1966 and 1996. Few Ferruginous Hawks (*Buteo regalis*) were recorded along BBS routes prior to 1980, although their representation improved subsequently. As is true for many raptors, this species is not well sampled by the BBS methodology and was recorded in small numbers throughout its range. Population increases after 1980 were largely responsible for the increasing trends shown over the entire survey period (Table 1). These increases were evident across most of the breeding range (Fig. 4).

Upland Sandpipers (*Bartramia longicauda*) were more adequately surveyed by the BBS methodology than was the preceding species. Population increases were most evident from the Great Plains westward, whereas declines were concentrated from the Great Lakes into Minnesota and Wisconsin (Fig. 5). The remnant, locally distributed populations elsewhere in eastern North America are currently poorly monitored by the BBS. Although some regional variability exists in the temporal patterns of trends in this species, the continental increases were most consistent between 1978 and 1992 (Fig. 6).

Sedge Wrens (*Cistothorus platensis*) are op-

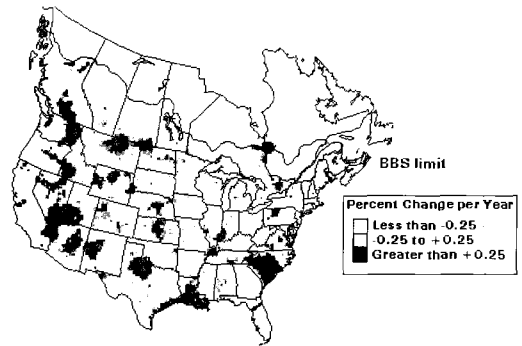


FIGURE 2. Population trend map for grassland bird group, 1966–1996. The map presents areas of consistent population change, grouped into categories of declining ($< -0.25\%$ change per year), indeterminate (-0.25 to $+0.25\%$ change per year), and increasing ($> +0.25\%$ change per year) trends.

portunistic breeders, apparently exhibiting little site fidelity (Burns 1982). This species' erratic seasonal movements may obfuscate population-trend estimates, and they should thus be viewed with caution. The long-term trend was generally positive, reflecting increases during the 1980–1996 interval. In contrast, most trend estimates for the species were negative during the 1966–1979 interval. Increases between 1966 and 1996 were most prevalent from the Dakotas into Manitoba and portions of Minnesota, whereas declines prevailed eastward from Iowa and Wisconsin and in Saskatchewan (Fig. 7).

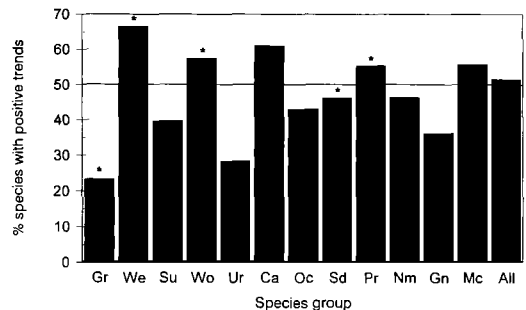


FIGURE 3. Percentages of increasing species for all BBS bird groups, 1966–1996. Gr = grassland birds, We = wetland birds, Su = shrub and successional birds, Wo = woodland birds, Ur = urban birds, Ca = cavity nesters, Oc = open-cup nesters, Sd = short-distance migrants, Pr = permanent residents, Nm = neotropical migrants, Gn = ground- and low-nesting birds, Mc = midstory- and canopy-nesting birds, All = all species. An asterisk (*) denotes a significant ($P < 0.05$) deviation from 50%.

TABLE 1. BBS CONTINENTAL TREND ESTIMATES FOR GRASSLAND BIRDS

Species	1966-1996				1966-1979			1980-1996		
	Trend ^a	p ^b	N ^c	RA ^d	Trend	P	N	Trend	P	N
Northern Harrier	-0.6	-	891	0.49	-1.4	-	397	-0.7	-	745
Ferruginous Hawk	5.2	***	186	0.25	2.6	-	34	7.2	**	170
Ring-necked Pheasant	-1.0	**	1,206	7.30	-0.8	-	735	-0.6	-	1,060
Sharp-tailed Grouse	0.3	-	124	0.55	-4.8	-	53	1.8	-	105
Mountain Plover	-2.7	**	33	0.31	2.0	-	9	3.7	-	29
Upland Sandpiper	1.3	***	581	2.22	3.0	**	315	-0.9	-	486
Long-billed Curlew	-1.4	-	202	1.45	1.7	-	74	-2.0	-	155
Short-eared Owl	-2.8	-	132	0.21	4.1	-	54	-0.8	-	90
Horned Lark	-1.3	***	1,805	27.02	-0.4	-	1,064	-2.0	***	1,559
Sedge Wren	2.2	**	307	1.14	-3.3	**	162	1.9	-	262
Sprague's Pipit	-4.7	***	108	1.41	-6.6	***	51	-4.5	-	94
Dickcissel	-1.6	***	783	16.29	-5.5	***	559	0.4	-	706
Cassin's Sparrow	-2.5	***	203	16.31	0.4	-	96	-0.2	-	186
Vesper Sparrow	-0.8	**	1,462	7.84	-1.9	***	816	0.1	-	1,232
Lark Bunting	-0.9	-	332	42.97	-4.0	**	154	0.2	-	288
Savannah Sparrow	-0.6	**	1,477	8.40	0.2	-	810	-0.2	-	1,336
Baird's Sparrow	-1.6	-	115	1.87	-4.7	**	52	-1.1	-	95
Grasshopper Sparrow	-3.6	***	1,404	3.97	-4.6	***	857	-2.1	***	1,193
Henslow's Sparrow	-8.8	***	149	0.15	-6.0	**	99	-10.4	***	80
Le Conte's Sparrow	1.4	-	154	0.73	-1.9	-	44	4.6	***	138
McCown's Longspur	1.1	-	59	4.57	3.5	-	27	2.7	-	44
Chestnut-collared Longspur	-0.1	-	145	9.27	1.6	-	76	1.1	-	125
Bobolink	-1.6	***	1,134	5.35	1.1	**	761	-3.8	***	1,026
Eastern Meadowlark	-2.6	***	1,921	20.29	-1.4	***	1,338	-3.0	***	1,761
Western Meadowlark	-0.6	**	1,480	44.48	-1.4	**	800	-0.3	-	1,348

Note: See American Ornithologists' Union 1983 for scientific names.

^a Average percent change per year.

^b ** 0.01 < P < 0.05, *** P < 0.01.

^c Number of BBS routes on which each species has been recorded.

^d Relative abundance; expressed as mean number of individuals per BBS route within the range of the species.

