

SHOULD HETEROGENEITY BE THE BASIS FOR CONSERVATION? GRASSLAND BIRD RESPONSE TO FIRE AND GRAZING

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Abstract. In tallgrass prairie, disturbances such as grazing and fire can generate patchiness across the landscape, contributing to a shifting mosaic that presumably enhances biodiversity. Grassland birds evolved within the context of this shifting mosaic, with some species restricted to one or two patch types created under spatially and temporally distinct disturbance regimes. Thus, management-driven reductions in heterogeneity may be partly responsible for declines in numbers of grassland birds. We experimentally altered spatial heterogeneity of vegetation structure within a tallgrass prairie by varying the spatial and temporal extent of fire and by allowing grazing animals to move freely among burned and unburned patches (patch treatment). We contrasted this disturbance regime with traditional agricultural management of the region that promotes homogeneity (traditional treatment). We monitored grassland bird abundance during the breeding seasons of 2001–2003 to determine the influence of altered spatial heterogeneity on the grassland bird community. Focal disturbances of patch burning and grazing that shifted through the landscape over several years resulted in a more heterogeneous pattern of vegetation than uniform application of fire and grazing. Greater spatial heterogeneity in vegetation provided greater variability in the grassland bird community. Some bird species occurred in greatest abundance within focally disturbed patches, while others occurred in relatively undisturbed patches in our patch treatment. Henslow's Sparrow, a declining species, occurred only within the patch treatment. Upland Sandpiper and some other species were more abundant on recently disturbed patches within the same treatment. The patch burn treatment created the entire gradient of vegetation structure required to maintain a suite of grassland bird species that differ in habitat preferences. Our study demonstrated that increasing spatial and temporal heterogeneity of disturbance in grasslands increases variability in vegetation structure that results in greater variability at higher trophic levels. Thus, management that creates a shifting mosaic using spatially and temporally discrete disturbances in grasslands can be a useful tool in conservation. In the case of North American tallgrass prairie, discrete fires that capitalize on preferential grazing behavior of large ungulates promote a shifting mosaic of habitat types that maintain biodiversity and agricultural productivity.

Key words: conservation biology; disturbance; diversity; grassland birds; heterogeneity; Henslow's Sparrow; rangelands; Tallgrass Prairie Preserve, Oklahoma; Upland Sandpiper.

INTRODUCTION

All ecosystems are variable in space and time. The focus of experimental ecology has largely been on reducing variability to conform to traditional statistics and experimental designs. This has led to a form of land management and an understanding of landscapes that are simplistic and based on a paradigm of uniformity

where land management ignores or even manages against heterogeneity (Fuhlerdorf and Engle 2001). For example, a fundamental principle of rangeland management is to maintain uniform and moderate grazing across the entire landscape (Holechek et al. 1998). These types of disturbances to ecosystem structure and function are often justified with evolutionary history and ecological theories, but with minimal consideration of spatial and temporal patterns. However, in recent decades, ecologists have recognized that spatial and temporal patterns are critical to the sustainability and maintenance of ecosystems. This has led to the suggestion that heterogeneity is actually the precursor to biological diversity and that it should be the

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basis for ecosystem management and conservation (Christensen 1997, Ostfeld et al. 1997, Wiens 1997, Fuhlendorf and Engle 2001). Recognition of the importance of ecosystem complexity and heterogeneity has presented a challenge to applied ecologists and resource managers because it suggests the need for an alternative paradigm for ecosystem management.

Rangelands have been described as inherently heterogeneous, where composition and vegetation structure vary with topo-edaphic features and species interactions at multiple spatial scales (Patten and Ellis 1995, Fuhlendorf and Smiens 1998, 1999). When disturbances such as fire and grazing are allowed to occur on grassland landscapes without intense agricultural management, spatial patterns become very important, multiple disturbances begin to interact, patch-level heterogeneity increases, and biological diversity is expected to increase (Hobbs et al. 1991, Vinton et al. 1993, Hartnett et al. 1996, Askins 2000, Fuhlendorf and Engle 2004). For example, the fire–grazing model predicts that bison (*Bison bison*) preferentially select high-quality vegetation regrowth within recently burned portions of the landscape (Coppedge and Shaw 1998). When only one part of the landscape is burned, intense grazing occurs on burned patches, while adjacent unburned patches receive less grazing pressure (Fuhlendorf and Engle 2001). Abundant fuel in unburned patches leads to a higher probability of future fires within these patches, while past fires and focal grazing in recently burned areas leads to a lower probability of reoccurring fire. Thus, fire alters grazing behavior, and grazing alters the extent and intensity of future fires, resulting in a shifting mosaic of patch types that differ in plant community composition and structure across the landscape (Steuter 1986, Hobbs et al. 1991, Hamilton 1996, Fuhlendorf and Engle 2004). Empirical evaluation of the heterogeneity paradigm has not been evaluated for grassland ecosystems, and management systems have not been developed to promote heterogeneity and provide habitat for co-existing species with variable habitat requirements (Fuhlendorf and Engle 2001).

