Influence of Prescribed Fire History on Habitat and Abundance of Passerine Birds in Northern Mixed-Grass Prairie

ELIZABETH M. MADDEN[1,2], ANDREW J. HANSEN[1], and ROBERT K. MURPHY[3]

[1]Biology Department, Montana State University, Bozeman, Montana 59717, USA
[2]Present address: Medicine Lake National Wildlife Refuge, Medicine Lake, Montana 59247, USA
[3]U.S. Fish and Wildlife Service, Des Lacs National Wildlife Refuge Complex, Kenmare, North Dakota 58746, USA

Madden, Elizabeth M., Andrew J. Hansen, and Robert K. Murphy. 1999. Influence of prescribed fire history on habitat and abundance of passerine birds in northern mixed-grass prairie. Canadian Field-Naturalist 113(4): 627–640.

To more effectively manage remaining native grasslands and declining populations of prairie passerine birds, linkages between disturbance regimes, vegetation, and bird abundance need to be more fully understood. Therefore, we examined bird-habitat relationships on mixed-grass prairie at Lostwood National Wildlife Refuge (NWR) in northwestern North Dakota, where prescribed fire has been used as a habitat management tool since the 1970s. We sampled bird abundance on upland prairie at 310 point count locations during 1993 and 1994 breeding seasons. We also measured vegetation structure and composition at each location. Complete fire histories were available for each point, with over 80% having been burned one to four times in the previous 15 years. Post-fire succession generally transformed vegetation structure from short, sparse, and grassy with few forbs and low litter immediately after fire, to increasing and moderate amounts of forbs, litter, and shrubs two to eight years postfire, to tall, dense, shrubby prairie with little forb, grass, or litter understory when fire was absent (>80 years). Most grassland birds (six of nine species examined) at Lostwood NWR were absent from prairie untreated with fire. Species richness and abundances of Baird's Sparrows (*Ammodramus bairdii*), Bobolinks (*Dolichonyx oryzivorus*), Grasshopper Sparrows (*A. savannarum*), Le Conte's Sparrows (*A. leconteii*), Sprague's Pipits (*Anthus spragueii*), and Western Meadowlarks (*Sturnella neglecta*) were positively related to an index of amount of fire, and these species were absent from unburned units. In contrast, Common Yellowthroats (*Geothlypis trichas*) and Clay-colored Sparrows (*Spizella pallida*) both reached highest abundance on unburned prairie. To provide maximum grassland bird diversity, managers of mesic, mixed-grass prairie generally should provide areas with short (2-4 year), moderate (5-7 year), and long (8-10 year, or more) fire return intervals. Because long-term rest may create habitat unfavorable for most species of grassland passerines in mesic, northern mixed prairie, periodic defoliations by disturbances such as fire should be considered essential to restore and maintain native biodiversity.

Key Words: Baird's Sparrow, *Ammodramus bairdii*, Sprague's Pipit, *Anthus spragueii*, grassland, habitat management, grassland birds, fire ecology, plant succession, mixed-grass prairie, North Dakota, Great Plains.

Grassland bird populations have been declining more precipitously in recent decades than those of any other group of North American birds (Droege and Sauer 1994). These population declines parallel vast reductions in native prairie habitats that grassland birds depend on. Native grasslands throughout North America have been severely degraded, fragmented, and reduced by cumulative effects of overgrazing, fire suppression, invasion by exotic plants, and conversion to cropland (review in Samson and Knopf 1996). For example, estimated declines in extent of tallgrass prairie range from 83 to 99% and exceed those reported for any other North American ecosystem, including old-growth forest and temperate rainforest (Samson and Knopf 1994). Mixed-grass prairie has declined by 72 to 99% from Manitoba to Nebraska.

Individual bird species do not respond alike to common grassland management practices, with various species preferring specific habitat conditions along a continuum of prairie succession (reviews in Kirsch et al. 1978; Ryan 1990; Dobkin 1992). Species that prefer vegetation communities promoted by human activities such as annual mowing or grazing, and fire suppression generally have benefited in recent years. In contrast, those species requiring more natural disturbance regimes (i.e., periodic fire and grazing) have suffered the worst declines (Dobkin 1992; Knopf 1994, 1996). For example, 14 of 19 widespread grassland species and six of nine endemic species are declining (Knopf 1996).

Remaining tracts of prairie thus become increasingly valuable for native species, and their proper management critical for maintaining native biodiversity. To manage these resources effectively, we must understand linkages between disturbance regimes, vegetation, and bird communities; yet relatively few studies have addressed effects of fire on prairie passerines. Those conducted typically included only a single burn and control (Huber and Steuter 1984; Pylypec 1991), or followed responses only one to three years postfire (Forde et al. 1984; Herkert 1994). These studies documented general declines in species diversity and abundance immediately following fire, and variable population increases of some species one to three years postfire. Assessments of fire effects that consider only immediate post-fire response ignore a large portion of the natural disturbance cycle on the Great Plains. Only one long-term study of fire effects on birds has been completed in mixed-grass prairie (Johnson 1997).

Our goal was to document longer-term effects of fire by examining multiple, independent burns done over an extended period (15 years) in mixed-grass prairie. The objective of this study was to quantify relationships between fire history and bird abundance and species richness in northern mixed-grass prairie. We also assessed vegetation structure and composition as it related to post-fire succession.

Study Area

Lostwood National Wildlife Refuge (NWR) covers 109 km^2 of rolling to hilly, mixed-grass prairie in northwestern North Dakota (48°37'N; 102°27'W). It lies within the Missouri Coteau (Bluemle 1980), a strip of dead-ice, glacial moraine characterized by knob-and-kettle topography (685–747 m elevation). Large tracts of grassland are interspersed with ≈4000 wetland basins and ≈500 clumps of Quaking Aspen (*Populus tremuloides*). Major vegetation is a needle-grass-wheatgrass (*Stipa* spp.- *Agropyron* spp.) association (Coupland 1950), and habitat composition is 55% native prairie, 21% previously-cropped prairie (revegetated with tame and native prairie plants), 20% wetland, 2% trees, and 2% tall shrubs (Murphy 1993). Climate is semi-arid and mean annual precipitation (1936–1989) on the refuge is 42 cm, with most (>75%) falling as rain between April and September.

Before European settlement in the early 1900s, the landscape of Lostwood NWR was a treeless expanse of mixed-grass prairie, maintained in a shorter grass, or even barren state by frequent fire and Bison (*Bison bison*) impacts (Murphy 1993). The region likely supported a 5- to 10-year fire-return interval (Wright and Bailey 1982: 81; Murphy 1993, Bragg 1995). Although some of present-day Lostwood NWR was tilled and farmed during the early 1900s, most (70%) upland areas remained unbroken and were either rested or lightly grazed season-long by livestock during the 1930s–1970s. With settlement came suppression of wildfires, and a concomitant loss of early successional, herbaceous vegetation. Western Snowberry (*Symphoricarpos occidentalis*), aspen, and exotic grasses (Kentucky Bluegrass [*Poa pratensis*], Smooth Brome [*Bromus inermis*], and Quack Grass [*Agropyron repens*]) proliferated and now dominate the mixed-grass community of Lostwood NWR.

Since the 1970s, the U.S. Fish and Wildlife Service (USFWS) has used prescribed fire to reduce woody vegetation and restore a more natural diversity of successional stages to Lostwood NWR. The refuge was divided into ≈20 prescribed burn units (range = 5–2265 ha; $\bar{x}$ = 310 ha). During 1978–1993, 63 burns were conducted and 5–35% of the refuge was burned annually. Decisions on when to burn a given unit were based on land management objectives, thus, fire treatments were not randomly assigned to burn units. Most burns (75%) were conducted in summer (mid-July through August) and the remainder in late spring (late April through early May). Burns typically were done in 10–30 km/h wind, 20–40% relative humidity, and 10–30°C, and generally removed 80–95% of aboveground vegetation.