SPECIES WITH NONSIGNIFICANT POPULATION TRENDS

Nine grassland bird species had nonsignificant trend estimates, although for six of these species the trends were in a negative direction (Table 1). Sharp-tailed Grouse (*Tympanuchus phasianellus*) and Short-eared Owls (*Asio flammeus*) were poorly sampled by the BBS methodology, and estimates may not be representative of actual

population trends (Table 1). Other species, including Le Conte's Sparrow (*Ammodramus leconteii*) and McCown's Longspur (*Calcarius mccownii*), have restricted ranges or are otherwise infrequently encountered along BBS routes. Their population trends were generally imprecisely estimated and should also be viewed with caution. Four other species are summarized

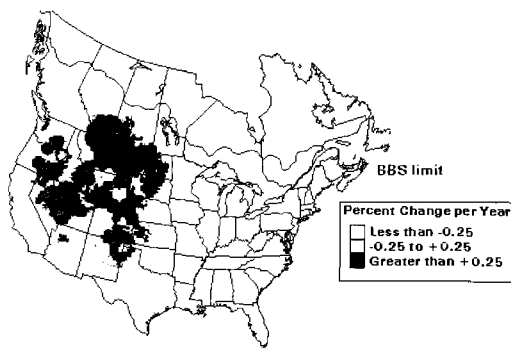


FIGURE 4. Ferruginous Hawk population trend map, 1966-1996.

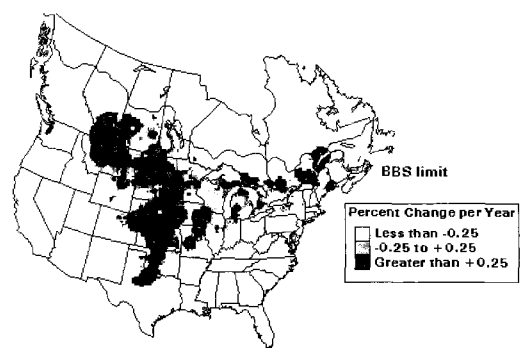


FIGURE 5. Upland Sandpiper population trend map, 1966-1996.

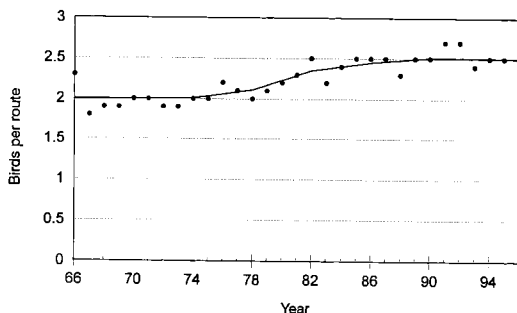


FIGURE 6. Continental indices for Upland Sandpiper, 1966–1996.

below to illustrate the temporal and geographic patterns in their trends.

Northern Harriers (*Circus cyaneus*) were widely encountered in relatively small numbers throughout their range. BBS data indicate that the most consistent declines occurred from the Great Plains westward through the intermountain states, although increases were evident in portions of the Dakotas, Montana, and Wyoming (Fig. 8). Consistent increases were also evident from Wisconsin eastward to the maritime provinces and in the states bordering the Pacific coast. This species' continental population trends remained negative from 1966 to 1996 (Table 1).

Long-billed Curlews (*Numenius americanus*) are not particularly conspicuous during the breeding season except when they vocalize at dawn (Fitzner 1978). Their relative abundance may be under-represented by the BBS methodology (Redmond et al. 1981). Also, reports of nonbreeders along BBS routes may have obscured population trends in some areas. Despite these potential limitations, BBS data suggest that Long-billed Curlews declined throughout the western Great Plains but tended to increase west

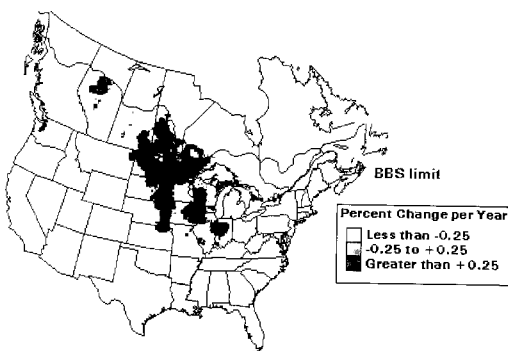


FIGURE 7. Sedge Wren population trend map, 1966–1996.

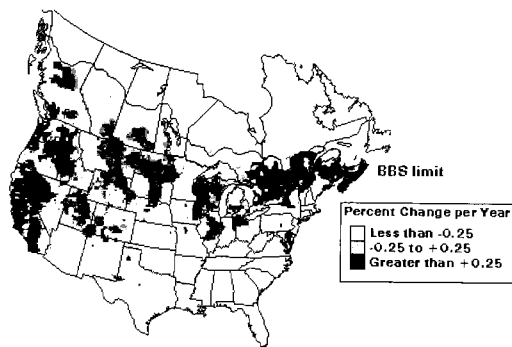


FIGURE 8. Northern Harrier population trend map, 1966–1996.

of the Rocky Mountains except in Utah (Fig. 9). No consistent temporal patterns were evident in these trends (Table 1).

Lark Buntings (*Calamospiza melanocorys*) can be nomadic during the breeding season, and these short-term movements may obscure or accentuate long-term population trends (Stewart 1975, Andrews and Righter 1992). Along BBS routes, population declines predominated throughout most of the Lark Bunting's range (Fig. 10). Increasing populations were small and localized, except in Montana. Population declines during 1966–1979 were largely responsible for the long-term trends in this species, although the estimates became more positive after 1980 (Table 1).

As a result of their limited distribution on the northern Great Plains and historic declines in some populations (Stewart 1975), Baird's Sparrows (*Ammodramus bairdii*) have received considerable attention. The BBS population trend map indicates that declines were prevalent in North Dakota and along the northern periphery of this species' range, whereas increases were evident elsewhere (Fig. 11). The trend estimates

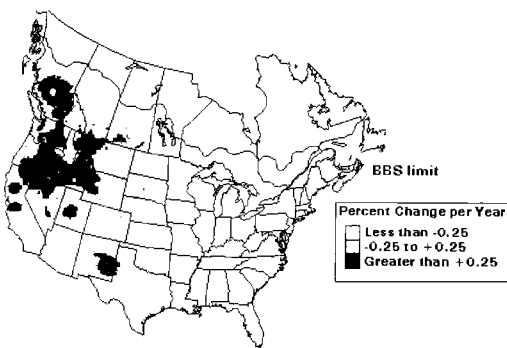


FIGURE 9. Long-billed Curlew population trend map, 1966–1996.