In this study, we compared a traditional management model that promotes homogeneity to a heterogeneity-based model (i.e., fire–grazing model) where fire and grazing are allowed to interact to create a shifting mosaic (Fuhlendorf and Engle 2001). Our specific objectives were to test if (1) altering the temporal and spatial pattern of fire and grazing in a tallgrass prairie (heterogeneity management model) results in a shifting mosaic of vegetation compared with management in which fire and grazing are applied annually in a spatially uniform pattern (traditional management model) and (2) a shifting mosaic translates into increased heterogeneity at higher trophic levels, specifically in the grassland bird community. This paper does not focus on modeling the habitat of individual species, but focuses instead on testing the idea that heterogeneity should be the basis of conservation and ecosystem

management on rangelands. We considered increased heterogeneity or variability in the grassland bird community within a treatment to be an indicator of increased biodiversity. We predicted that the application of spatially variable fire and grazing in tallgrass prairie will increase spatial heterogeneity, thus allowing the coexistence of a suite of grassland bird species with more breadth in habitat structure requirements.

METHODS

Site description

Our study took place on the Tallgrass Prairie Preserve (TGPP) in north-central Oklahoma, USA (36°50' N, 96°25' W), owned and operated by The Nature Conservancy. The preserve lies within the southern portion of the Flint Hills region of the Great Plains and contains one of the last remaining extensive tallgrass prairies in North America. The climate is temperate, with hot summers (average high of 33.9°C for July 2001–2003) and cold winters (average low of –4.8°C for January 2001–2003). Growing-season (April–October) precipitation for the area was 341 mm, 661 mm, and 821 mm in 2001, 2002, and 2003, respectively. Long-term average (1971–2000) growing precipitation (April–October) for the area was 719 mm. Dominant grass species include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Nash), Indian grass (*Sorghastrum nutans* Nash), and switchgrass (*Panicum virgatum* L.).

Experimental design

We chose four pastures within the TGPP that varied from 400 ha to 900 ha. To examine patch-level heterogeneity, we divided each pasture into six approximately equal-sized patches. All pastures were fenced only on the exterior boundary with no fences dividing the patches, so the division was merely for organizational purposes. Two pastures were used for the heterogeneity-based treatment (patch treatment; $n = 2$). In each of these patch treatment pastures, one patch was burned in spring (March) and another patch in late summer or autumn (August–December; average patch size 100 ha) of each year (2001–2003) (Table 1). Therefore, each patch in the patch treatment was burned once (in either spring or autumn) every three years, and at any given point in time one-third of the pasture had been burned within the past year, one-third was burned one to two years prior, and one-third had not been burned for at least two years. Cattle were stocked in patch treatment pastures from mid-April through mid-July at a rate of 1.2 ha/270-kg steer. Cattle had free access to all patches within each pasture, so cattle could choose between burned and unburned patches in the patch treatment. Recently burned patches were preferentially grazed by cattle (see Fuhlendorf and Engle 2004), thus creating patches with focal disturbances within the patch treatment. Patches that had not been recently burned were less preferred by cattle, allowing

TABLE 1. Burn schedule for patch and traditional treatments at the Tallgrass Prairie Preserve, north-central Oklahoma, USA.

Treatment and year	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5	Patch 6
Patch						
2001	0–12	0–12	(>25)	(>25)	(>36)	(>36)
2002	13–24	13–24	0–12	0–12	(>36)	(>36)
2003	25–36	25–36	13–24	13–24	0–12	0–12
Traditional						
2001	burned	burned	burned	burned	burned	burned
2002	burned	burned	burned	burned	burned	burned
2003	burned	burned	burned	burned	burned	burned

Notes: Values in the patch treatment group indicate the number of months since the patch was burned. Traditional patches were burned every year. Parentheses indicate patches that were not yet burned within the context of the patch treatment.

vegetation to recover. This shifting of focal disturbance (fire and grazing) resulted in a mosaic of recently burned patches, recovering patches, and unburned patches that we lumped into categories according to months since focal disturbance in the patch treatment (Table 1). Unburned patches (>36 months) were those patches in the patch treatment that had not been burned yet during our study (Table 1).