Methods

Study Design and Plot Selection

We measured bird abundance and vegetation characteristics on 160 (1993) and 150 (1994) sample points distributed over nine independent burn units. We selected sampling points from a grid of potential points that encompassed the study area. The sampling scheme was systematic in 1993, but was randomized in 1994 to meet sampling assumptions for statistical testing. Points were > 250 m apart to provide statistical independence in terms of birds and vegetation (Hutto et al. 1986; Ralph et al. 1993), and were randomly selected from potential points that met the following criteria: (1) located in "upland prairie" as delineated by the National Wetland Inventory map of cover types of Lostwood NWR (USFWS, unpublished report), (2) > 200 m from any aspen clump, (3) > 50 m from roads or firebreaks, and (4) ungrazed by livestock for > 10 years. In 1994, we reduced the buffer from aspen to 100 m based on 1993 sampling observations, and added a 50-m buffer from any seasonally-flooded wetland zone because of high water levels. Points within a given burn unit were not independent in terms of fire history, thus data within a unit were averaged for all statistical analyses.

Fire History

Fire history for each point count location was compiled from Lostwood NWR maps and narratives (Table 1). Fire history was described as: (1) number of years since the point was burned (0.5–8.0 or >80 years), and (2) number of times the point was burned in previous 15 years (0–4 times). Areas burned recently tended to have been burned many times. This could potentially confound results, making it difficult to discern relative impacts of each variable. Both variables played a role in defining fire history, thus we combined them using an index to describe the amount of fire an area had experienced:

Fire Index (FI) = Number of Burns/Years Since Last Fire

Using this formula, sampled burn units were scaled along a gradient from 0.0 (no fire) to 6.0 (many burns, the last recently) (Table 1). Although there may be problems extrapolating this index to all fire histories, it appeared to aptly depict the nine

TABLE 1. Fire history* on prescribed burn units sampled at Lostwood National Wildlife Refuge, North Dakota.

		1993				1994			
Burn name	Size (ha)	Sample points	Number of burns	YSF[a]	Fire index[b]	Sample points	Number of burns	YSF[a]	Fire index[b]
Unburned - West	526	17	0	>80	0.00	12	0	>80	0.00
Unburned - South Central Core	445	15	0	>80	0.00	18	0	>80	0.00
Green Needle	398	11	1	6	0.17	6	1	7	0.14
Wilderness	2265	34	2	5	0.40	25	2	6	0.33
North Dead Dog Slough	89	5	4	7	0.57	9	4	8	0.50
Kruse	645	23	2	3	0.67	20	3	0.5	6.00
Aspen	518	10	2	0.5	4.00	20	2	2	1.00
Thompson Lake	372	14	4	1	4.00	20	4	2	2.00
Teal Slough	494	28	4	1	4.00	20	4	2	2.00

*source: USFWS (unpublished data)

[a]YSF = Years since last fire.

[b]Fire Index = number of burns/years since last fire. The index varies from 0.0, no fire experienced in >80 years, to 6.0, several fires with the last less than one year previous.

burn units sampled in this study along a plausible gradient of amount of fire experienced.

Bird Abundance Sampling

We conducted three bird counts at each sample point during 29 May–7 July 1993 and 26 May–24 June 1994. Bird abundance was estimated using 50-m fixed-radius point counts (Hutto et al. 1986) in 1993, and point counts with five distance categories in 1994 (Buckland et al. 1993; Madden 1996). During each count, an observer stood at a point for 10 minutes and recorded all birds seen or heard, and the distance category to each bird when first detected. To minimize observer differences and maximize accuracy of measurements, we (1) spent two weeks prior to data collection practicing bird identification, point count techniques, and distance measurements, especially for birds detected aurally; (2) observed each point before approaching it to record distances from the point to birds that might be disturbed by our approach; and (3) used flags marking distance category boundaries at each point to ensure accurate distance estimation. When assignment to a distance category was uncertain, we measured the distance to a bird's location by pacing after the count was completed. We conducted counts one-half hour before sunrise until approximately 09:00 CST only on mornings when weather conditions did not impede detection of birds (i.e., no rain, fog, or wind >15 km/h). Observers and the order in which points were visited were rotated to minimize sampling bias. Although all bird species were recorded, only passerine species were well-represented on point counts and included in the final data set.

We calculated the mean number of singing males of each species per 50-m (1993) or 75-m (1994) radius point count (average of three visits). (A 75-m, rather than 50-m, radius cut-off was used for 1994 data to increase the number of birds sampled [Rotella et al. 1997]). Abundance of Brown-headed Cowbirds (scientific names for bird species are listed in Table 3) was calculated differently: we divided total number of cowbirds seen or heard at a count by two, for comparability with singing male data for other species. Total passerine abundance was simply the total number of singing male passerines at each point averaged over three visits. We calculated species richness for singing males using the total number of species observed within 50 m (1993) or 75 m (1994) of each point during three visits (i.e., cumulative richness). To avoid bias due to differences in numbers of points sampled in each burn unit, we chose a random subsample of five (1993) or six (1994) points (i.e., lowest common denominator) from each burn unit to calculate richness.

Vegetation Sampling

Vegetation structure and general composition were measured at each bird sampling point during 28 June–7 August 1993 and 28 June–28 July 1994. Twenty subsample points were located along two transects within each fixed-radius bird plot. Both transects were positioned on the same random compass bearing (i.e., parallel), each a different random number of paces from plot center.

At each subsample point, we estimated visual obstruction from a height of 1 m and a distance of 4 m using a Robel pole (Robel et al. 1970). Litter depth was measured directly (cm) by lowering a 6-mm diameter rod vertically into the litter layer 30 cm east of the Robel pole. Dead vegetation from previous years that was standing but no longer vertical was considered litter where it formed a mat-like layer, roughly continuous with the ground. Using the same rod, we counted the total number of "hits" or contacts of vegetation on the rod in each dm height interval (Wiens 1969). Each hit was recorded as either live (current year's growth) or dead (previous years' growth). Total number of hits represented vertical density. We also calculated the percentage of total hits represented by live vegetation. Percentage areal cover of shrubs, forbs, and grasses was visually estimated (Daubenmire 1959) within a 1-m diameter circular frame centered on each Robel pole. Finally, each subsample was assigned to one of nine general plant species associations: native grass, Kentucky Bluegrass, native grass/Kentucky Bluegrass, broad-leaved exotic grass, shrub, shrub/broad-leaved exotic grass, shrub/Kentucky Bluegrass, shrub/native grass, and wetland (Madden 1996).

For each vegetation structure variable, we calculated the mean and coefficient of variation (CV) for the 20 subsamples near each point. Coefficient of variation measures horizontal "patchiness" or heterogeneity of a particular vegetation attribute (Roth 1976). Plant associations were expressed as the mean frequency of a given association in the 20 subsamples. Fourteen vegetation structure variables and nine plant associations were considered.

Data Analyses

Data for 1993 and 1994 were analyzed separately because several bird species differed significantly in abundance between the two breeding seasons, and weather differences were also extreme. Only bird species detected at >10% of points were included in statistical analyses. We used Kruskal-Wallis 1-way Analysis of Variance (SAS Institute 1988) to test hypotheses that there were no differences in vegetation or bird abundance among categories of burns. Burn categories were: (1) Years since last fire (1–3, 5–7, or >80 years in 1993 and 2, 6–8, or >80 years in 1994), and (2) Number of burns in last 15 years (0, 1–2, or 4). Results of these analyses are presented fully by Madden (1996).