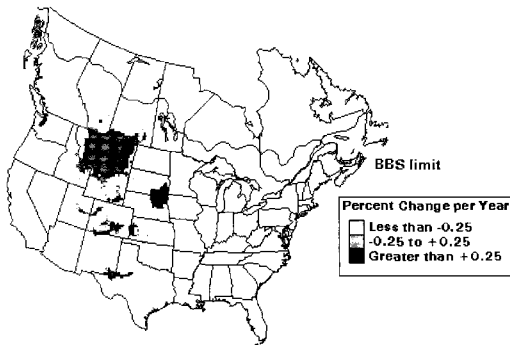


FIGURE 10. Lark Bunting population trend map, 1966–1996.

were nonsignificant for the entire survey period, although a significant decline occurred during 1966–1979 (Table 1).

SPECIES WITH DECLINING POPULATION TRENDS

Most of the 13 species that experienced significant declines in their continental populations during 1966–1996 were widely distributed and well sampled by the BBS (Table 1). Mountain Plovers (*Charadrius montanus*), however, were recorded on a relatively small number of routes which precluded a detailed analysis of the species' population trends. Other species, including Sprague's Pipit (*Anthus spragueii*) and Henslow's Sparrow (*Ammodramus henslowii*), have relatively limited breeding distributions but experienced consistent significant rangewide declines between 1966 and 1996. Cassin's Sparrows (*Aimophila cassinii*) exhibit considerable annual fluctuations in abundance which produce imprecise trend estimates, but they have shown a declining tendency since the mid-1970s. Examples of other temporal and geographic patterns in population trends shown by declining species are described below.

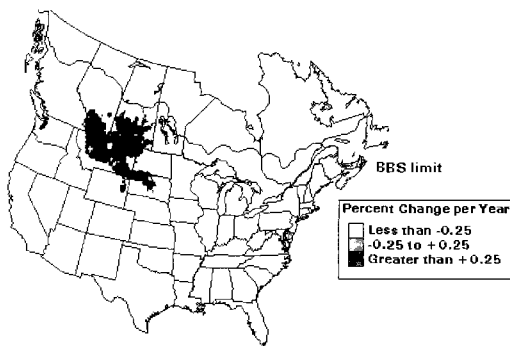


FIGURE 11. Baird's Sparrow population trend map, 1966–1996.

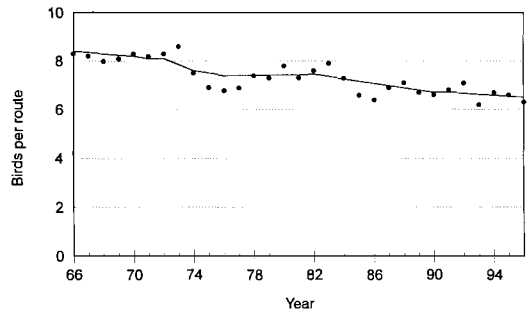


FIGURE 12. Continental indices for Ring-necked Pheasant, 1966–1996.

Populations of Ring-necked Pheasants (*Phasianus colchicus*) exhibited consistent trends during 1966–1979 and 1980–1996 (Table 1). The surveywide indices declined noticeably during the mid-1970s, followed by a slight recovery and then another decline during 1982–1985 (Fig. 12). Increasing populations were most evident in the Great Plains, whereas declines were widespread from the Rocky Mountains westward and from Wisconsin and Illinois east into New England (Fig. 13).

BBS data indicate that Horned Lark (*Eremophila alpestris*) populations experienced widespread declines between 1966 and 1996 (Table 1, Fig. 14). Declining trends were prevalent in most regions of the continent, although local increases were evident from the western Great Lakes across the northern Great Plains and into the intermountain western states.

The status and distribution of the Dickcissel (*Spiza americana*) have always been confounded by the species' irregular population movements (Emlen and Wiens 1965, Ewert and Cantino 1967). These movements normally produce influxes near the northern periphery of the breeding range that are inversely correlated with

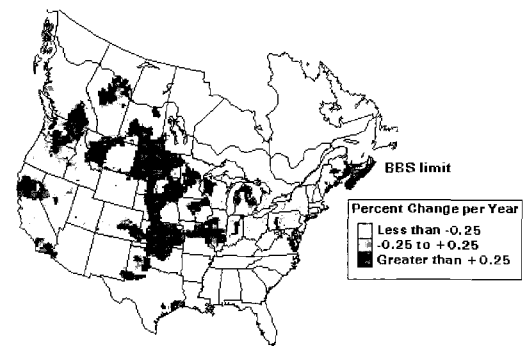


FIGURE 13. Ring-necked Pheasant population trend map, 1966–1996.

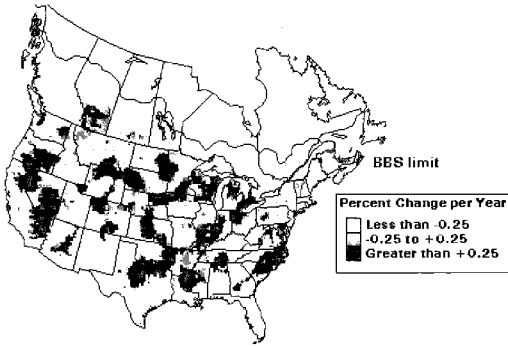


FIGURE 14. Horned Lark population trend map, 1966–1996.

habitat suitability in the southern portion of the range (Fretwell 1986). Perhaps as a result of these irregular movements, the geographic patterns in the long-term trends of Dickcissels are not uniform (Fig. 15). Declines were most prevalent across the northern half of the range and in central Texas. Increases predominated from northern Texas through Oklahoma into Kansas and from Arkansas and Louisiana east into Alabama and Tennessee. The continental annual indices exhibited a distinct decline from 1966 through the late 1970s, followed by variable but fairly stable counts (Fig. 16A). Declines during the first 10 yr of the BBS were evident in the Eastern and Central BBS regions, but populations in both regions were reasonably stable between 1980 and 1996 (Figs. 16B and C).

Vesper Sparrow (*Poocetes gramineus*) populations showed consistent declines from Minnesota, Wisconsin, and Indiana eastward and from Montana and South Dakota south to northern New Mexico, northern Arizona, and Nevada (Fig. 17). Increasing populations predominated from Illinois across Iowa to Kansas and northward into North Dakota. The continental indices

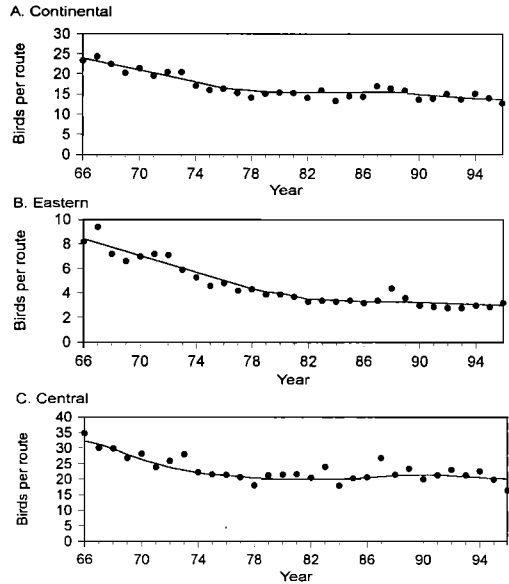


FIGURE 16. BBS annual indices for Dickcissel populations, 1966–1996: A = continental, B = Eastern BBS region, C = Central BBS region.

varied, but declines were most evident before the mid-1970s (Fig. 18). This temporal pattern reflected similar trends in the Central and Western BBS regions; populations in the Eastern BBS region declined throughout the survey period (Fig. 17).

