Effects of Prescribed Fire on Vegetation and Passerine Birds in Northern Mixed-Grass Prairie

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ABSTRACT  Prescribed fire is used widely to manage grasslands on National Wildlife Refuges and other public lands in the northern Great Plains, but its effects on habitat use or production of wildlife in the region are poorly understood. During 1998–2003, we used point counts to examine effects of prescribed fire on vegetation and passerines in a mixed-grass prairie complex in north-central North Dakota, USA (n = 7 units, each 40–70 ha). Vegetation structure and, to a lesser extent, plant community composition varied with year of study (likely related to changes in annual precipitation) and with number of growing seasons since fire. Fire altered plant structure, especially the amount of residual vegetation, which in turn influenced bird species richness and abundance. The number of indicated pairs for sedge wren (Cistothorus platensis), clay-colored sparrow (Spizella pallida), Le Conte’s sparrow (Ammospiza leucotis), Savannah sparrow (Passerculus sandwichensis), and bobolink (Dolichonyx oryzivorus) were lowest during the first postfire growing season but generally increased and stabilized within 2–3 postfire growing seasons. Our results support the premise that grassland passerines are well-adapted to frequent, periodic fires, generally corresponding to those occurring prior to Euro–American settlement of the region. Prescribed fire is important for reducing tree and shrub invasion, restoring biological integrity of plant communities, and maintaining or enhancing populations of grassland-dependent bird species. Managers in the northern mixed-grass prairie region should not be overly concerned about reductions in bird abundances that are limited mostly to the first growing season after fire.

KEY WORDS fire effects, grassland bird, habitat, mixed-grass prairie, North Dakota, prescribed fire, vegetation.

Mixed-grass prairie has declined 70–90% across states and provinces in the northern Great Plains, mainly due to conversion for agriculture (Samson et al. 2004). This trend continues unabated for prairies in North Dakota and South Dakota, USA (Higgins et al. 2002b, Government Accountability Office 2007, Stephens et al. 2008). The quality of remaining prairies is increasingly diminished by fragmentation, the spread of woody and introduced plants, suppression or misapplication of fire, and certain livestock grazing practices (Samson and Knopf 1994, Grace et al. 2001, Grant and Murphy 2005, Grant et al. 2009). Concurrent with these changes are reductions in breeding populations of most grassland-dependent bird species, including those endemic to the northern Great Plains (Igl and Johnson 1997, Sauer et al. 2008). Prairie is an endangered ecosystem in North America (Samson et al. 2004) and the decline in prairie avifauna may be among the most prominent conservation crises of the century (Brennan and Kuvlesky 2005, Askins et al. 2007). Annually, about 10,000–20,000 ha of grassland, mostly northern mixed-grass prairie, are periodically burned on national wildlife refuges (NWRs) in the Dakotas and eastern Montana, USA. Fire is used primarily to maintain or improve habitat for wildlife, restore native vegetation, and reduce accumulated fuels associated with catastrophic wildfire. Although fire has been used widely as a management tool in the northern Great Plains for 40 years, and is a well-known ecological driver in the system (Bragg 1995), data on its effects specific to plant communities and animal populations are scarce. Reliable data on effects of fire on wildlife and wildlife habitats in northern mixed-grass prairie are restricted to a few site-specific studies (e.g., Johnson 1997) or effects are inferred from different grassland ecosystems, especially tallgrass prairie. Consequently, managers can only vaguely predict effects of prescribed fire on prairies and indigenous wildlife populations in the region. Depending on timing, frequency, and intensity, prescribed fire may or may not have the anticipated effect on plant communities or animal populations.

Within northern mixed-grass prairie, Johnson (1997), Madden et al. (1999), and Danley et al. (2004) examined effects of fire on bird abundance within the Missouri Coteau landform of North Dakota (Bluemle 2000). Recently, Ludwick and Murphy (2006) examined effects of fire on bird abundance in the Drift Prairie landform (100 km W of our study). Pylypec (1991) documented postfire changes in bird abundance for one treatment plot and adjacent control plot in fescue prairie in Saskatchewan, Canada. Huber and Steuter (1984) used a treatment–control approach to explore...
fire effects on birds in South Dakota. Fire effects also have been documented for birds breeding in other grassland systems, especially tallgrass prairie (e.g., Herkert 1994; Herkert and Glass 1999; Powell 2006, 2008; Coppege et al. 2008). Prescribed fire remains controversial for some grassland managers because of reported reductions in bird use of recently burned grasslands (Naugle et al. 2000).

Our objectives were to evaluate short-term effects of fire on structure and composition of vegetation and on species richness and bird abundance (i.e., indicated pairs) of passerines in northern mixed-grass prairie. In cases where fire influenced the number of indicated pairs, we also explored the potential for explaining these effects based on fire-induced changes in vegetation. Finally, we addressed the role of fire as an ecological process in northern mixed-grass prairie.