Because it was difficult to tease out relative impacts of the two variables of fire history, we then used simple linear regression (Chatterjee and Price 1991) to quantify relationships between vegetation or birds and the fire index (which combined the two fire variables). Regressions were performed on means of vegetation attributes or bird abundances for each of the burn units rated by fire index. The smaller radius (50-m) point counts used in 1993 yielded low numbers of bird observations, and resulting data were primarily zeros for most species. Too many zero records in the data violated the assumptions of normality and constant variance required for use of linear regression models, and we were unsuccessful in our attempts to normalize data and stabilize variances using transformations. Therefore, only 1994 bird data were used in this part of the analysis. Several vegetation variables also did not meet regression assumptions and were not analyzed further: frequency of shrub/exotic grasses and shrub/Kentucky bluegrass in 1993, and CV litter depth and frequency of shrub in both years. Burn units that had not had a full growing season of vegetation recovery (i.e., years since last fire = 0.5) were omitted from regression analyses. Burned during the previous August, these areas generally had extreme vegetation and bird responses, unreflective of the longer-term fire effects we sought to document. Areas burned in the spring previous (i.e., years since last fire = 1.0), having had one full growing season for vegetation to recover, were included.

Because many variables of vegetation structure were correlated, we also used principal components analysis (SAS Institute 1988) to identify major gradients in vegetation structure. Although most ecological data violate some fundamental assumptions of principal components analysis (e.g., normality) for purposes of hypothesis testing, the technique is useful for synthesizing and describing patterns in data (Gauch 1982: 143). We plotted 1994 sample points by fire history on a plot of the first two principal components to describe each burn unit's location in principal component vegetation space. We then plotted a 95% confidence ellipse (Wilkinson 1990) based on the mean for each fire interval and superimposed the ellipses onto a single graph for comparative purposes.

Results

Vegetation and Fire

Relationships between individual vegetation variables and the fire index, as measured by slope of regression line, were similar both years, even if not significant ($P < 0.05$) in both (Table 2). Grass cover increased with amount of fire, whereas shrub cover, CV grass cover, and vegetation density decreased. Variances in vegetation variables (CVs), which reflected structural heterogeneity, generally decreased with amount of fire as did litter depth. Native grass/Kentucky Bluegrass and broad-leaved, exotic grasses increased in frequency with amount of fire.

Four principal components had eigenvalues greater than 1.0, accounting for 81% and 83% of the variation in vegetation structure in 1993 and 1994, respectively. Only the first two components are examined here because the third and fourth components explained relatively little of the variation, and also because more than two dimensions are difficult to visualize. Eigenvectors and gradients were remarkably similar for these two components between years. The first axis (PC1) accounted for 39% and 38% of the variation in 1993 and 1994, and represented a gradient from short, sparse, grass-dominated vegetation to tall, dense, shrub-dominated vegetation (Figure 1). The second axis (PC2) accounted for 18% and 20% of the variation in 1993 and 1994, and represented a gradient from deep litter and forb-dominated vegetation to mostly live vegetation with few forbs and low litter (Figure 1).

TABLE 2. Relationships between vegetation variables and fire index (see text for explanation of fire index) based on simple linear regression (n = 8 burn units). Only results for vegetation variables with significant ($P < 0.05$) regression relationships in at least one year are reported.

	1993		1994		Response
Vegetation variable	R^2	P	R^2	P	to fire[a]
Shrub cover	0.56	0.03	0.53	0.04	-
Grass cover	0.86	0.00	0.83	<0.01	+
CV forb cover	0.11	0.42	0.53	0.04	-
CV grass cover	0.49	0.05	0.55	0.04	-
CV visual obstruction	0.22	0.24	0.68	0.01	-
Litter depth	0.90	0.00	0.15	0.35	-
Density (# hits)	0.65	0.02	0.66	0.01	-
% live vegetation	0.90	0.00	0.38	0.10	+
CV % live vegetation	0.67	0.01	0.26	0.20	-
Kentucky Bluegrass/native grass	0.48	0.06	0.60	<0.01	+
Broad-leaved exotic grass	0.73	0.01	0.34	0.13	+
Shrub/Kentucky Bluegrass	[b]	[b]	0.50	0.05	-
Shrub/native grass	0.50	0.05	0.40	0.09	-

[a]Fire response based on slope (+ or -) of regression line.
[b]Variable did not meet regression assumptions in 1993.

Confidence ellipses for 1994 burn units in PC vegetation space indicated that the unit with the most distinct vegetation was the area burned several times, the last occurring the previous August (i.e., about 0.5 years earlier) (Figure 1). Its confidence ellipse was located at the extreme negative end of PC1, defined by short, sparse grassy cover, and the extreme positive end of PC2, indicating low litter and few forbs. An area burned twice, the last being two years previous, was also distinct, but closer to the graph origin (i.e., "average" vegetation characteristics). This area fell to the short, sparse, grassy (negative) side of PC1 and was centered on zero on PC2, indicating moderate litter and forbs.

Areas last burned two years previous, but four times in the last 15 years, fell wholly in the short and sparse, litter-, grass-, and forb-dominated quadrat of the graph and overlapped slightly with an area burned one time, seven years previous. This one-burn area fell mostly in the quadrat defined by tall, dense, shrub- and forb-dominated vegetation with much litter. Complete overlap with this ellipse occurred for areas last burned six years ago (two times) and eight years ago (four times). This illustrates great similarity in vegetation structure six to eight years postfire. The confidence ellipse for unburned units overlapped no others and was located on the tall, dense, shrub-dominated side of PC1, and toward the low litter, few forbs side of PC2.

Birds and Fire

We observed 19 and 24 passerine bird species on 50- and 75-m radius plots in 1993 and 1994, respectively (Table 3). Nine and ten species were detected at > 10% of points in 1993 and 1994. Savannah Sparrows and Clay-colored Sparrows were by far the most frequently encountered species; both occurred more than twice as frequently as other species during both years. Several species were completely absent from unburned (> 80 years) units both years (Tables 4 and 5). Baird's Sparrows, Grasshopper Sparrows, Le Conte's Sparrows, Sprague's Pipits, and Western Meadowlarks were never detected during three visits to each of 62 point count locations in unburned units. Bobolinks also were absent from unburned areas except for two detections of a singing male at one point in 1993. In contrast, none of ten species examined was completely absent from units treated with fire.

Abundances of eight bird species and species richness had significant ($P < 0.05$) long-term relationships with amount of fire in 1994 (Table 6, Figure 2). Six species and species richness responded positively to amount of fire: Baird's Sparrow, Bobolink, Grasshopper Sparrow, Le Conte's Sparrow, Sprague's Pipit, and Western Meadowlark. These species reached highest abundance in units with a fire index rating of 2.0 (i.e., burned four times, the last being two years prior). Two species responded negatively to fire: Clay-colored Sparrow and Common Yellowthroat. Both were most abundant in units with a fire index of 0.0 (i.e., unburned in >80 years). Savannah Sparrow, Brown-headed Cowbird, and total passerine abundance did not respond significantly to amount of fire.