Savannah Sparrows (*Passerculus sandwichensis*) have expanded their breeding range during the twentieth century, most noticeably in the midwestern states where their breeding distribution has spread southward from the upper Great Lakes (Monroe et al. 1988, Peterjohn and Rice 1991). Despite this range expansion, populations declined from Ontario, Minnesota, and Iowa eastward between 1966 and 1996 (Fig. 19).

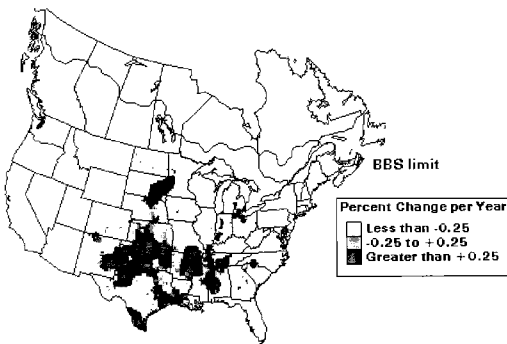


FIGURE 15. Dickcissel population trend map, 1966–1996.

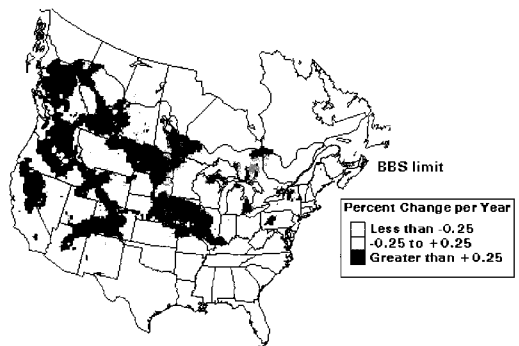


FIGURE 17. Vesper Sparrow population trend map, 1966–1996.

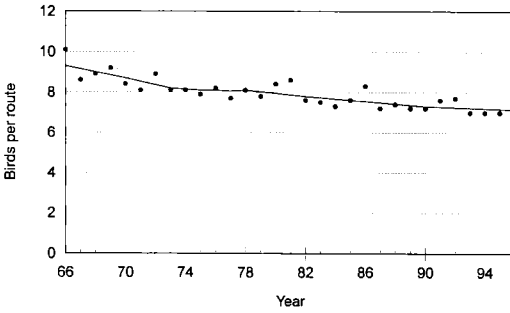


FIGURE 18. Continental indices for Vesper Sparrow, 1966–1996.

A mosaic of increases and decreases was evident elsewhere, with increases most prevalent in the Rocky Mountains and northern Great Plains. Regional trends exhibited increases in the Western BBS region and more variation, including a fairly distinct decline during the late 1970s, in the Central BBS region (Figs. 20A and B). The continental indices also showed the most marked declines in the late 1970s (Fig. 20C).

Grasshopper Sparrows (*Ammodramus saviannarum*) showed some of the most consistent declines of any grassland bird. The declines prevailed throughout most of the Grasshopper Sparrow's range (Fig. 21), although some local increases were evident in the western states and elsewhere. These trends were fairly consistent from 1966 to 1996, with a slight moderation in the rate of decline in recent years.

BBS data indicate that Bobolinks (*Dolichonyx oryzivorus*) have generally declined throughout their breeding range (Fig. 22). Areas with increasing populations were small and locally distributed, most notably from North Dakota to western Ontario and in Pennsylvania. The continental indices were fairly stable through the late 1970s, followed by a consistent decline

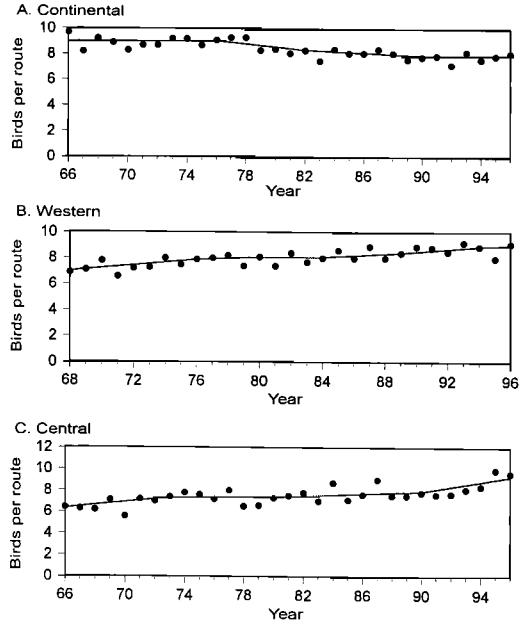


FIGURE 20. BBS annual indices for Savannah Sparrow populations, 1966–1996: A = continental, B = Western BBS region, C = Central BBS region.

(Fig. 23). The general population declines in 1980–1996 contrasted sharply with the population estimates for 1966–1979, when the continental population significantly increased (Table 1).

Eastern Meadowlarks (*Sturnella magna*) also exhibited consistent declines on the BBS. Declining populations prevailed throughout most of the range except in the southwestern states (Fig. 24). The long-term trends were almost entirely negative, and most declines were significant. These declining trends prevailed during the 1966–1979 and 1980–1996 intervals (Table 1).

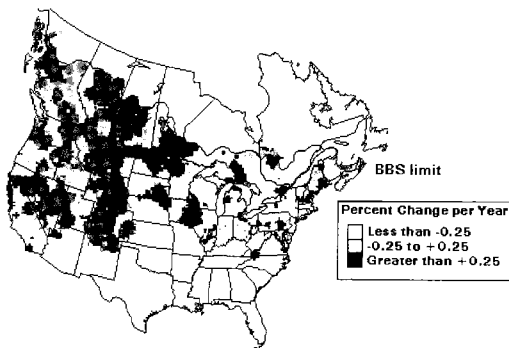


FIGURE 19. Savannah Sparrow population trend map, 1966–1996.