Remaining pastures were assigned as the homogeneity-based treatment (traditional treatment; $n = 2$) and were designed to mimic agricultural management used over much of the region where our study was conducted (Robbins and Ortega-Huerta 2002). Management of these pastures consisted of annual spring burning (all patches burned in a single fire every year) and stocked with cattle from mid-April through mid-July at a rate of 1.2 ha/270-kg steer. Although we uniformly burned traditional pastures, we arbitrarily divided each unit into six patches designated as “all-burn patches” to compare the traditional treatment with the patch treatment at the patch level. As with the patch treatments, pastures in the traditional treatment also were fenced only on the exterior boundary with no fences dividing the patches. Because cattle preferentially grazed burned patches in the patch treatment, effective stocking density (number of cattle per grazed area) on burned patches in the patch treatment was roughly three times the stocking density in the traditional treatment in which cattle did not preferentially select any recently burned patch over another.

FIELD METHODS

Grassland birds

We estimated the abundance of breeding birds in each patch within replicate pastures using point count method during spring (15 May–1 July) from 2001 to 2003 (Ralph et al. 1993). Point counts resulted in indices of bird abundance that could be used to test for differences in the abundance of a given bird species among patch types and treatments. We established 100-m radius point count locations evenly spaced within each pasture to determine the abundance of birds by species (Ralph et al. 1993). All point count locations were 300 m apart and were located ≥ 150 m from fences

and roads. Each pasture ($n = 4$) contained six patches, and each patch contained four point count locations evenly spaced, or 24 point count locations/pasture. All point count locations were sampled four times from 15 May to 30 June. Observers recorded all bird species seen or heard within 100-m radius of each point count location for 10 min. Point count locations were mapped with a handheld GPS unit accurate to ± 5 m. Point count locations and order of point count locations between sessions were alternated between two observers to avoid bias. Counts were not conducted during periods of heavy rain or wind > 8 km/hour. Each point count was conducted between 0630 and 1030 hours Central Daylight Time (CDT). Most birds were identified by song, but binoculars (10 \times) were used to verify bird identification when necessary.

Vegetation

Vegetation composition and structure were measured in two sampling sessions, concurrent with bird point counts, once during the early growing season (15 May–5 June, 2001–2003) and about one month later, to monitor within-growing season changes in habitat structure that may have been related to bird abundance. At each point count location, we measured canopy cover of plant functional groups (tallgrass, shortgrass, grass-like, forb, shrub), cover of bare ground and litter as described by Fuhlendorf and Engle (2004), and vegetation structure (vegetation height, angle of obstruction; Harrell and Fuhlendorf 2002) to determine treatment effects. We sampled vegetation composition and structure in 0.10-m² quadrats centered on each point count location (5 quadrats placed 20 m apart on a line in four cardinal directions from the center of each point count; 20 plots/point) (Daubenmire 1959). Vegetation height (centimeters) and angle of obstruction (degrees), measurements of vegetation structure (Harrell and Fuhlendorf 2002), were recorded at the southeast corner of each quadrat.

Statistical analysis

Structure of the grassland bird community and vegetation functional groups at the patch level were subjected to indirect gradient analysis using Detrended