Discussion

Vegetation and Fire

In our study, repeated fire reduced shrub cover, litter build-up, and vegetation height and density, but increased grass cover and percentage of live vegetation on mixed-grass prairie. Fire decreased horizon-

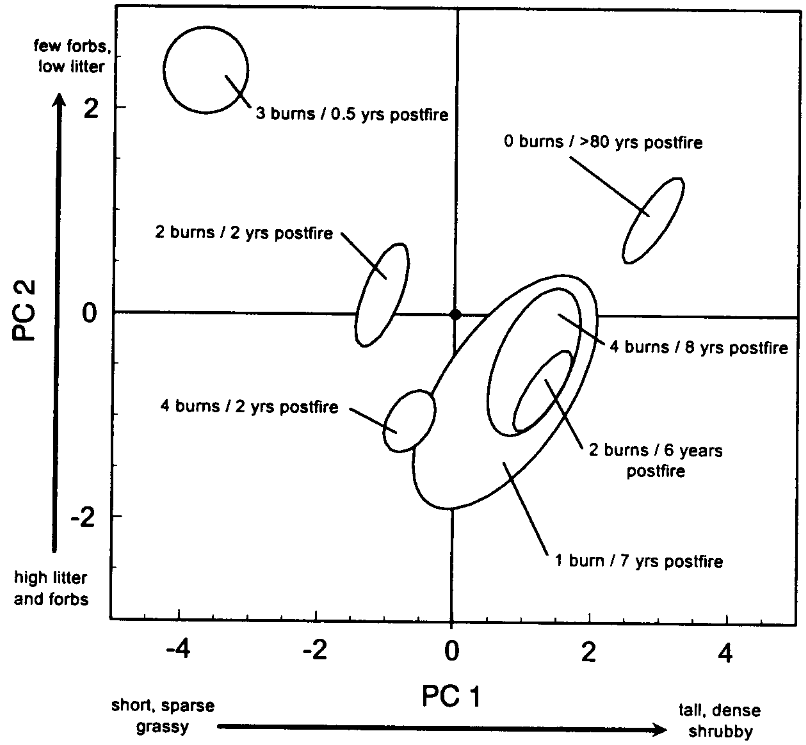

FIGURE 1. Composite confidence ellipses for areas with different burn histories in 1994. Ellipses represent 95% confidence intervals around the mean position of sample points with similar burn histories, located with reference to Principal Components 1 and 2.

tal patchiness of grasses, forbs, live vegetation, and visual obstruction, and increased litter patchiness. These results are consistent with previous findings concerning the role of fire in maintaining mixed-grass prairie vegetation. Annual die-offs of grass and the resulting litter build-ups necessitate some type of defoliation in these semi-arid environments where plant decomposition is otherwise slow (Kucera 1981; Wright and Bailey 1982; Bragg 1995). Fire reduces vegetation biomass and litter and increases growth and reproduction of native vegetation (Kucera 1981; Wright and Bailey 1982). Vegetation in burned tall-grass prairie generally begins growing earlier, matures earlier, and produces more flowering stalks, especially of native plants (Ehrenreich 1959). This enhanced growth is attributed to reduced litter, warmer soil temperatures, increased light for emerging shoots, and greater nutrient availability after burning (Ehrenreich 1959; Daubenmire 1968; Kucera 1981).

Exotic and native grasses alike increased with prescribed fire at Lostwood NWR. In northern mixed-grass prairie, fire is sometimes considered for reducing exotic grasses such as Smooth Brome (Romo and Grilz 1990), but our data from multiple burns over 15 years do not support this. Refuge personnel concur with our findings and report that Smooth Brome increased in all management units of Lostwood NWR during the 1970s–1990s, regardless of treatment history (K. A. Smith, personal communication). Fire impacts on individual plant species depend largely on treatment timing in relation to plant phenology (Higgins et al. 1989). Prescribed burns on any given management unit at Lostwood NWR were conducted from spring to late summer, obscuring effects of the timing of burns on changes in exotic grass coverage.

Suppression of woody vegetation is a more obvious and well-documented effect of fire on grassland habitats (review in Higgins et al. 1989). High coverages and frequencies of shrubs were successfully reduced with fire at Lostwood NWR.

During post-fire succession on mixed-grass prairie at Lostwood NWR, vegetation structure was generally transformed from short, sparse, and grassy with few forbs and low litter immediately after fire, to increasing and moderate amounts of forbs, litter, and shrubs two to eight years postfire, to tall, dense, shrubby prairie with little forb, grass, or litter understory when fire was absent (> 80 years). Although relatively low litter seems surprising for unburned units, parts of these units were covered by decadent snowberry shrub with little or no understory, and any existing understory was usually lush, green growth of smooth brome. These extensive shrub stands likely account for the low litter readings in the longest-idled burn units.

The similarity of 2 to 8 year postfire vegetation structure to "average" characteristics (i.e. closest to origin on graph; see Figure 1), and the more extreme locations of 0.5-year and >80-year post-fire vegetation near the ends of the vegetation gradients is consistent with the estimated historic fire return interval of 5–10 years in mixed-grass prairie.

Birds and Fire

Most grassland birds (six of nine species examined) at Lostwood NWR were absent from mixed prairie untreated with fire for long periods. Abundances of Baird's Sparrows, Bobolinks, Grasshopper Sparrows, Le Conte's Sparrows, Sprague's Pipits, and Western Meadowlarks were positively related to amount of fire, and these species were absent from unburned units. Brown-headed Cowbirds and Savannah Sparrows showed inconclusive responses to fire. Savannah Sparrow abundance apparently is more associated with intermediate stages of post-fire succession (Madden 1996), and Brown-headed Cowbirds exploit a wide variety of habitats (Lowther 1993). Clay-colored Sparrows and Common Yellowthroats showed consistent, distinctly negative reactions to fire, which was not surprising, given both species are commonly associated with shrubby habitats.

Most short-term studies of fire effects simply point out that, for many bird species, abundance is depressed for one to several years postfire and then recovers (Forde et al. 1984; Huber and Steuter 1984; Pylypec 1991). Our data go a step further and illustrate that, in the longer term, most grassland species were absent from mesic prairie untreated with fire for long periods. This was also suggested by a study of shrubby versus shrubless prairie on the Missouri Coteau in south-central North Dakota (Arnold and Higgins 1986), where many true grassland species were absent (Baird's Sparrow, Savannah Sparrow) or reduced (Grasshopper Sparrow, Bobolink) on shrubby prairie such as that associated with a lack of fire.

Trends in species abundance were similar in another fire-effects study on the Missouri Coteau in North Dakota (Johnson 1997), with Bobolinks, Western Meadowlarks, and Grasshopper, Baird's, and Savannah Sparrows most common 2–5 years postfire, and declining after about five years postfire.

TABLE 3. Passerine bird species (singing males) detected during point counts, 1993 and 1994, Lostwood National Wildlife Refuge, North Dakota.

		% occurrence[a]	
Bird species	Scientific name	1993 (n = 160)	1994 (n = 150)
Eastern Kingbird	*Tyrannus tyrannus*	8.8	3.3
Horned Lark	*Eremophila alpestris*	0.6	1.3
House Wren	*Troglodytes aedon*	–	0.7
Sedge Wren	*Cistothorus platensis*	–	3.3
Marsh Wren	*Cistothorus palustris*	–	0.7
Gray Catbird	*Dumetella carolinensis*	0.6	–
Sprague's Pipit	*Anthus spragueii*	10.6	12.0
Yellow Warbler	*Dendroica petechia*	0.6	1.3
Common Yellowthroat	*Geothlypis trichas*	18.8	24.7
Clay-colored Sparrow	*Spizella pallida*	66.3	92.0
Vesper Sparrow	*Pooecetes gramineus*	6.3	8.0
Savannah Sparrow	*Passerculus sandwichensis*	63.8	92.7
Baird's Sparrow	*Ammodramus bairdii*	16.9	35.3
Grasshopper Sparrow	*Ammodramus savannarum*	20.6	41.3
Le Conte's Sparrow	*Ammodramus leconteii*	1.3	12.0
Nelson's Sharp-tailed Sparrow	*Ammodramus nelsoni*	–	2.7
Song Sparrow	*Melospiza melodia*	0.6	1.3
Chestnut-collared Longspur	*Calcarius ornatus*	0.6	0.7
Bobolink	*Dolichonyx oryzivorus*	27.5	44.0
Red-winged Blackbird	*Agelaius phoeniceus*	0.6	2.0
Western Meadowlark	*Sturnella neglecta*	13.1	18.0
Brewer's Blackbird	*Euphagus cyanocephalus*	2.0	2.0
Brown-headed Cowbird	*Molothrus ater*	20.0	21.3
American Goldfinch	*Carduelis tristis*	–	0.7

[a]Percentage of 50-m (1993) or 75-m (1994) radius points at which the species was detected (within the given radius).