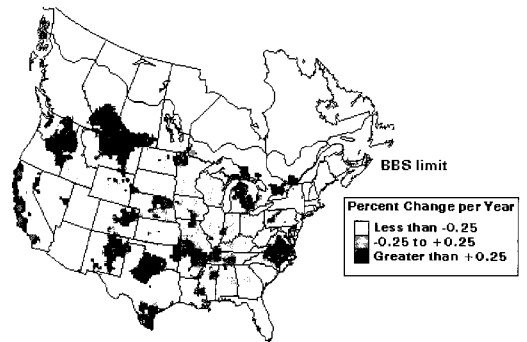


FIGURE 21. Grasshopper Sparrow population trend map, 1966–1996.

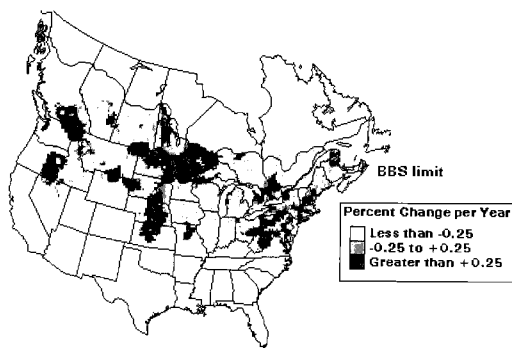


FIGURE 22. Bobolink population trend map, 1966–1996.

Robbins et al. (1986) reported declines in Eastern Meadowlark populations associated with the severe winters of 1976–1978. These declines were most apparent in the Midwest, especially in Illinois, Indiana, Michigan, and Kentucky (Figs. 25A–D). Populations in Indiana recovered in 3 yr, but no substantial recovery was evident in the other states.

Western Meadowlarks (*S. neglecta*) have undergone a range expansion in the twentieth century, spreading eastward into the Great Lakes region (Lanyon 1956, DeVos 1964). This expansion largely occurred before the start of the BBS, and Western Meadowlark populations generally declined between 1966 and 1996 (Table 1). These declines were evident throughout most of the Western Meadowlark's range, although increases occurred from southern California across the southwestern states to Texas and locally northward along the Rocky Mountains and Great Plains (Fig. 26).

DISCUSSION

Although BBS data indicate the trends of grassland bird populations, they do not identify the factors responsible for these trends. Some factors, such as habitat alteration, degradation, and destruction, may be common to many grassland birds, whereas other factors may influence only certain species or may operate in only portions of a species' range. The factors believed to be responsible for the reported population trends are discussed below, although for many species the causes of their population trends have not been conclusively identified.

SPECIES WITH INCREASING POPULATION TRENDS

Ferruginous Hawk populations have experienced significant declines and range contractions in the past 100 yr, but these trends were most evident before 1960 (Houston and Bechard 1984, Schmutz 1984, Houston and Schmutz

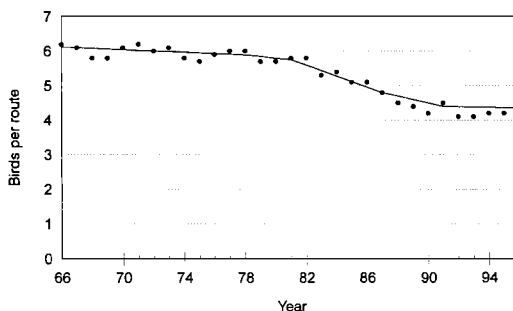


FIGURE 23. Continental indices for Bobolink, 1966–1996.

1999). The conversion of native grasslands to agricultural fields was largely responsible for these trends (Schmutz 1984). Contributing factors included persecution, reductions in prey populations, fewer fires, and shortages of suitable nest sites (Houston and Bechard 1984).

Ferruginous Hawk population trends after 1960 have been less certain. Since most tillable lands had already been converted into agricultural fields, additional declines in response to habitat loss have been relatively small (Houston and Bechard 1984). The declines apparently have been reversed in portions of the species' range, where Ferruginous Hawks may have increased during the late 1980s (Harlow and Bloom 1989). These increases were reflected in the positive BBS trend estimates for 1980–1996 (Table 1). Short-term population increases in Ferruginous Hawks are not unexpected, as the birds are known to be fairly nomadic and local influxes have been documented in response to prey availability (Gilmer and Stewart 1983). Additional data from the BBS and other sources are needed to determine if the increases since 1980 reflect short-term fluctuations or a long-term reversal of historic declines.

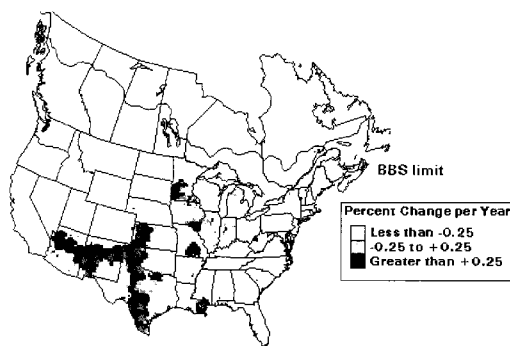


FIGURE 24. Eastern Meadowlark population trend map, 1966–1996.

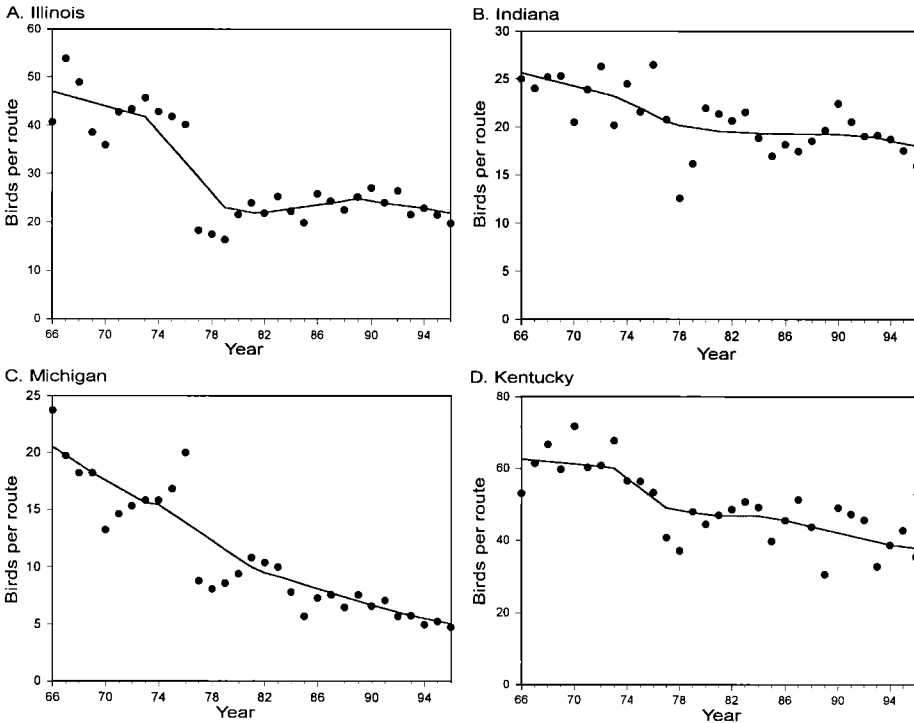


FIGURE 25. BBS annual indices for Eastern Meadowlark populations, 1966–1996: A = Illinois, B = Indiana, C = Michigan, D = Kentucky.