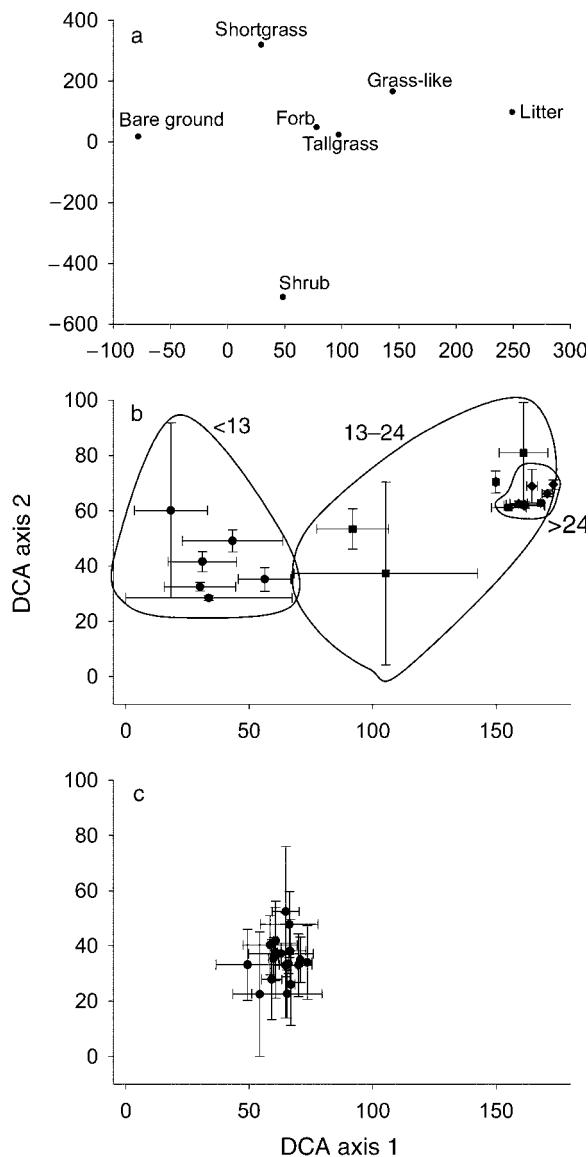


FIG. 1. Plots of the first two axes of the detrended correspondence analysis for vegetation data observed in the early growing season (15 May–5 June, 2001–2003) at the Tallgrass Prairie Preserve, north-central Oklahoma, USA. The plots represent (a) scores for functional groups, bare ground, and litter; (b) site (patch) scores for the patch treatment; and (c) site (patch) scores for the traditional treatment. Envelopes encompassing site scores indicate months since focal disturbance (<13, 13–24, >24). Year symbols (diamond, 2001; square, 2002; triangle, 2003) indicate the year of observation, not year of treatment.

Correspondence Analysis (DCA) with default options within PCORD software (Jongman et al. 1987, Fuhlen-dorf and Engle 2004). DCA has been used to summarize general similarities and differences among grassland bird communities and can elucidate compositional dynamics over time (Collins 2000). We averaged point counts within patches (four point count locations/patch) for bird abundance and vegetation data to evaluate the

effect of treatment at the patch level on vegetation and the grassland bird community. DCA arranges sites by compositional similarity, which reflects total environmental variation, so we used the range of DCA site scores and the standard deviation among patches within a pasture for tallgrass, forb, litter, bare ground, vegetation height, and angle of obstruction to assess patch-level heterogeneity. We determined the order of influence of vegetation functional group and grassland bird species in the DCAs by using species loading scores reported by PCORD. Loading scores estimate the relative influence of an individual variable on the DCA. Thus, higher species scores indicate species with greater influence on community structure. We used linear regression to examine relationships between the DCA of vegetation data and the DCA of bird data and to interpret environmental gradients represented by DCA axes.

We also used univariate analysis of variance (ANOVA) to test for significant differences in vegetation composition and structure and the abundance of grassland bird species within patches. Based on the results of the DCA, for the ANOVA we pooled the data across years into classes of months since focal disturbance (0–12, 13–24, 25–36, >36) for the patch treatment and pooled all data for the traditional treatment. We also analyzed heterogeneity within each pasture as the standard deviation of vegetation variables among patches within a single pasture. Only bird species within the grassland bird guild and those known to commonly use grasslands were included in our analyses of the bird community (Zimmerman 1993, 1997). We analyzed 10 grassland bird species that met the aforementioned criteria and were sufficiently abundant to provide statistically reliable results.

RESULTS

Vegetation response

Vegetation differed minimally between early and late sampling sessions; thus, all vegetation data reported are from the early growing season sampling period (15 May–5 June, 2001–2003). The first two axes of the DCA accounted for 53% of the variance in the data. DCA axis 1 and 2 had eigenvalues of 0.332 and 0.054, respectively. On DCA axis 1, the order of functional groups, based on the species loading scores, was litter, grass-like, tallgrass, and bare ground (Fig. 1a). For DCA axis 2, the order of influence of functional group variables based on the species loading scores was shrub, shortgrass, grass-like, and litter (Fig. 1a). DCA axis 1 site scores and time since focal disturbance were strongly correlated ($r = 0.90$). Low DCA site scores on axis 1 represent recently disturbed patches, and high DCA site scores on axis 1 represent patches that have >24 months since focal disturbance of fire and grazing. Thus, multivariate vegetation structure is influenced primarily by a gradient of time since focal disturbance.