TABLE 4. Bird species abundance and standard error (SE) in relation to years since last fire, Lostwood National Wildlife Refuge, 1993. Abundance is mean number of singing males per 50-m radius point count.

	Years since last fire						
	< 1 (*n*=10)[a]	1 (*n*=42)	3 (*n*=23)	5 (*n*=34)	6 (*n*=11)	7 (*n*=5)	> 80 (*n*=32)
Bird species	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Baird's Sparrow	0.00 (0.00)	0.13 (0.03)	0.13 (0.06)	0.11 (0.04)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Brown-headed Cowbird	0.27 (0.20)	0.14 (0.04)	0.08 (0.03)	0.10 (0.05)	0.00 (0.00)	0.00 (0.00)	0.03 (0.02)
Bobolink	0.00 (0.00)	0.48 (0.06)	0.07 (0.03)	0.05 (0.02)	0.06 (0.04)	0.13 (0.13)	0.04 (0.04)
Clay-colored Sparrow	0.33 (0.12)	0.25 (0.06)	0.34 (0.07)	0.53 (0.09)	0.61 (0.12)	0.27 (0.12)	0.57 (0.08)
Common Yellowthroat	0.00 (0.00)	0.02 (0.01)	0.00 (0.00)	0.05 (0.02)	0.03 (0.03)	0.20 (0.13)	0.24 (0.04)
Grasshopper Sparrow	0.00 (0.00)	0.17 (0.04)	0.30 (0.08)	0.06 (0.02)	0.03 (0.03)	0.07 (0.07)	0.00 (0.00)
Savannah Sparrow	0.17 (0.07)	0.32 (0.05)	0.57 (0.09)	0.32 (0.06)	0.79 (0.09)	0.73 (0.12)	0.25 (0.06)
Sprague's Pipit	0.00 (0.00)	0.08 (0.03)	0.10 (0.04)	0.02 (0.01)	0.03 (0.03)	0.20 (0.13)	0.00 (0.00)
Western Meadowlark	0.00 (0.00)	0.09 (0.03)	0.10 (0.04)	0.07 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
All passerines	0.97 (0.29)	1.82 (0.12)	1.73 (0.16)	1.35 (0.14)	1.61 (0.15)	1.67 (0.21)	1.22 (0.14)
Species richness	2.10 (0.31)	3.55 (0.19)	3.04 (0.26)	2.59 (0.20)	2.55 (0.25)	3.00 (0.32)	2.25 (0.20)

[a]*n* = number of point counts

In contrast to our study, however, none of these species was completely absent from the unburned control plot. Johnson's control plot had been idle for 11 years when his study was initiated, but had been grazed for 55 years prior to that. The two unburned plots in our study were likely in a more degraded grassland condition, as one had been completely idle (no burning or grazing) for >80 years, and the other had received only light season-long grazing until 16 years before this study. These differences between studies highlight the need for grassland managers to consider site-specific information when determining treatment needs, as well as the need for research replication across a range of conditions and grassland types.

Total species richness at Lostwood NWR was generally highest in areas experiencing periodic, frequent fire and lowest in unburned areas. Other studies of grassland passerines have shown species richness highest in idle or shrubby, late successional stages associated with lack of fire (Renken 1983; Arnold and Higgins 1986; Zimmerman 1992). These studies, however, included some trees, shrub thickets, and/or wetlands in plots, which inflated total species richness by adding non-prairie species associated with woody habitats. Because we limited our plots to upland prairie and avoided aspen groves and wetlands, we exclusively sampled grassland habitats, and thus mainly grassland bird species. Had we included aspen groves, common on unburned prairie at Lostwood NWR, total species richness would have been highest on unburned prairie due to presence of many woodland bird species. For grassland managers charged with maintaining a native bird community, emphasis on woody, later successional stages simply because they support greater avian

TABLE 5. Bird species abundance and standard error (SE) in relation to years since last fire, Lostwood National Wildlife Refuge, 1994. Abundance is mean number of singing males per 75-m radius point count.

	Years since last fire					
	<1 (*n*=20)[a]	2 (*n*=60)	6 (*n*=25)	7 (*n*=6)	8 (*n*=9)	>80 (*n*=30)
Bird species	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Baird's Sparrow	0.30 (0.10)	0.37 (0.06)	0.09 (0.04)	0.06 (0.06)	0.07 (0.05)	0.00 (0.00)
Brown-headed Cowbird	0.08 (0.05)	0.09 (0.02)	0.21 (0.07)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)
Bobolink	0.52 (0.09)	0.41 (0.06)	0.16 (0.06)	0.06 (0.06)	0.15 (0.11)	0.00 (0.00)
Clay-colored Sparrow	0.68 (0.14)	0.86 (0.08)	1.53 (0.17)	1.50 (0.17)	1.22 (0.33)	2.25 (0.15)
Common Yellowthroat	0.02 (0.02)	0.03 (0.02)	0.08 (0.04)	0.22 (0.14)	0.22 (0.08)	0.39 (0.06)
Grasshopper Sparrow	0.20 (0.06)	0.44 (0.06)	0.29 (0.06)	0.50 (0.11)	0.00 (0.00)	0.00 (0.00)
Le Conte's Sparrow	0.00 (0.00)	0.10 (0.03)	0.05 (0.03)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Savannah Sparrow	0.93 (0.16)	0.99 (0.08)	1.27 (0.13)	1.61 (0.38)	1.52 (0.19)	0.91 (0.10)
Sprague's Pipit	0.02 (0.02)	0.10 (0.03)	0.01 (0.01)	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)
Western Meadowlark	0.07 (0.04)	0.11 (0.02)	0.11 (0.04)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
All passerines	2.93 (0.28)	3.61 (0.17)	4.01 (0.24)	4.00 (0.56)	3.26 (0.32)	3.71 (0.22)
Species richness	4.10 (0.23)	4.98 (0.21)	4.48 (0.31)	3.67 (0.49)	3.22 (0.28)	3.03 (0.18)

[a]n = number of point counts

TABLE 6. Relationships between bird abundance and amount of fire (1994) based on linear regressions of abundance on the fire index (n = 8). Fire index is explained in the text.

Bird species	R^2	P	Response to fire[a]
Baird's Sparrow	0.79	<0.01	+
Bobolink	0.97	<0.01	+
Grasshopper Sparrow	0.49	0.05	+
Le Conte's Sparrow	0.79	<0.01	+
Sprague's Pipit	0.65	0.02	+
Western Meadowlark	0.64	0.02	+
Species richness	0.75	0.01	+
Clay-colored Sparrow	0.74	0.01	–
Common Yellowthroat	0.67	0.01	–
Savannah Sparrow	0.09	0.48	NS
Brown-headed Cowbird	0.18	0.30	NS
All passerines[b]	0.01	0.84	NS

[a]Response to fire based on slope (+ or -) of regression line.
[b]Total number of singing male passerines/point.

diversity may be inappropriate (Knopf and Samson 1994; Johnson 1996). In strictly grassland habitats, our data suggest that mesic, mixed-grass prairie treated with some type of periodic disturbance such as fire will support maximum species richness of grassland birds.