STUDY AREA
We conducted our study on the 23,900-ha J. Clark Salyer NWR in Bottineau County, North Dakota (about 48°45’N, 100°50’W). The refuge was within the northern mixed-grass prairie region (Partners in Flight Physiographic Area 37; Fitzgerald et al. 1999). More specifically, our study site was within the Drift Prairie landform, characterized by native sod in deep (12–15-cm surface, 25–30-cm subsurface), level loams (Bluemle 2000). Drift prairie on J. Clark Salyer NWR consisted of 25-km-long, narrow (0.5- to 2.0-km-wide) tracts along shallow impoundments of the Souris River. Drift prairie tracts were bordered by cropland (dryland farming for small grains), interspersed with scattered tracts (16–130 ha) of either annually grazed, privately owned drift prairie or former cropland seeded to introduced grasses and forbs for conservation purposes (e.g., to inhibit soil erosion, provide bird nesting cover).

Our study area was typical of many grassland tracts managed by the United States Fish and Wildlife Service and other conservation agencies or organizations in the northern Great Plains. Specifically, these grassland tracts were 1) chiefly native prairie invaded by cool-season, introduced plants and often native woody vegetation (Grant et al. 2009), 2) managed mainly by rest (i.e., no disturbance), with periodic defoliation by fire, livestock grazing, or haying, 3) usually large enough to contain area-sensitive species (e.g., northern harrier [Circus cyaneus], marbled godwit [Limosa fedoa]), 4) characterized by scattered small wetlands or nearby, large semi-permanent wetlands (Stewart and Kantrud 1971), and 5) bordered by annually tilled cropland or, to a lesser extent, by grazed native prairie or nonnative grassland.

Vegetation was a needlegrass–wheatgrass (Stipa–Agropyron) association intermingled with 2 exotic grasses, Kentucky bluegrass (Poa pratensis) and smooth brome (Bromus inermis). Herbaceous plant communities were interspersed with patches of low shrub dominated by western snowberry (Symphoricarpos occidentalis). The study area was managed with prescribed fire in 100–200-ha blocks every 2–6 years since the late 1960s, except during 1985–1994, when the frequency and extent of prescribed fire in North Dakota was curtailed by drought. Cattle had not grazed the area since 1950 or before. Climate was subhumid continental, with average monthly temperatures ranging from −15°C in January to 20°C in July (T. A. Grant, United States Fish and Wildlife Service, unpublished data). Annual precipitation fluctuated during 1998–2003, but mean annual level was near the long-term average (x = 44.2 cm vs. 43 cm).

METHODS
Study Design
We designed a manipulative study to isolate fire effects from other effects (e.g., area effects or effects of other treatments such as grazing or haying) expected to influence grassland bird species richness and abundance. With this focus, we used a 400-ha tract of prairie composed of 7 contiguous units, each with a unique fire schedule (Table 1). All burn units had similar vegetation structure and composition at a bird-territory scale (e.g., <5 ha) and similar habitat-area and edge metrics (e.g., distance to cropland edge) at a local landscape scale.

Beginning in 1997, we burned selected units in August–September (Table 1) to mimic naturally occurring late-summer fires. The primary variable of interest (i.e., treatment) was the number of growing seasons since the last fire had occurred (postfire growing seasons). We grouped study unit burn schedules (41 total 1998–2003) into 1 (i.e., current growing season), 2, 3, or ≥4 postfire growing seasons (range = 1–12). For example, the number of postfire growing seasons for unit F, which was burned in autumn 1998 and again in autumn 2002, was ≥4 in 1998, 1 in 1999, 2 in 2000, 3 in 2001, ≥4 in 2002, and 1 in 2003 (Table 1).

Data Collection
For bird surveys, we used systematic sampling with a random start point to locate 4–7 100-m-radius plots within each of 7 burn units (37 plots). We placed edges of plots >50 m from cropland, wetland, or adjacent plots. Following Hutto et al. (1986), we surveyed each plot twice between 25 May and 30 June when conditions did not impede detection of birds (i.e., no precipitation and wind <15 km/hr). We

### Table 1. Growing seasons since last fire for 7 units within a 400-ha mixed-grass prairie complex on J. Clark Salyer National Wildlife Refuge, North Dakota, USA, 1998–2003. For purposes of analysis, we categorized the 41 unit-year combinations into 1 (n = 11), 2 (n = 11), 3 (n = 7), or ≥4 (n = 12) growing seasons since last fire.

<table>
<thead>
<tr>
<th>Yr</th>
<th>Unit</th>
<th>Area (ha)</th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>69</td>
<td>8</td>
<td>9a</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>43</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4a</td>
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<td>2</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>69</td>
<td>5</td>
<td>6a</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>69</td>
<td>5a</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>49</td>
<td>12a</td>
<td>1</td>
<td>2</td>
<td>1b</td>
<td>2</td>
<td>3</td>
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<td></td>
<td>H</td>
<td>47</td>
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<td>2</td>
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<td>4a</td>
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<td>41</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>1</td>
</tr>
</tbody>
</table>

a Indicates yr during which we completed late-summer prescribed burns.