Upland Sandpiper populations suffered significant declines in the late nineteenth and early twentieth centuries as a result of market hunting and habitat destruction (Bent 1929). Their numbers recovered, however, when hunting ceased. More recent declines have been evident in the eastern portion of the species' range since the 1940s, and only small isolated populations remain in most of this region (Peterjohn and Rice 1991, Carter 1992). BBS trend estimates were

consistent with this pattern; there were declines in the Eastern BBS region, but relatively few Upland Sandpipers were recorded on those BBS routes, and the eastern regional trend estimates thus had little influence on the continental trend estimates.

Increases in the Great Plains were largely responsible for the positive continental trend estimates for Upland Sandpipers. Factors that contributed to these positive trends merit additional study since the increases occurred in areas where most other grassland birds declined. Breeding Upland Sandpipers occupy much larger home ranges than other grassland birds (Mitchell 1967), so nesting pairs may be less affected by unfavorable agricultural practices in individual fields. These sandpipers also prefer to nest where the grass cover is of mixed short and medium heights (Kirsch and Higgins 1976, Ailes 1980). Hence, they tolerate moderate levels of grazing, especially in habitats where the grass cover may otherwise be too tall. This ability to tolerate some disturbance may have allowed populations to increase in recent decades. Overgrazing, standing water, burning, and mowing, however, can still make breeding habitats unsuitable for this species (Mitchell 1967).

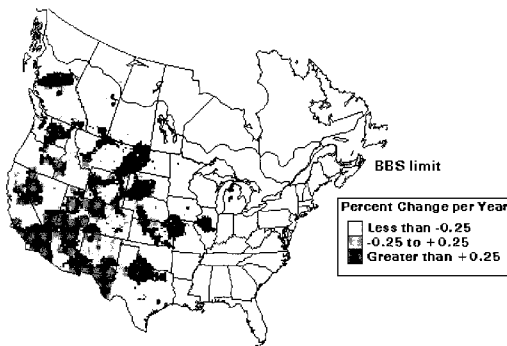


FIGURE 26. Western Meadowlark population trend map, 1966–1996.

Factors on the Upland Sandpiper's South American winter range may also have influenced BBS population trends. Unfortunately, this species' winter ecology is poorly understood (White 1988). Although pesticide use and unfavorable agricultural practices remain threats, deforestation and the subsequent creation of grasslands are probably beneficial for Upland Sandpipers. Some range extensions have been reported in deforested areas of South America (White 1988).

The erratic intraseasonal movements of Sedge Wrens may not have greatly influenced the BBS trend estimates since these movements are most evident in late summer after breeding surveys have been completed (Meanley 1952, Schwillling 1982). Bedell (1996), for example, documented Sedge Wrens on some Nebraska BBS routes in August, even though the species had never been recorded during the June surveys. Although lack of site fidelity during the breeding season may contribute to considerable annual fluctuations in abundance of this species (Burns 1982), the BBS data may reasonably reflect population trends in June. How these June population trends relate to the entire Sedge Wren population, however, cannot be determined until the birds' seasonal movements are better understood.

Despite fluctuations, some marked declines have been apparent in Sedge Wren populations in the twentieth century, especially in the northeastern states and near the eastern Great Lakes (Brewer et al. 1991, Peterjohn and Rice 1991, Gibbs and Melvin 1992). These trends have continued in recent decades, with declines along BBS routes most consistent in the eastern half of the species' range. Habitat loss appears to have been the most important factor contributing to these declines, although burning and overgrazing may have been important in some areas (Gibbs and Melvin 1992).

In contrast, Sedge Wren population increases on the Great Plains during 1980–1996 were largely responsible for generally positive continental trend estimates in 1980–1996 and 1966–1996 (Table 1). These increases were most evident in the 1990s. Since Sedge Wrens frequently occupy grasslands created by the Conservation Reserve Program (CRP; Johnson and Schwartz 1993), increased habitat availability may have contributed to these increases. Also, increased annual precipitation has improved wetland conditions in this portion of the Great Plains (U.S. Fish and Wildlife Service 1997), expanding the extent of damp grassland habitats favored by nesting Sedge Wrens.

SPECIES WITH NONSIGNIFICANT POPULATION TRENDS

For those species that are poorly sampled by the BBS, trend estimates may not represent the

true status of their breeding populations. Any discussion of factors responsible for these reported trends would be speculative. Only those species adequately surveyed by the BBS are discussed below.

The BBS trends for Northern Harrier populations were similar to those reported by Martin (1989), Serrentino and England (1989), and Sweet (1991). Martin (1989) indicated that several factors combine to prevent clear interpretation of population trends for this species. Its specialized predation on voles (*Microtus* spp.) produces extensive nomadic movements which, in concert with a fluctuating prey base, obscure distinguishing between actual trends and normal fluctuations. Precipitation extremes also influence population levels since droughts or floods can affect habitat suitability and prey populations. Severe winter weather and its effects on prey populations can also influence short-term fluctuations in Northern Harrier populations (Hamerstrom 1986). In the BBS data, these marked short-term fluctuations were apparent only in the annual indices for states and provinces and in physiographic strata. Where long-term declines were documented, as in portions of the northeastern and midwestern United States, habitat destruction and intensified agricultural use of remaining grasslands are believed to have been largely responsible (Serrentino and England 1989, Sweet 1991). Reforestation has also eliminated many suitable grasslands in the Northeast (Serrentino and England 1989).

Breeding Long-billed Curlews are associated with shortgrass steppe communities on the western Great Plains and with grasslands in the Great Basin. They prefer habitats that have been heavily grazed where the vegetation is less than 10 cm high and the soils are moist (Knopf 1988). Populations were decimated by uncontrolled hunting in the nineteenth and early twentieth centuries, causing a noticeable contraction of the breeding range (Page and Gill 1994). The conversion of native grasslands to agricultural fields has not permitted a sustained population recovery (Page and Gill 1994), and the breeding range has experienced some local contractions since 1960 (McCallum et al. 1977, Renaud 1980). Since Long-billed Curlews prefer grazed habitats, major threats to their breeding populations are the continued conversion of grasslands into cultivated fields and the loss of wetlands, which may eliminate the moist soils preferred for feeding (Knopf 1988, Page and Gill 1994). These factors may be responsible for the general population declines of Long-billed Curlews along BBS routes on the western Great Plains between 1966 and 1996. However, loss of coastal foraging habitats during the winter, exposure to toxic

chemicals, and increased predation may also have contributed to the declines of some populations (Page and Gill 1994). Factors that may have contributed to the apparent increase in populations along BBS routes in the Great Basin have not been identified.