Fire History and Management

Fire has played a major role in maintaining Great Plains grasslands (review in Higgins 1986). But, without trees to carry records of burning in fire scars, it is difficult to estimate pre-settlement frequencies of grassland fires. Extrapolating from fire histories in grasslands under pine forests, Wright and Bailey (1982: 81) estimated a 5- to 10-year fire frequency for North American grasslands. Fire probably occurred, on average, every six years in northern mixed prairie, but up to every 25 years in the dry, western part of the mixed prairie, based on rates of fuel accumulation and woody plant invasion (Bragg 1995). This distinction between dry and mesic mixed prairie is important, because fire effects on vegetation and birds vary with moisture conditions (Higgins et al. 1989; Wright and Bailey 1982). In general, grasslands receiving more moisture have higher productivity and thus are more fire-dependent (Kucera 1981). Mixed-grass prairie of the Dakotas, including Lostwood NWR, generally is more mesic than that of Saskatchewan, Alberta, and Montana (Wright and Bailey 1982), and thus has more rapid accumulation of residual vegetation and a correspondingly higher fire frequency. Thus, a fire frequency that maximizes plant and bird diversity in mesic mixed prairie could be negative in dry mixed prairie.

Results of fire effects are further complicated because prescribed burns at Lostwood NWR were not merely "maintenance" burns on healthy mixed-grass prairie, but treatments to rectify more than 80 years of unnatural fire suppression and shrub accumulation (renovation burns). Renovation burns in areas of dense shrub build-up are characteristically different (e.g., hotter) than burns in herbaceous prairie. Most of Lostwood NWR's prairie remains less than pristine, and conclusions about bird and vegetation response to fire must consider this. But, because many remaining grasslands (especially on public land) have management histories similar to those of Lostwood NWR, our results can be used to anticipate outcomes as fire is restored to these systems.

Pre- and Post-Settlement Endemic Bird Populations

After receiving a series of renovation burns, native prairie at Lostwood NWR probably supports a breeding passerine community roughly similar to that of pre-settlement prairie. High numbers of endemic prairie species such as Baird's Sparrows and Sprague's Pipits in these repeatedly-burned areas are consistent with pre-settlement descriptions by Coues (1878). As he traveled near present-day Lostwood NWR in 1873, Coues remarked repeatedly on the "trio of the commonest birds" encountered: Baird's Sparrows, Sprague's Pipits, and Chestnut-collared Longspurs. Baird's Sparrows outnumbered all other birds together in some areas, and Sprague's Pipits were sometimes "...so numerous that the air seemed full of them..." (Coues 1878: 560). After less than 100 years of settlement and agricultural development, Baird's Sparrows and Sprague's Pipits had declined to the point that they were no longer among even the 15 most common birds in North Dakota (Stewart and Kantrud 1972). Population declines in these species have paralleled large reductions in extent and quality of native prairie habitats (see Goossen et al. 1993; Samson and Knopf 1996).

The third species of Coues' "commonest trio," Chestnut-collared Longspurs, were not among the common bird species during this study: only two breeding males were seen (both on units one-year

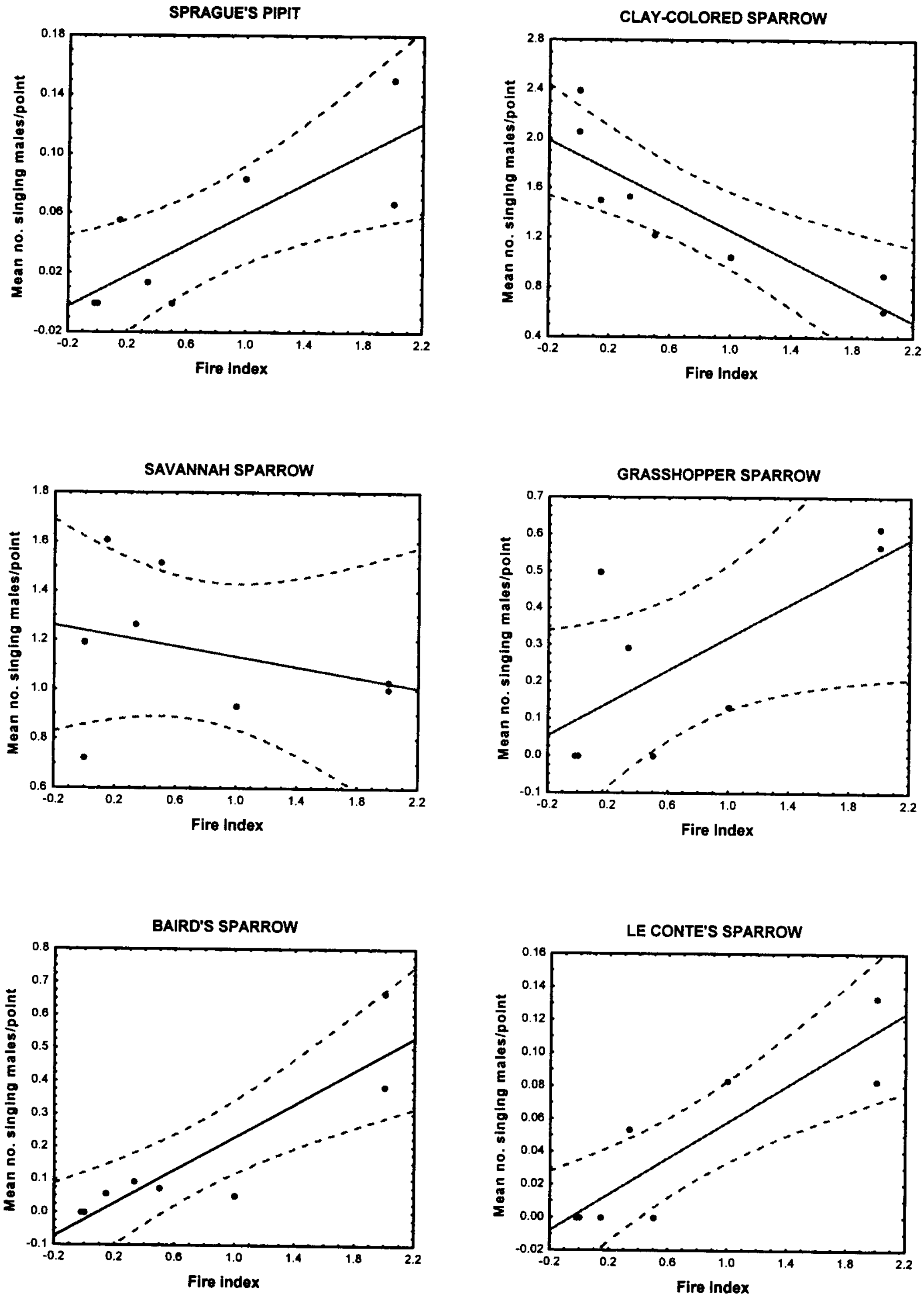

FIGURE 2. Observed relationships between bird species abundance and amount of fire, Lostwood National Wildlife Refuge, North Dakota, 1994. Abundance is mean number of singing males per point. See text for explanation of fire index. Dotted lines indicate 95% confidence intervals of the regression line.