b We excluded unit G from study in 2001 because we burned it in spring 2001 rather than late-summer 2000 as scheduled.
used 3 experienced observers (E. M. Madden, J. S. Dockens, and T. A. Grant, 2 consecutive yr each) to tally birds by sight and sound during 5-minute visits. We switched order of visitation so we sampled each plot once each during an early (0515–0645 hr) and late (0645–0800 hr) period. We derived indicated pairs for each visit from observations of either singing males, observed pairs, or, in the case of brown-headed cowbirds (*Molothrus ater*), number of females (Madden et al. 1999, 2000; Davis 2004; Grant et al. 2004a). We used the greater of the 2 counts in our analyses. Because the design of our bird surveys was tightly controlled, we believe that the probability of detection (given that a species was present) was similar among burn treatments for any species of grassland bird recorded during our study. Therefore, we based our comparisons of burn treatments on actual counts (indicated pairs) rather than estimates of absolute abundance, which would have required species-specific estimates of detection probability and introduced additional sources of variability (Johnson 2008). Methods for estimating absolute abundance from point-count surveys have met with limited success because necessary assumptions are difficult to meet in field studies and techniques used to address imperfect detectability in studies like ours may well be more damaging than imperfect detectability itself (Johnson 2008, Efford and Dawson 2009).

Each year we measured structure and general composition of vegetation during late June through mid-July on the same 100-m-radius plots used to survey birds. Following Madden et al. (2000) we measured vegetation structure along 2 parallel 70-m transects established at each side of plot center. At each sample point spaced every 10 m along transects (16 points/plot), we measured the following: litter depth, defined as thickness (cm) of dead, unconsolidated (mostly horizontal) plant matter; standing dead vegetation, defined as the percentage of standing vegetation that is dead; and maximum vegetation height (cm), defined as the tallest vegetation contact. Following Grant et al. (2004a, b) we recorded general vegetation composition using 4 100-m belt transects radiating from the center of each plot. Beginning at a plot center, we first established a belt transect along a random compass bearing and then placed subsequent transects at 90°, 180°, and 270° from the first. At 0.5-m increments along each transect (800 belt-segment records/plot) we recorded canopy coverage of plant community associations common to the region (Grant et al. 2004d). To avoid area bias due to over-sampling near the center of each plot, we systematically omitted 0.5-m-segment data within each of 10 10-m bands extending from plot center, such that remaining segments (*n* = 421) were proportionally distributed according to the area within each 10-m band (Grant et al. 2004 a, b). We summarized vegetation composition into 7 categories, including low shrub, native grass–forb, Kentucky bluegrass, smooth brome, leafy spurge (*Euphorbia esula*), other tall weeds, and wetland. We used geographic information system technology and 1,7920 aerial photographs acquired in 1997 to delineate the distance from each plot center to the nearest cropland and wetland edges.

**Modeling Fire and Habitat Effects**

We anticipated annual variation in vegetation attributes and indicated pairs of breeding birds based on annual fluctuations in local and regional conditions, especially, but not solely, precipitation. We also recognized inherent differences among study units in terms of features such as edge:interior ratio. The burn schedule (Table 1) allowed us to construct models that could distinguish fire effects (no. of postfire growing seasons as a categorical variable) from effects of year and study unit under the assumption that such effects were additive (i.e., no interactions). That assumption seemed reasonable given the close proximity of study plots and that features like edge:interior ratio did not change year to year.

We measured annual precipitation as the amount received from 1 July of the previous year to 30 June of the current year. Because year effects accounted for potential effects of precipitation, we did not include precipitation as a covariate in any of our models. We did, however, compute correlation coefficients to describe the relationship between precipitation and either vegetation or bird abundance metrics.

We used an information-theoretic approach (Burnham and Anderson 2002) to assess evidence for effects of fire on the structure and composition of vegetation. For each habitat variable, we considered 2 a priori models, one that included effects of year (categorical) and study unit and another that also included an effect of fire (i.e., no. of postfire growing seasons as a categorical effect). We chose the information-theoretic approach because it allowed us to quantify, using evidence ratios, support for the fire-effect hypothesis. Percentage variables (e.g., % cover of Kentucky bluegrass), although not derived from counts, have distributional properties similar to binomial random variables (i.e., variance is greatest for values near 50% and smallest for values near 0% and 100%). McCullagh and Nelder (1989) demonstrated the use of quasi-likelihood estimation techniques to model these types of data. We used the GLIMMIX procedure (SAS Institute 2004) to conduct analyses of percent-composition variables. We used a similar approach to analyze litter depth and maximum vegetation height except that we assumed that these variables followed log-normal distributions. In all cases, we examined Pearson residual diagnostics to determine whether our distributional assumptions were appropriate. Because we surveyed the same plots each year, these repeated measures were potentially correlated. We modeled the correlation with a REPEATED statement, assuming an exchangeable correlation structure. Repeated-measure models for percent cover of leafy spurge would not converge; therefore, we report results based on the assumption of independent residuals. Quasi-likelihood estimation techniques are not based on a full likelihood function and, thus, we could not compute Akaike’s Information Criterion (AIC; Burnham and Anderson 2002). However, the GLIMMIX procedure reports pseudo-AIC values that we used to compute model weights and evidence ratios similar to those described by Burnham and Anderson (2002).
Using an approach similar to that for vegetation, we modeled the number of indicated bird pairs and species richness as Poisson random variables with means that we could express as a log-linear function of year (categorical and possibly a surrogate for precipitation), study unit, and number of postfire growing seasons (categorical). The quasi-likelihood Poisson model for western meadowlark (Sturnella neglecta) would not converge, even when we treated the repeated measures as independent. Therefore, we assumed a normal distribution with correlated errors to analyze counts of western meadowlark.