Breeding Lark Buntings are conspicuous occupants of short- and mixed-grass communities of the Great Plains. Their nomadic movements are poorly understood, but fluctuations in precipitation levels and the influence of these fluctuations on habitat conditions and food availability are believed to be primarily responsible for these movements (Stewart 1975, Andrews and Righter 1992). Large influxes of Lark Buntings may appear for a single year or for several years in any portion of the species' range, only to disappear quickly when conditions change (Shane 1996). Regional populations may show cyclical fluctuations, and Shane (1996) has theorized that a single population cycle may require several decades to complete. Until this species' population fluctuations are better understood, the biological significance of BBS trend estimates for Lark Buntings remains in question.

Despite these fluctuations, the generally negative trends for Lark Bunting populations between 1966 and 1996 were associated with the destruction and degradation of their preferred grassland habitats (Andrews and Righter 1992). These buntings are also nomadic during the winter months (Shane and Seltman 1995), and changing habitat conditions in their winter range may have contributed to population trends. Since 1990, however, Lark Buntings have benefited from habitats created by the CRP on the Great Plains (Johnson and Igl 1995). These new habitats have allowed some populations to expand and may have contributed to the more positive population trend estimates since 1980.

Baird's Sparrows have not been extensively studied, and the factors affecting their population trends are poorly understood. They frequent mixed-grass communities or, in more arid regions, the taller grasslands bordering wetlands, lakes, or other water sources. They prefer relatively undisturbed grasslands and avoid intensively grazed areas (Stewart 1975). Habitat destruction and degradation during the breeding season have been associated with population declines in the past (Stewart 1975). Habitats created by the CRP may have benefited this species in the 1990s (Johnson and Igl 1995). Factors influencing grassland habitats on the winter range in the southwestern United States and Mexico may also influence population trends of Baird's Sparrows; their winter distribution is poorly understood (Phillips et al. 1964), however, and

their habitat preferences and ecological requirements are largely unknown.

SPECIES WITH DECLINING POPULATION TRENDS

Many of the factors important in the declines of grassland bird populations are common to most species. These factors are discussed first, followed by a summary of the species-specific factors that have contributed to declining trends.

Habitat destruction

The destruction of grassland habitats has been implicated in the declines of all grassland birds. The loss of native grasslands in North America has been dramatic, especially in the eastern half of the continent (Vickery 1996). Most of these grasslands disappeared before the twentieth century, but the conversion of shortgrass communities into agricultural habitats has continued (Knopf 1988). The conversion of non-native pastures and hayfields into other agricultural habitats has also been prevalent during the past 50 yr (Herkert 1994).

Until recently, few new grasslands had been created to compensate for habitats converted into agricultural fields or urban development or lost through forest regeneration. Reclamation of strip mines in portions of the northern Appalachian Mountain region created extensive grasslands in areas that were formerly forested, producing local increases in some grassland birds (Whitmore and Hall 1978). Reproductive success may be low in these habitats, however, so they may actually serve as population "sinks" for some species (Wray et al. 1982).

Beginning in the 1980s, the CRP was initiated to reduce agricultural overproduction. Millions of hectares of cropland were converted to grasslands or other perennial cover, with the greatest enrollment of area in the central United States (Young and Osborn 1990). Although the CRP lands represent a very small proportion of all agricultural lands in North America, creation of these habitats has benefited grasslands birds and even reversed the long-term declines of some regional populations (Johnson and Schwartz 1993, Johnson and Igl 1995). This reversal of some population trends in association with the creation of CRP lands demonstrates the importance of habitat availability in influencing population trends in grassland birds.

Habitat fragmentation

Although the effect of habitat fragmentation on woodland bird communities has been the subject of many studies, little information is available on its effects on grassland birds. Herkert (1994) examined area relationships of grassland birds in Illinois and noted that both area

and vegetative structure significantly influenced the composition of grassland bird communities. Five species were area sensitive in Illinois, and only Dickcissels were unaffected by this factor. In Maine, Vickery et al. (1994) found similar results, suggesting that large area requirements for grassland birds may be an important factor influencing habitat use and that fragmentation of remaining grassland habitats may play a significant role in the population trends of some species.

Habitat degradation

Grazing has been implicated in the declines of some local grassland bird populations, but its impact on regional populations is difficult to assess. Some species, such as Grasshopper Sparrow, may benefit from light to moderate grazing in portions of their range but be adversely affected in other areas (Vickery 1996). Other species may be fairly sensitive to grazing across their range and may serve as indicators of overall habitat quality (Bock and Webb 1984, Baker and Guthry 1990). Species that prefer shortgrass habitats, such as Long-billed Curlew and Horned Lark, may benefit from intensive grazing under some circumstances (Knopf 1988).

Agricultural practices, particularly those associated with hay cropping, have also been detrimental to many grassland birds. Hayfields are being cropped more frequently and at earlier dates (Rodenhouse et al. 1993), which under many circumstances prohibits grassland birds from successfully raising young during the breeding season (Warner and Etter 1989, Bollinger et al. 1990). Since hayfields provide most of the remaining grassland habitats in eastern North America (Herkert 1994), this agricultural practice may have serious adverse effects on the regional populations of grassland birds.

Grazing, fire, and agricultural practices also influence the successional stages of grassland communities. Habitats that have not been disturbed for 5–10 yr are favored by a few species such as Upland Sandpiper, Grasshopper and Henslow's sparrows, and Eastern Meadowlark (Bollinger 1995), which are less numerous in or completely absent from younger grasslands. Hence, regular disturbance to grasslands may favor generalist species such as Savannah Sparrow but may contribute to the declines of species favoring more mature grasslands (Bollinger 1995).

Mortality from toxic chemicals

Direct mortality of grassland birds from poisoning by toxic chemicals such as Carbofuran and Fenthion has been reported in a few cases (Stone 1979, Deweese et al. 1983). The geographic extent of this problem is poorly under-

stood, however. Species that spend considerable time in agricultural fields, such as Ring-necked Pheasant and Horned Lark, may be most susceptible to the toxic effects of these chemicals.

Nest parasitism

Brown-headed Cowbirds (*Molothrus ater*) are known to parasitize the nests of most grassland-nesting passerines (Friedmann 1963). Rates of nest parasitism are generally believed to be low, but there is much interspecific variability in parasitism rates within sites (Hill 1976) as well as intraspecific variability across a species' range (Vickery 1996). Nest parasitism has been shown to have a negative impact on the recruitment of Dickcissels (Zimmerman 1983) and may have a similar effect on other species.