TABLE 2. Heterogeneity of tallgrass, forb and litter cover, bare ground, height, and angle of obstruction (AOB) observed in the early growing season (15 May–5 June, 2001–2003) stratified by year and treatment (traditional and patch).

Year and treatment	Tallgrass cover	Forb cover	Litter cover	Bare ground	Height	AOB
2001						
Patch	12.7 (2.3)	5.7 (0.03)	43.1 (0.8)	13.6 (5.0)	10.3 (0.2)	11.9 (1.1)
Traditional	7.6 (3.7)	4.7 (0.6)	3.9 (2.3)	7.1 (2.0)	1.4 (0.6)	6.3 (0.5)
2002						
Patch	19.9 (0.6)	7.0 (1.5)	43.2 (1.3)	18.1 (0.2)	8.9 (0.2)	7.8 (0.3)
Traditional	5.5 (2.1)	3.8 (1.3)	0.4 (0.3)	3.2 (0.1)	1.6 (0.3)	1.3 (0.4)
2003						
Patch	19.3 (1.1)	5.9 (2.6)	38.9 (3.0)	21.3 (3.5)	9.5 (0.4)	9.4 (1.9)
Traditional	8.8 (1.4)	3.1 (0.7)	0.1 (0.1)	6.8 (2.1)	2.2 (0.2)	3.2 (1.2)

Notes: Heterogeneity is measured as the standard deviation among patches within a single management unit. Standard errors of heterogeneity are in parentheses.

The range of patch site scores along DCA axis 1 within a treatment was an indicator of spatial and temporal variability or heterogeneity, because it described the variability in composition among patches within a single treatment. The range of site scores across all patches and years for DCA axis 1 in the patch treatment was 18 to 173 (Fig. 1b). In contrast, the range of site scores across all patches and years for DCA axis 1 in the traditional treatment was 49 to 74 (Fig. 1c). Thus, variability was 5.5 times greater (based on ranges of DCA axes) in the patch treatment compared with the traditional treatment, indicating greater vegetation heterogeneity and habitat diversity in the patch treatment. Heterogeneity (as indexed by standard deviation among patches) of tallgrasses and bare ground in the patch treatment increased after the initial year of the study and maintained higher variability than the traditional treatment for the duration of the study (Table 2). Heterogeneity in litter among patches was as much as 40 times greater in the patch treatment than the traditional treatment throughout the study (Table 2). Changes in the traditional treatment consisted primarily of an increase in tallgrass cover and a decrease in forb and bare ground cover over the three years of the study (2001–2003), which can be attributed to a 2.4-fold increase in growing season precipitation. There was

minimal heterogeneity in any functional group within the traditional treatment.

Cover of functional groups indicated similar patterns as the DCA. Differences between treatment averages were minimal, with the exception of cover of litter and bare ground at the pasture scale (Table 3), but highly significant for some variables at the patch level. Analyses of variance indicated significant differences across patches for tallgrass ($P < 0.001$), shortgrass ($P = 0.009$), grass-like ($P = 0.019$), litter ($P < 0.001$), and bare ground ($P < 0.001$). Within the patch treatment, bare ground increased, and tallgrass and litter cover decreased in patches with recent focal disturbance (<13 months; Fig. 2). Patches with >13 months since focal disturbance increased in cover of tallgrasses and litter, and decreased in bare ground with increasing time since focal disturbance. Annual spring fire in the traditional treatment eliminated nearly all litter cover, whereas litter was eliminated only in patches with recent focal disturbance (<13 months) in the patch treatment. Litter accumulated rapidly as patches recovered from focal disturbance (>13 months) in the patch treatment (Fig. 2). Bare ground followed opposite patterns of litter. Several patches in the patch treatment that had a focal disturbance 13–36 months before sampling had similar functional group composition to patches that had not been burned in >36 months prior to the beginning of the

TABLE 3. Percent cover of tallgrass, forb, litter, and bare ground, height, and angle of obstruction (AOB) observed in the early growing season (15 May–5 June, 2001–2003) stratified by year and treatment.