We identified habitat features most associated with indicated pairs or species richness. In this analysis, we considered 14 plausible models. The simplest model included only an effect for year. Twelve models also contained an effect for year and one of the following habitat variables: low shrub, native grass–forb, Kentucky bluegrass, smooth brome, leafy spurge, tall weed, wetland, litter depth, maximum height, standing dead, distance to cropland (log-transformed), and distance to wetland (log-transformed). One additional model contained effects of year and study unit and allowed for the possibility that bird species responded to a combination of habitat variables or to some unmeasured habitat feature. When this model was the best model, we conducted exploratory analyses involving 2-way combinations of habitat variables to better understand the nature of the relationship between habitat features and bird abundance. We assumed a Poisson distribution for the counts (except western meadowlark, for which we used a normal distribution) and modeled correlations among repeated counts with an exchangeable correlation structure using the GLIMMIX procedure. We ranked models from best to worst on the basis of \( \Delta \text{AIC} \) (\( \text{AIC} \) adjusted for small samples for the model in question minus that for the model with min. \( \text{AIC} \)) western meadowlark) or \( \Delta \)-pseudo-\( \text{AIC} \), values.

In our final analyses, we investigated whether bird response to fire (i.e., when species richness or indicated pairs varied with the no. of postfire growing seasons) could be explained on the basis of fire-induced changes in structure or composition of vegetation. We used results from our analysis of habitat features associated with bird abundance as a starting point for selecting candidate models, considering only models with \( \Delta \)-values \( \leq 6.0 \). We derived additional models by adding an effect of fire (i.e., no. of postfire growing seasons) to each candidate model that met the above criterion. We also considered a model that included only effects of year and fire. Thus, if \( m \) models met our starting criterion, we considered \( 2m + 1 \) models in our analysis. If birds responded primarily to fire-induced changes in vegetation structure and composition, we expected the \( m + 1 \) models that included an explicit effect of fire, in addition to effects for vegetation structure or composition, to be inferior to vegetation-only models. Conversely, if fire altered the suitability of a unit for birds beyond modification of vegetation structure or composition, we expected models that also included an effect of fire to be superior to vegetation-only models. Specifically, \( \Delta \text{IC} \) values \( \leq -4 \) (\( \text{IC} \) is either \( \text{AIC} \) or a pseudo-\( \text{AIC} \) produced by the GLIMMIX procedure and \( \Delta \text{IC} \) is vegetation-only model minus vegetation + fire model) suggest that fire-induced changes in vegetation were sufficient to explain a species’ response to fire. Values \( \geq 4 \) indicate that the model containing an explicit fire effect was superior to the vegetation-only model, suggesting that the species’ response to fire could not be explained solely on the basis of measured changes in vegetation structure or composition. Values between \(-4 \) and \( 4 \) provide no clear evidence.

**RESULTS**

We observed few effects of fire on general community composition of vegetation (Table 2), except that cover of Kentucky bluegrass increased about 7% with 3+ postfire growing seasons compared to first and second postfire growing seasons (Fig. 1). Less compelling (Table 2), but of more biological importance, was a 7.5% decline in cover of native grasses and forbs with \( \geq 4 \) postfire growing seasons compared to \( 2\text{–}3 \) postfire growing seasons (Fig. 1). In contrast, fire strongly altered the structure of vegetation, especially the amount of residual vegetation (i.e., dead plant material from a previous growing season; Table 2). Maxi-

**Table 2.** Evidence for an effect of fire on structure and composition of vegetation, J. Clark Salyer National Wildlife Refuge, North Dakota, USA, 1998–2003. For each vegetation variable, the null model included effects of year and study unit. The fire model contained those effects plus an effect of fire (i.e., no. of postfire growing seasons). The evidence ratio (\( = \exp(0.5 \Delta \text{IC}) \)) provides the relative evidence for the hypothesis that the variable is affected by fire; ratios >30 provide strong evidence for an effect of fire.

<table>
<thead>
<tr>
<th>Habitat variable</th>
<th>Null IC (K = 14)*</th>
<th>Fire IC (K = 17)*</th>
<th>( \Delta \text{IC}^a )</th>
<th>Evidence ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation composition</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Native grass–forb (%)</td>
<td>464.7</td>
<td>467.8</td>
<td>-3.1</td>
<td>0.2</td>
</tr>
<tr>
<td>Kentucky bluegrass (%)</td>
<td>410.9</td>
<td>402.7</td>
<td>8.2</td>
<td>61.5</td>
</tr>
<tr>
<td>Smooth brome (%)</td>
<td>237.1</td>
<td>241.5</td>
<td>-4.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Tall weeds (%)</td>
<td>1,015.7</td>
<td>1,045.7</td>
<td>-30.0</td>
<td>0</td>
</tr>
<tr>
<td>Leafy spurge (%)</td>
<td>60.6</td>
<td>67.4</td>
<td>-6.8</td>
<td>0</td>
</tr>
<tr>
<td>Low shrub (%)</td>
<td>372.4</td>
<td>377.5</td>
<td>-5.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Vegetation structure</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter depth (cm)</td>
<td>458.1</td>
<td>117.9</td>
<td>340.1</td>
<td>&gt;1,000</td>
</tr>
<tr>
<td>Standing dead (%)</td>
<td>277.8</td>
<td>-39.9</td>
<td>317.8</td>
<td>&gt;1,000</td>
</tr>
<tr>
<td>Max. ht (cm)</td>
<td>44.3</td>
<td>1.8</td>
<td>42.5</td>
<td>&gt;1,000</td>
</tr>
</tbody>
</table>