Adverse winter weather

Unusually severe winter weather is known to significantly reduce populations of some bird species (Robbins et al. 1986, Sauer and Droege 1990, Sauer et al. 1996). These reductions are normally short-term, with populations returning to normal within several years following the return to normal weather patterns. These weather conditions are most likely to affect species breeding in the northern United States, although during exceptionally harsh winters, such as occurred during 1975–1977, harsh conditions can extend south to the Gulf Coast states. Among grassland birds, species that winter in the northern United States, such as Ring-necked Pheasant and Eastern Meadowlark, appear to be most susceptible to these conditions.

Species-specific factors

Habitat destruction, fragmentation, and degradation are common causes of declines of all grassland species, but additional factors may have contributed to the population trends evident between 1966 and 1996.

Factors responsible for declines in Ring-necked Pheasant populations included intensified agricultural land-use practices (resulting in reduced habitat availability), increased use of pesticides, and adverse weather conditions (Dahlgren 1988). Adverse weather normally produced short-term population fluctuations, as exemplified by declines during the mid-1970s in portions of the range, whereas the other factors were largely responsible for long-term declines.

The loss of agricultural fields to reforestation and development contributed to Horned Lark population declines in eastern North America (Laughlin and Kibbe 1985, Buckelew and Hall 1994). Factors responsible for this species' decline elsewhere are poorly understood. Since Horned Larks are frequently associated with ag-

ricultural fields throughout their range, their extensive decline may indicate that some agricultural practices have contributed to these negative trends. For example, mortality of Horned Larks has been reported after exposure to certain pesticides (Beason 1995). In contrast, population increases in the intermountain region of the western United States corresponded with the conversion of sagebrush (*Artemisia*) habitats to grasslands (Knick and Rotenberry 1999).

Several factors contributed to trends in Dickcissel populations. This species is well adapted to residing in agricultural landscapes, inhabiting hayfields, pastures, weedy fallow fields, and weedy margins of ditches and roadsides. Conversion of these habitats to cultivated fields and more frequent mowing of hayfields, however, contributed to declines in some areas (Fretwell 1986). Brood parasitism by Brown-headed Cowbirds had a negative effect on Dickcissel recruitment (Zimmerman 1983), as did increased nest predation in certain habitats (Zimmerman 1984). Factors on the Dickcissel's tropical winter range are also believed to be important; the birds are viewed as pests in grain fields, and control operations at winter roosts have caused extensive mortality (Fretwell 1986, Basili and Temple 1999).

Several factors contributed to declines in Vesper Sparrow populations in eastern North America. Loss of grassland habitat to reforestation and urbanization was a major factor, although "clean farming" practices such as the removal of hedgerows and more frequent mowing of hayfields also contributed to declines (Laughlin and Kibbe 1985, Brauning 1992). The Vesper Sparrow is one of the first species to occupy reclaimed strip mines, however, and it has expanded its range in heavily forested portions of West Virginia and surrounding states since 1960 (Whitmore and Hall 1978).

The factors responsible for the trends in Savannah Sparrow populations are poorly understood (Wheelwright and Rising 1993). In the eastern United States, reforestation, conversion of grasslands to cultivated crops, and more frequent mowing of hayfields contributed to declines (Laughlin and Kibbe 1985, Peterjohn and Rice 1991). Factors associated with population trends in western North America, where areas of increase and decline were interspersed, were not identified.

Habitat destruction, fragmentation, and degradation have been the primary factors responsible for declines in Grasshopper Sparrow populations since 1966 (Vickery 1996). Because this species prefers relatively large grassland tracts (Herkert 1994, Vickery et al. 1994, Bollinger 1995), it may be particularly susceptible

to changes in habitat availability. Additionally, early mowing of hayfields can result in abandonment of breeding territories and can contribute to local annual fluctuations in abundance (Smith 1963).

In addition to habitat destruction, the factor most frequently cited for declines in Bobolink populations is more frequent mowing of hayfields (Bollinger et al. 1990). Many hayfields are cut in late May and at regular intervals throughout the summer, which does not provide Bobolinks with an opportunity to successfully raise a brood between mowing operations. Also, habitat preferences and other aspects of the species' winter biology are poorly understood, so factors on its South American winter range may also have contributed to population declines.

Eastern Meadowlarks tend to winter farther north than most other grassland birds, which may explain their greater susceptibility to periodic severe winter weather, as shown in the BBS annual indices. Their population declines, however, have generally been attributed to habitat destruction, more frequent mowing of hayfields, and similar factors affecting the populations of most grassland birds (Peterjohn and Rice 1991, Brauning 1992). Breeding meadowlarks are very sensitive to disturbance around the nest, either by people or livestock. Certain agricultural practices, such as spring tillage (which can reduce nest success and increase adult mortality), are also detrimental to breeding populations (Lanyon 1995).

Factors responsible for declines in Western Meadowlark populations are believed to be similar to those described for Eastern Meadowlarks (Lanyon 1994). Extensive droughts in the 1930s may have contributed to this species' eastward range expansion into the Great Lakes area, but causes for this expansion and subsequent decline have never been fully explained (Lanyon 1956).

CONCLUSIONS AND CONSERVATION IMPLICATIONS

BBS data indicate negative population trends for most grassland bird species between 1966 and 1996. The declines were fairly consistent throughout the survey period and, for many species, prevailed across most of the breeding range. A few exceptions existed, with Ferruginous Hawks, Upland Sandpipers, and Sedge Wrens exhibiting significant increases. The general declines in grassland birds shown by the BBS, however, reflected similar trends reported in the decades prior to the 1960s.

Although BBS data can be used to identify temporal and geographic patterns in population trends, the data do not identify the causes of these patterns. Other sources of information

must be used to establish the factors responsible for these trends. The common factors of habitat destruction, fragmentation, and degradation influence population trends of most grassland bird species. Agricultural practices such as earlier and more frequent mowing of hayfields may also contribute to population declines in some species, whereas other factors may be important for individual species or in specific geographic areas. These factors affect each species differently and produced the variety of geographic and temporal patterns in population trends evident in the BBS estimates.

Despite the prevalence of negative trend estimates, the situation is not entirely bleak for grassland birds. The CRP has shown that deterioration of grassland habitats can be reversed over the short term, even on fairly large geographic scales. Efforts to mitigate some of the other adverse factors discussed above can only help grassland birds. Grassland birds have evolved in relatively harsh and constantly changing habitats, requiring considerable adaptability in order to survive in this environment. With some assistance from humans, this adaptability may allow many of these species to recover if habitat availability and conditions improve.

The reversal of population declines resulting from the habitats created by the CRP is just the first step toward an overall improvement in the status of grassland birds. The conservation of these species must receive greater priority, particularly in the Great Plains where grassland bird communities are richest. Additional research is needed to better understand how these species respond to the factors that affect their population trends. This understanding may be crucial for the development of successful efforts to produce a long-term reversal of the general decline in grassland bird populations.

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