Year and treatment	Tallgrass cover (%)	Forb cover (%)	Litter cover (%)	Bare ground (%)	Height (cm)	AOB (degrees)
2001						
Patch	57 (4)	27 (2)	59 (2)	13 (3)	21 (1)	79 (1)
Traditional	55 (1)	28 (2)	6 (1)	28 (2)	11 (1)	70 (1)
2002						
Patch	49 (3)	17 (1)	40 (5)	17 (3)	20 (2)	83 (1)
Traditional	66 (9)	16 (1)	18 (2)	18 (2)	17 (2)	86 (2)
2003						
Patch	61 (7)	13 (4)	52 (6)	14 (6)	24 (4)	83 (3)
Traditional	68 (1)	10 (1)	0 (0)	15 (2)	16 (1)	85 (1)

Note: Standard errors are in parentheses.

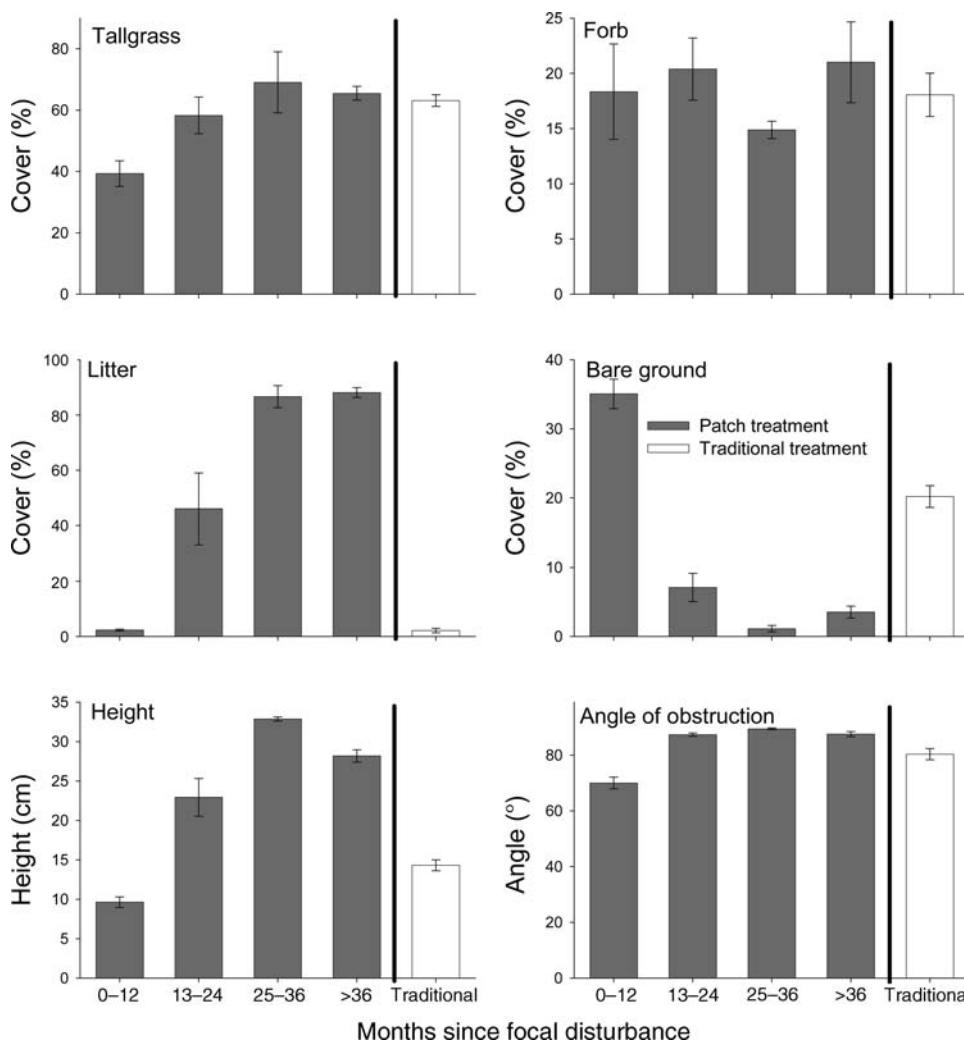


FIG. 2. Percent cover of dominant plant functional groups (tallgrasses and forbs), litter, and bare ground and habitat structure measures observed in the early growing season (15 May–5 June, 2001–2003) in the patch (grouped by months since focal disturbance) and traditional treatments. Error bars indicate standard errors across patch-by-year combinations.

study, indicating a recovery of vegetation to pretreatment levels (Figs. 1b and 2).