* IC is either Akaike’s Information Criterion (AIC) or a pseudo-AIC produced by the GLIMMIX procedure. \( K \) is the no. of parameters. \( \Delta \text{IC} \) is the difference in IC values between the null and fire models.
mum vegetation height, litter depth, and standing dead vegetation were lowest during the first postfire growing season (Fig. 1). Standing dead vegetation and maximum vegetation height increased by 39% and 7 cm, respectively, during the second postfire growing season and stabilized thereafter, whereas plant litter accumulated 1–2 cm during each postfire growing season (Fig. 1). Vegetation height and litter depth varied among years, likely in response to changes in amount of annual precipitation received during the previous growing season (Fig. 2). For example, annual precipitation was correlated with accumulation of plant litter ($r = 0.94$, $n = 6$ yr).

We observed 22 bird species known to be associated with grasslands on 37 plots during 1998–2003 (Table 3). Savannah sparrow (Passerculus sandwichensis), bobolink (Dolichonyx oryzivorus), clay-colored sparrow (Spizella pallida), brown-headed cowbird, and Le Conte’s sparrow (Ammodramus leconteii) accounted for 83% of indicated pairs. Three species endemic to the northern Great Plains were either absent (Sprague’s pipit [Anthus spragueii]) or uncommon (Baird’s sparrow [Ammodramus bairdii] and chestnut-collared longspur [Calcarius ornatus]). Bird species richness and the number of indicated pairs (by species) varied among years, and possibly with annual precipitation (Fig. 2). For example, the number of indicated pairs for all bird species combined was correlated with precipitation received during the previous growing season ($r = 0.84$, $n = 6$).

Species richness and the number of indicated pairs for all species combined were lowest during the first postfire growing season, but increased during the second postfire growing season and stabilized thereafter (Fig. 3). Fire affected 5 of 8 species for which we had sufficient samples (Table 4). Indicated pairs for Savannah sparrow, clay-colored sparrow, Le Conte’s sparrow, bobolink, and sedge

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**Figure 1.** The relationship between the number of postfire growing seasons (1, 2, 3, or 4) and either percent cover of native grasses and forbs, percent cover of Kentucky bluegrass, standing dead vegetation, litter depth, or maximum vegetation height on J. Clark Salyer National Wildlife Refuge, North Dakota, USA, 1998–2003. Estimates are least-squares means (Milliken and Johnson 1984) from a model with additive effects for year, study unit, and postfire growing seasons. Error bars represent 95% confidence intervals.

**Figure 2.** Bird species richness, indicated pairs (by species), litter depth, maximum vegetation height, and annual precipitation during 1998–2003 on J. Clark Salyer National Wildlife Refuge, North Dakota, USA. We recorded annual precipitation from 1 July of the previous growing season to 30 June of the current year.
Wren (Cistothorus platensis) were lowest during the first postfire growing season (Fig. 4). Indicated pairs for Savannah sparrow and clay-colored sparrow increased about 0.5 pairs/plot during the second postfire growing season and stabilized or slightly increased thereafter. In contrast, indicated pairs for Le Conte's sparrow, bobolink, and sedge wren peaked during the second or third growing season after fire (Fig. 4). Fire had little influence on indicated pairs for brown-headed cowbird, western meadowlark, or grasshopper sparrow (Ammodramus savannarum; Table 4).

Standing dead vegetation was associated with species richness, indicated pairs for all bird species combined, and indicated pairs of sedge wren, clay-colored sparrow, Le Conte's sparrow, Savannah sparrow, and brown-headed cowbird (Table 5). Indicated pairs of sedge wren and grasshopper sparrow declined as cover of leafy spurge increased. Sedge wren pairs increased as cover of tall weeds, especially sweet clover (Melilotus officinalis), increased. Indicated pairs of grasshopper sparrow declined as cover of low shrub increased (Table 5). Indicated pairs for bobolink and western meadowlark were not associated with any habitat feature we measured (Table 5).