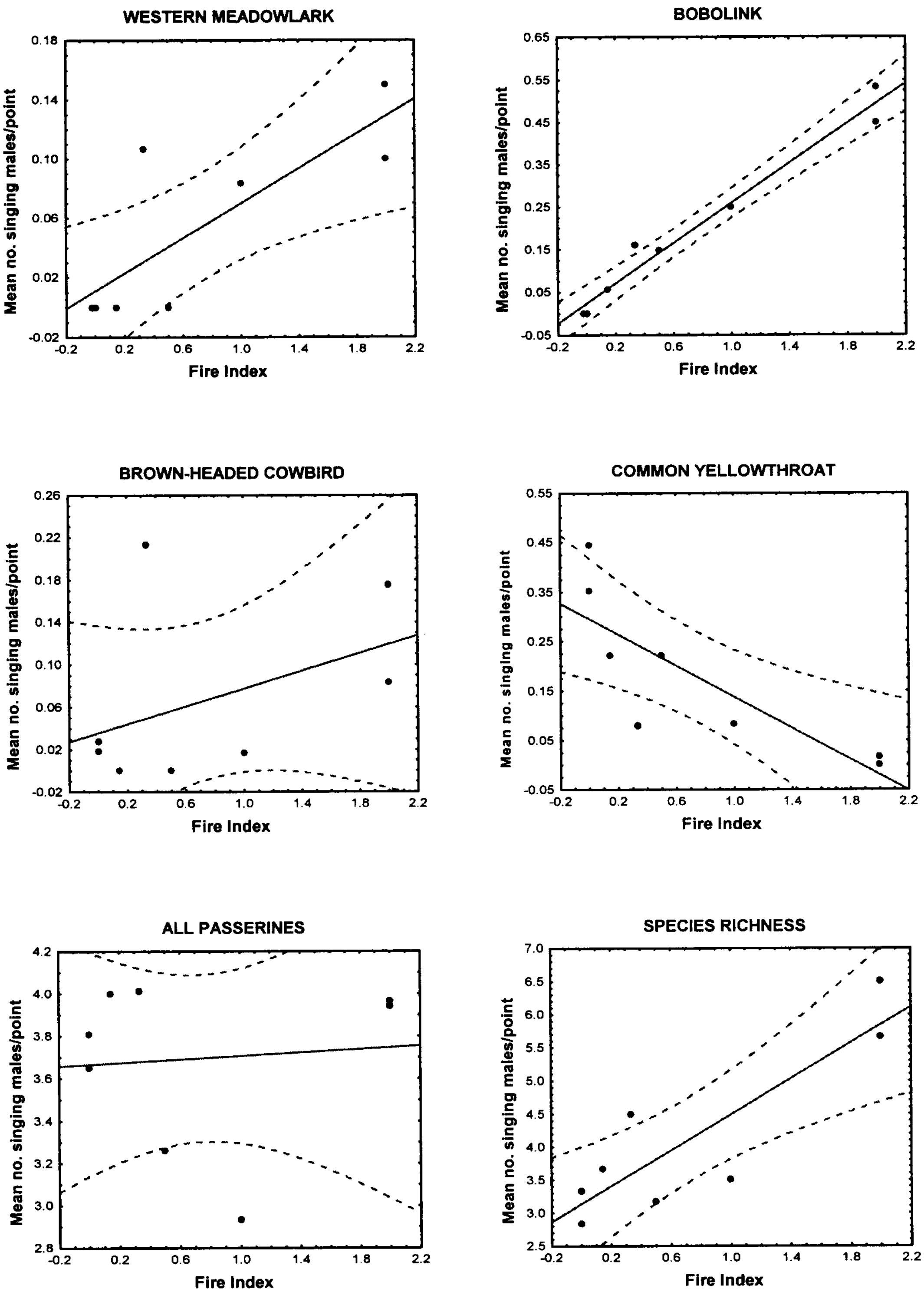

FIGURE 2. (*continued*)

postfire) (Madden 1996). In mixed-grass prairie, Chestnut-collared Longspurs use short, sparse cover that typically is associated with annual livestock grazing under heavy stocking rates (Kantrud 1981; Dale 1983; Renken 1983; Huber and Steuter 1984) or, historically, with frequent fire and Bison grazing (Knopf 1996). Longspurs were still abundant on Lostwood NWR in the 1930s when the refuge was created (Gabrielson 1943: 145). However, they disappeared by the 1970s after decades of fire suppression and either season-long grazing by cattle at light stocking rates, or no grazing at all (USFWS, Lostwood NWR, refuge files). After aggressive grassland management was initiated on Lostwood NWR in the late 1970s–1980s, longspurs began to re-colonize areas experiencing frequent fire. Although still relatively rare, Chestnut-collared Longspurs continue to be observed at Lostwood NWR, especially where grazing is beginning to be introduced following several prescribed burn treatments (USFWS, Lostwood NWR, unpublished report, 1998).

Role Of Fire in the Maintenance of Grasslands

Considering results from this study along with current thinking on fire frequency, we conclude that grassland vegetation and birds are strongly adapted to, and may depend on, frequent (every 5–10 years) fire in mesic parts of North America's northern mixed-grass prairie such as the Missouri Coteau of North Dakota.

Management at Lostwood NWR has successfully restored fire as a dynamic process in the mixed prairie, and abundances of breeding, endemic passerines have increased. Because the northern Great Plains supports several species of endemic passerines (e.g., Baird's Sparrow, Sprague's Pipit), conservation of habitats used by these species should be emphasized. Clay-colored Sparrows responded negatively to fire (although they were not completely absent from burned areas), however, indicating that a mosaic of all stages of fire succession is needed to provide suitable habitat for all birds present (Ryan 1990). Grassland species among other bird orders (Charadriformes, Galliformes, Anseriformes, Falconiformes) also respond positively to fire or decline in its absence on the northern Great Plains (Kirsch and Kruse 1973; Kirsch and Higgins 1976; Huber and Steuter 1984; Higgins et al. 1989; Murphy 1993) and would benefit from incorporation of fire into native prairie management.

Effects of fire on grassland communities both within and among sub-regions of the Great Plains are extremely variable (Wright and Bailey 1982; Bragg 1995), and factors such as the pre-burn vegetation community, soil conditions, season and frequency of burning, and grazing history all affect post-fire conditions. Appropriate sizes and configurations for burn units have not been established, and further study is warranted. On midwestern prairies, burning of 20–30% of an area each year is suggested as a general guideline for bird management on large (>80 ha) tracts (Herkert 1994). On extensive tracts of prairie such as Lostwood NWR, effects of large-scale burning on small, ecologically sensitive fauna such as butterflies (Lepidoptera) must also be considered (Oates 1995).

Managers of mesic, mixed-grass prairie generally should provide areas with short (2-4 year), moderate (5-7 year), and long (8-10 year, or more) fire return intervals to provide maximum grassland bird diversity. Combination of fire with other defoliation tools (grazing, mowing) will, of course, modify these intervals. Most grassland species we examined (Baird's Sparrow, Sprague's Pipit, Bobolink, Grasshopper Sparrow, Western Meadowlark, Le Conte's Sparrow) would benefit from short intervals, but Savannah Sparrow and Clay-colored Sparrow would likely be most abundant with moderate and long fire return intervals, respectively. Decisions on whether to emphasize any one fire frequency will depend on overall management goals, and thus include anticipated impacts on other native prairie biota (e.g., butterflies, amphibians). Because long-term rest may create habitat unfavorable for most species of grassland passerines in mesic, northern mixed prairie, periodic defoliations by disturbances such as fire should be considered essential to restore and maintain native biodiversity.

Acknowledgments

This study was funded by the Non-Game Migratory Bird Program and Refuges and Wildlife Division of the U.S. Fish and Wildlife Service, Region 6. Field assistance was provided by B. Johnson and L. Rawinski. K. Smith, manager of Lostwood NWR, furnished management history information and, with personnel of Des Lacs National Wildlife Refuge Complex, lent excellent logistical support. We thank T. Bidwell, D. Johnson, M. Restani, A. Erskine, and an anonymous reviewer for comments and advice on improving the manuscript.

Literature Cited

Arnold, T. W., and **K. F. Higgins.** 1986. Effects of shrub coverages on birds of North Dakota mixed-grass prairies. Canadian Field-Naturalist 100: 10–14.

Bluemle, J. P. 1980. Guide to the geology of northwestern North Dakota. Education Series 8, North Dakota Geologic Survey. 38 pages.

Bragg, T. B. 1995. Climate, soils and fire: The physical environment of North American grasslands. *In* The Changing Prairie. *Edited by* K. Keeler and A. Joerns. Oxford University Press, New York.

Buckland, S. T., K. P. Burnham, D. R. Anderson, and **J. L. Laake.** 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, New York. 446 pages.