Changes in vegetation structure, especially the amount of standing dead vegetation, seemed to explain observed patterns of postfire response in indicated pairs of clay-colored sparrow, Le Conte's sparrow, Savannah sparrow, and sedge wren. The best models for these species contained only vegetation variables with information criterion values 4.3–39.4 units smaller than the best model containing an explicit effect of fire, suggesting that these species responded to changes in vegetation structure induced by fire. Changes in vegetation structure did not, however, account for fire-induced response of bobolink (ΔIC = 12.1). This species may have responded to habitat features influenced by fire that we did not measure. Fire-induced changes in vegetation variables that we measured were not associated with the number of indicated pairs for all species combined (ΔIC = 17.4), most likely because individual bird species responded differently to the suite of fire and habitat variables we measured or possibly because we failed to measure attributes that were simultaneously influenced by fire and associated with bird abundance. Our data provided no clear evidence of an association between fire-induced changes in vegetation and species richness (ΔIC = 1.4).

**DISCUSSION**

**Short-Term Fire Effects**

Litter depth, standing dead vegetation, and maximum vegetation height were lowest during the first growing season after late-summer burning but generally increased during the second postfire growing season and stabilized.

**Figure 3.** Species richness and indicated pairs of all grassland bird species combined relative to the number of postfire growing seasons (1, 2, 3, or ≥4) on J. Clark Salyer National Wildlife Refuge, North Dakota, USA, 1998–2003. Estimates are least-squares means (Milliken and Johnson 1984) from a model with additive effects for year, study unit, and postfire growing seasons. Error bars represent 95% confidence intervals.

**Table 3.** Indicated pairs and average indicated pairs/100-m-radius plot (SE) for grassland bird species observed on 37 point-count plots at J. Clark Salyer National Wildlife Refuge, North Dakota, USA, 1998–2003.

<table>
<thead>
<tr>
<th>Species</th>
<th>Indicated pairs</th>
<th>Indicated pairs/point</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern harrier</td>
<td>11</td>
<td>0.05</td>
<td>0.02</td>
</tr>
<tr>
<td>Willet (Tringa semipalmata)</td>
<td>2</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Upland sandpiper (Bartramia longicauda)</td>
<td>10</td>
<td>0.05</td>
<td>0.02</td>
</tr>
<tr>
<td>Marbled godwit</td>
<td>5</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>Short-eared owl (Asio flammeus)</td>
<td>5</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>Eastern kingbird (Tyrannus tyrannus)</td>
<td>7</td>
<td>0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>Horned lark (Eremophila alpestris)</td>
<td>7</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Sedge wren</td>
<td>91</td>
<td>0.41</td>
<td>0.05</td>
</tr>
<tr>
<td>Common yellowthroat (Geothlypis trichas)</td>
<td>21</td>
<td>0.10</td>
<td>0.02</td>
</tr>
<tr>
<td>Clay-colored sparrow</td>
<td>289</td>
<td>1.30</td>
<td>0.09</td>
</tr>
<tr>
<td>Grasshopper sparrow</td>
<td>31</td>
<td>0.14</td>
<td>0.04</td>
</tr>
<tr>
<td>Baird's sparrow</td>
<td>7</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Le Conte's sparrow</td>
<td>117</td>
<td>0.53</td>
<td>0.05</td>
</tr>
<tr>
<td>Nelson's sparrow (Ammodramus nelsoni)</td>
<td>4</td>
<td>0.02</td>
<td>0.01</td>
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<tr>
<td>Savannah sparrow</td>
<td>663</td>
<td>2.99</td>
<td>0.10</td>
</tr>
<tr>
<td>Song sparrow (Melospiza melodia)</td>
<td>2</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Chestnut-collared longspur</td>
<td>17</td>
<td>0.08</td>
<td>0.03</td>
</tr>
<tr>
<td>Bobolink</td>
<td>477</td>
<td>2.15</td>
<td>0.13</td>
</tr>
<tr>
<td>Red-winged blackbird (Agelaius phoeniceus)</td>
<td>48</td>
<td>0.22</td>
<td>0.04</td>
</tr>
<tr>
<td>Western meadowlark</td>
<td>67</td>
<td>0.30</td>
<td>0.05</td>
</tr>
<tr>
<td>Brewer's blackbird (Euphagus cyanoccephalus)</td>
<td>23</td>
<td>0.10</td>
<td>0.05</td>
</tr>
<tr>
<td>Brown-headed cowbird</td>
<td>161</td>
<td>0.73</td>
<td>0.05</td>
</tr>
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</table>
thereafter. This postfire successional pattern corresponds with that reported elsewhere in North Dakota and northwestern Minnesota, USA (Dix 1960, Tester and Marshall 1961, Higgins 1986, Kruse and Bowen 1996). Although litter depth is among the most common vegetation variables measured in grassland bird habitat studies (Johnson et al. 2004, Fisher and Davis 2010), our models suggest that the percentage of standing dead vegetation is likely a more important attribute of bird habitat to assess. However, standing dead vegetation is more time-consuming to measure than litter depth and these 2 variables are usually correlated (Nenneman 2003), particularly in a study like ours where fire greatly reduced residual plant matter from previous growing seasons.

Recently burned prairies had fewer indicated pairs of passerines than prairies rested ≥2 growing seasons. In most cases, indicated pairs increased during the second postfire growing season and stabilized, or in some cases decreased,
thereafter. Our results are similar to postfire response patterns described by Johnson (1997) and Madden et al. (1999) for clay-colored sparrow, Savannah sparrow, bobolink, and Le Conte’s sparrow nesting in the Missouri Coteau landform of North Dakota. A longer postfire recovery period was needed for bird abundance to increase and stabilize for rescue prairie sites in Saskatchewan (Driver 1987, Pylypec 1991). Fire also influenced bird abundance in tallgrass prairie (Tester and Marshall 1961; Herkert 1994; Herkert and Glass 1999; Powell 2006, 2008). However, few fire-effect studies were able to empirically demonstrate bird–fire responses as a function of fire-induced changes in vegetation (e.g., Coppedge et al. 2008, our study).

Within the northern mixed-grass prairie, grassland passerines select nesting territories and nest sites based on vegetation attributes (Madden et al. 2000; Davis 2003, 2005; Nenneman 2003; Grant et al. 2004a). Fluctuations in annual precipitation also influence density and distribution of grassland bird populations in North Dakota (George et al. 1992, Niemuth et al. 2008), presumably via influences on habitat (e.g., Fig. 2). In particular, many grassland bird species require residual vegetation for nesting (Higgins 1986a, Johnson 1997, Nenneman 2003, Davis 2005). We suggest that postfire changes in bird abundance that we observed were, in part, the result of substantial and widespread reductions of residual vegetation available for constructing and concealing nests (i.e., fire-induced changes in residual vegetation is the primary mechanism influencing bird response), as supported by data from 2 additional studies conducted concurrently within our study area. Nest densities of clay-colored sparrow, Savannah sparrow, and bobolink also were lowest during the first postfire growing season but increased during subsequent growing seasons. For each of these species, the relationship between density of nests and number of postfire growing seasons closely matched the pattern of response we observed using indicated pairs as a measure of bird relative abundance (T. A. Grant, unpublished data). In another study, clay-colored sparrow and Savannah sparrow avoided nesting in recently burned grasslands and also selected nest sites with greater amounts of residual vegetation than available at random sites, regardless of the fire history of the area (Nenneman 2003). However, Nenneman (2003) also observed that when nests were located in recently burned areas, they were found in small patches (often \(<2 \text{m}^2\)) of unburned or lightly burned vegetation where some residual vegetation remained.

**Fire as an Ecological Process in Grasslands**

The northern Great Plains evolved with grazing and fire disturbances, as well as climatic variability (Higgins 1986b, Bragg 1995, Manske 2000). Historic and contemporary vegetation dynamics were mediated by the interaction and variation among these disturbances, particularly their frequency, intensity, and timing. Resulting habitat for grassland birds also was presumably heterogeneous; diversity in composition and structure of vegetation historically supported an assemblage of grassland birds that required specific criteria for nesting (Wiens 1974, Askins et al. 2007). Fire negligibly altered the general composition of vegetation during our 6-year study. Kentucky bluegrass cover was reduced, possibly offset by marginal increases in coverage of native grasses and forbs during 1–2 growing seasons postfire. However, short-term studies such as ours are rarely adequate to assess such changes because they often occur in small, incremental steps that are either not detected or rendered insignificant based on inadequate sampling (Murphy and Grant 2005). This is especially true given the dynamic nature of the northern Great Plains. When considered across many decades, fire (especially lack of fire) can profoundly influence the composition of vegetation in northern prairies. For example, composition of vegetation within our study area is modified from pristine conditions found prior to Euro–American settlement of the region. In contrast, cover dominated by native grasses and forbs accounted for 15% of the contemporary plant community, whereas Kentucky bluegrass– and smooth brome–dominated cover accounted for 26% and 43% cover, respectively (T. A. Grant, unpublished data). Mixed-grass prairie on NWRs elsewhere in the region also is degraded, mainly through invasions by smooth brome, Kentucky bluegrass, and woody plants (Madden et al. 2000, Grant and Murphy 2005, Murphy and Grant 2005, Grant et al. 2009). A common management history (i.e., 60–70 yr), consisting mainly of long-term rest, is implicated in these changes (Higgins et al. 2002a, Grant and Murphy 2005, Murphy and Grant 2005, Grant et al. 2009).