Chatterjee, S., and **B. Price.** 1991. Regression analysis by example. Second edition. John Wiley and Sons, New York. 278 pages.

Coues, E. 1878. Field notes on birds observed in Dakota and Montana along the forty-ninth parallel during the seasons of 1873 and 1874. United States Geologic and Geographic Survey Territorial Bulletin 4: 545–661.

Coupland, R. T. 1950. Ecology of mixed prairie in Canada. Ecological Monographs 20: 271–315.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33: 43–64.

Daubenmire, R. 1968. Ecology of fire in grasslands. Advances in Ecological Research 5: 209–298.

Dobkin, D. S. 1992. Neotropical migrant landbirds in the northern Rockies and Great Plains. U.S.D.A. Forest Service-Northern Region. Publication Number R1-93-34. Missoula, Montana.

Droege, S., and **J. Sauer.** 1994. Are more North American species decreasing than increasing? Pages 297–306 *in* Bird Numbers 1992. Distribution, monitoring and ecological aspects. *Edited by* E. J. M. Hagemeijer and T. J. Verstrael. Proceedings of the 12th International Conference of IBCC and EOAC, Noordwijkerhout, The Netherlands, Statistics Netherlands, Voorburg/Heerlen and SOVON, Beek-Ubbergen.

Ehrenreich, J. H. 1959. Effect of burning and clipping on growth of native prairie in Iowa. Journal of Range Management 12: 133–137.

Forde, J. D., N. F. Sloan, and **D. A. Shown.** 1984. Grassland habitat management using prescribed fire in Wind Cave National Park, South Dakota. Prairie Naturalist 16: 97–110.

Gabrielson, I. N. 1943. Wildlife refuges. MacMillian, New York. 257 pages.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York. 298 pages.

Goossen, J. P., S. Brechtel, K. D. DeSmet, D. Hjertaas, and **C. Wershler.** 1993. Canadian Baird's Sparrow Recovery Plan. Recovery of Nationally Endangered Wildlife Report Number 3. Canadian Wildlife Federation, Ottawa. 28 pages.

Herkert, J. R. 1994. Breeding bird communities of midwestern prairie fragments: the effects of prescribed burning and habitat-area. Natural Areas Journal 14: 128–135.

Higgins, K. F. 1986. Interpretation and compendium of historical fire accounts in the northern Great Plains. U.S. Fish and Wildlife Service Resource Publication 161. 39 pages.

Higgins, K. F., A. D. Kruse, and **J. L. Piehl.** 1989. Effects of fire in the northern Great Plains. South Dakota State University Extension Circular 760. 47 pages.

Huber, G. E., and **A. A. Steuter.** 1984. Vegetation profile and grassland bird response to spring burning. Prairie Naturalist 16: 55–61.

Hutto, R. L., S. M. Pletschet, and **P. Hendricks.** 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103: 593–602.

Johnson, D. H. 1996. Management of northern prairies and wetlands for the conservation of neotropical migratory birds. Pages 53–67 *in* Management of midwestern landscapes for the conservation of neotropical migratory birds. *Edited by* F. R. Thompson. U.S.D.A. Forest Service General Technical Report NC-187. St. Paul, Minnesota.

Johnson, D. H. 1997. Effects of fire on bird populations in mixed-grass prairie. Pages 181–206 *in* Ecology and conservation of Great Plains vertebrates. *Edited by* F. L. Knopf and F. B. Samson. Springer, New York.

Kantrud, H. A. 1981. Grazing intensity effects on the breeding avifauna of North Dakota native grasslands. Canadian Field-Naturalist 95: 404–417.

Kirsch, L. M., and **K. F. Higgins.** 1976. Upland Sandpiper nesting and management in North Dakota. Wildlife Society Bulletin 4: 16–22.

Kirsch, L. M., and **A. D. Kruse.** 1973. Prairie fires and wildlife. Proceedings of Tall Timbers Fire Ecology Conference 12: 289–303.

Kirsch, L. M., H. F. Duebbert, and **A. D. Kruse.** 1978. Grazing and haying effects on habitats of upland nesting birds. Transactions of the North American Wildlife and Natural Resources Conference 43: 486–497.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15: 247–257.

Knopf, F. L. 1996. Prairie legacies — birds. Pages 135–148 *in* Prairie conservation: preserving North America's most endangered ecosystem. *Edited by* F. Samson and F. Knopf. Island Press, Washington, D.C.

Knopf, F. L., and **F. B. Samson.** 1994. Scale perspectives on avian diversity in western riparian landscapes. Conservation Biology 8: 669–676.

Kucera, C. L. 1981. Grasslands and fire. Pages 90–111 *in* Fire regimes and ecosystem properties: proceedings of the conference. U.S.D.A. Forest Service General Technical Report WO-26. Washington, D.C. 594 pages.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* The birds of North America Number 47. *Edited by* A. Poole and F. Gill. Philadelphia, Pennsylvania: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union. 24 pages.

Madden, E. M. 1996. Passerine communities and bird-habitat relationships on prescribe-burned mixed-grass prairie in North Dakota. M.S. thesis, Montana State University, Bozeman, Montana. 153 pages.

Murphy, R. K. 1993. History, nesting biology, and predation ecology of raptors in the Missouri Coteau of northwestern North Dakota. Ph.D. dissertation, Montana State University, Bozeman, Montana. 212 pages.

Oates, M. R. 1995. Butterfly conservation within the management of grassland habitats. Pages 98–112 *in* Ecology and conservation of butterflies. *Edited by* A. S. Pullin. Chapman Hall, New York.

Pylypec, B. 1991. Impacts of fire on bird populations in a fescue prairie. Canadian Field-Naturalist 105: 346–349.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and **D. F. DeSante.** 1993. Handbook of field methods for monitoring landbirds. U.S.D.A. Forest Service General Technical Report PSW-GTR-144. Albany, California. 41 pages.

Renken, R. B. 1983. Breeding bird communities and bird-habitat associations on North Dakota Waterfowl Production Areas. M.S. thesis, Iowa State University, Ames. 90 pages.

Robel, R. J., J. N. Briggs, A. D. Dayton, and **L. C. Hulbert.** 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23: 295–297.

Romo, J. T., and **P. L. Grilz.** 1990. Invasion of Canadian prairies by an exotic perennial. Blue Jay 48: 131–135.

Rotella, J. J., E. M. Madden, and **A. J. Hansen.** 1999. Sampling considerations for estimating abundance of passerines in grasslands. Studies in Avian Biology Number 19.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57: 773–782.

Ryan, M. R. 1990. A dynamic approach to the conservation of the prairie ecosystem in the Midwest. Pages 91–106 *in* Management of dynamic ecosystems. *Edited by* J. M. Sweeney. North Central Section, The Wildlife Society, West Lafayette, Indiana.

Samson, F. B., and **F. L. Knopf.** 1994. Prairie conservation in North America. Bioscience 44: 418–421.

Samson, F. B., and **F. L. Knopf.** *Editors*. 1996. Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington, D.C. 339 pages.

SAS Institute Inc. 1988. SAS/STAT User's Guide, Version 6, third edition. SAS Institute Inc., Cary, North Carolina. 1028 pages.

Stewart, R. E., and **H. A. Kantrud.** 1972. Population estimates of breeding birds in North Dakota. Auk 89: 766–788.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8: 1–93.

Wilkinson, L. 1990. SYGRAPH: the system for graphics. SYSTAT Inc., Evanston, Illinois. 547 pages.

Wright, H. A., and **A. W. Bailey.** 1982. Fire ecology. John Wiley and Sons, New York. 501 pages.

Zimmerman, J. L. 1992. Density-independent factors affecting the avian diversity of the tallgrass prairie community. Wilson Bulletin 104: 85–94.

Received 18 January 1999
Accepted 13 May 1999