Degradation of prairies also may influence composition of bird communities in remaining prairies of the northern Great Plains, although these changes can be difficult to assess directly (Madden et al. 1999). The most common species (i.e., Savannah sparrow, bobolink; Table 3) we observed and that were observed by Ludwick and Murphy (2006) have broad geographical breeding ranges that encompass both mixed-grass and tallgrass prairie regions. Prior to Euro–American settlement of the region (circa 1900), Savannah sparrow and bobolink were common, often associated with lowland prairies near the Sours River (Coues 1878). In contrast, Baird’s sparrow, Sprague’s pipit,
and chestnut-collared longspur were described as the 3 most abundant songbird species in the region (Coues 1878). Although indicative of northern mixed-grass prairie, these species were rare or absent during our study (Table 3). All 3 species are endemic to the northern Great Plains and are more abundant on prairies dominated by native grasses and forbs (Wilson and Belcher 1989; Madden et al. 2000; Davis 2003, 2005; Grant et al. 2004a). Natural and anthropogenic fires occurred roughly every 5–6 years in northern mixed-grass prairie (Bragg 1995). Beginning with Euro–American settlement, these fires were suppressed (Umbanhowar 1996), facilitating increases in woody vegetation and introduced grasses (Grant and Murphy 2005, Murphy and Grant 2005), with corresponding adverse effects on many species of grassland passerines (Madden et al. 2000, Bakker et al. 2002, Grant et al. 2004a). For example, 80 years of fire suppression in the Missouri Coteau landform of northwestern North Dakota gradually transformed prairies that were previously short in stature and dominated by native grasses and forbs to prairies that were taller in stature and increasingly composed of trees, shrubs, and nonnative grasses (Murphy 1993, Madden et al. 1999). Many grassland bird species, especially Baird’s sparrow, Sprague’s pipit, and chestnut-collared longspur, were uncommon on these degraded prairies (Murphy 1993, Madden et al. 1999, Winter 1999). Reintroduction of fire during a 20-year period at Lostwood NWR (located in the Missouri Coteau landform) increased coverage of native vegetation and decreased coverage of introduced and woody plant species, thereby increasing use of prairies by several grassland bird species, including Baird’s sparrow and Sprague’s pipit (Madden et al. 1999, Danley et al. 2004).

A fire-effects study similar to that of Madden et al. (1999), but conducted at Des Lacs NWR, located in the Drift Prairie landform (100 km W of our study) did not corroborate results from Lostwood NWR (Ludwick and Murphy 2006). Despite frequent and widely applied reintroduction of fire during a 15-year period, several bird species endemic to the region remained rare or absent, most likely because introduced and woody plants altered the structure and composition of these prairies, perhaps irreparably (Murphy and Grant 2005, Ludwick and Murphy 2006). To an extent, these results are similar to our findings. Prescribed fire was used for >40 years within our study area, at frequencies comparable to those prior to Euro–American settlement. Yet, Baird’s sparrow and chestnut-collared longspur remained rare and Sprague’s pipit was absent, suggesting that fire frequency alone may not explain changes in vegetation and bird community composition over time. This claim is supported by additional anecdotal evidence. Beginning in 2004, prescribed grazing was reintroduced to the study site for the first time in >50 years (use of prescribed fire continues). Subsequently, longspurs occupied areas within the study site not used during our study or that of Grant et al. (2004a) and Sprague’s pipit established territories during the past 3 breeding seasons for the first time in >20 years (T. A. Grant, personal observation). Restoration of prairie plant and bird communities may be similarly challenging for prairies on NWRs and other publicly owned lands elsewhere in the northern Great Plains, which may be especially true within the Drift Prairie landform where remaining prairie tracts are often smaller in size, have greater edge to interior ratios, and are more degraded by introduced plants (particularly smooth brome) than tracts in the Missouri Coteau (T. A. Grant, unpublished data).

Fire has been perceived as a controversial management tool in cases where bird densities are reduced the year after a fire (reviewed in Naugle et al. 2000). Short-term effects have been routinely assessed by comparing burned sites against similar unburned areas. Such treatment–control assessments may conclude that prescribed fire is detrimental or at best neutral to the species of grassland bird in question (Naugle et al. 2000), despite evidence that birds are flexible and occupy adjacent unburned habitat rather than die or emigrate from the area as a result of fire. Of particular concern are recommendations for infrequent use of fire (mainly as a tool to reduce accumulated litter) because of short-term reductions in grassland bird densities, primarily limited to the tract where fire was applied. These concerns are rendered moot in the northern mixed-grass prairie where fire is currently used on too few areas and at intervals insufficient to meaningfully reduce populations of grassland birds. Of greater concern should be long-term changes in the avian community associated with decades of fire suppression, because these changes may be irreversible. In other regions, especially in large remnant tracts of tallgrass prairie, prescribed fire may be more extensively and frequently applied compared to the presettlement period, and in these cases fire may act to degrade grassland bird habitat (With et al. 2008). Management approaches that ignore the ecological role of fire for maintaining prairies are likely insufficient for achieving desired results if restoration is an important objective.

**MANAGEMENT IMPLICATIONS**

Our results support the premise that grassland passerines are well-adapted to frequent, periodic fires, generally corresponding to those occurring prior to Euro–American settlement of the region. However, only a small fraction of prairies in the northern Great Plains are managed such that the interaction of drought, fire, and grazing mimic natural conditions (i.e., frequency, timing, and extent of disturbances) under which grassland plant and animal species were adapted. To meet United States Fish and Wildlife Service goals for restoring or maintaining prairie plant and animal populations, the extent and frequency of prescribed fire will need to increase above current levels in northern mixed-grass prairie. More importantly, management approaches that better mimic formative ecological processes, including fire, offer improved opportunities for maintaining and restoring the ecological integrity of prairies (Samson et al. 2004, Grant et al. 2009) and the full assemblage of bird species that utilize these prairies (Madden et al. 1999, 2000; Coppedge et al. 2008; Powell 2008; this study). Only by understanding habitat requirements of grassland birds, as well as the role of processes (such as fire) that shaped the region’s ecology, can
managers effectively restore and maintain prairies on NWRs and elsewhere in the northern Great Plains.

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