Vegetation height and angle of obstruction (AOB) varied among years and between treatments (Table 3). Vegetation height was greater in the patch treatment than the traditional treatment in 2001 and 2003 (Table 3). AOB did not differ between patch and traditional treatments in 2002 and 2003 (Table 3). Analysis of variance indicated that both of these structural parameters were significantly different among patches ($P < 0.001$). In the patch treatment, height increased with increasing time since focal disturbance (Fig. 2). AOB was lower in recently burned patches within the patch treatment than in the recovering patches within the patch treatment or traditional treatment (Fig. 2). Heterogeneity in height was five times greater in the patch treatment than the traditional treatment throughout the study (Table 2). Heterogeneity in AOB was two

to four times greater in the patch treatment than the traditional treatment throughout the study (Table 2).

Grassland birds

The first two axes of the DCA accounted for 35% of the variance in the grassland bird data. DCA axis 1 and 2 had eigenvalues of 0.149 and 0.034, respectively. On DCA axis 1, the order of influence of bird species, based on the species loading scores, were Henslow’s Sparrow, Mourning Dove (*Zenaida macroura*), Upland Sandpiper, and Dickcissel (Fig. 3a). For DCA axis 2, the order of influence of bird species based on the species loading scores were Lark Sparrow, Red-winged Blackbird (*Agelaius phoeniceus*), Common Nighthawk (*Chordeiles minor*), and Mourning Dove (Fig. 3a). Correlation between DCA axis 1 site scores and time since focal disturbance was $r = 0.90$; thus, DCA axis 1 represents a gradient of grassland bird species responding to

increasing time since focal disturbance, similar to the vegetation data. The range of patch site scores in DCA axis 1 was an indicator of spatial and temporal variability or heterogeneity in the grassland bird community. The range of site scores across all patches and years for DCA axis 1 in the patch treatment was 0–131 (range of 131; Fig. 3b). The range of site scores across all patches and years for DCA axis 1 in the traditional treatment was 40 to 73 (range of 33; Fig. 3c). Thus, variability in the avian community was four times greater in the patch treatment compared with the traditional treatment, indicating greater heterogeneity in the patch treatment, which was primarily due to variable time since focal disturbance (Fig. 3b). The range of DCA axis 1 scores in the traditional treatment was limited to the intermediate portion of the range occupied by the patch treatment, indicating that the patch treatment had greater variability in the bird community than the traditional treatment.

Analysis of variances indicated differences among patches depending on months since focal disturbance in the patch treatment and the traditional treatment. Significant differences occurred for Dickcissels ($P = 0.005$), Eastern Meadowlark ($P = 0.0005$), Grasshopper Sparrow ($P = 0.019$), Upland Sandpiper ($P < 0.0001$), Killdeer (*Charadrius vociferous*; $P = 0.0002$), and Henslow's Sparrow ($P < 0.0001$). Abundance of Upland Sandpiper, and Killdeer increased in patches with recent focal disturbances (<13 months) in the patch treatment, and those patches had higher abundance of these species than the traditional treatment (Figs. 3b and 4). Abundance of Upland Sandpipers was five times greater in patches with recent focal disturbance (<13 months) compared with the other patches in the patch treatment, and 2.5 times greater in patches with recent focal disturbance (<13 months) in the patch treatment than the traditional treatment (Fig. 4). Lark Sparrows were not encountered in patches with 25–36 months of recovery or patches with >36 months since disturbance in the patch treatment (Fig. 4). Patches in the patch treatment shifted toward the right with increasing time since focal disturbance (i.e., recovery), regardless of year (Fig. 3b). That shift indicated an increasing abundance of Henslow's Sparrow and Dickcissel with increasing time since focal disturbance (Figs. 3b and 4). Abundance of Dickcissels was slightly lower in the traditional treatment than in patches with >36 months since disturbance within the patch treatment (Fig. 4). Henslow's Sparrows were not encountered in patches with recent focal disturbance (<13 months) in the patch treatment or in the traditional treatment (Fig. 4). Eastern Meadowlark reached peak abundance in patches in the intermediate recovering stages (13–36 months) in the patch treatment and reached the lowest abundance in patches with recent focal disturbance (<13 months) in the patch treatment (Fig. 4).

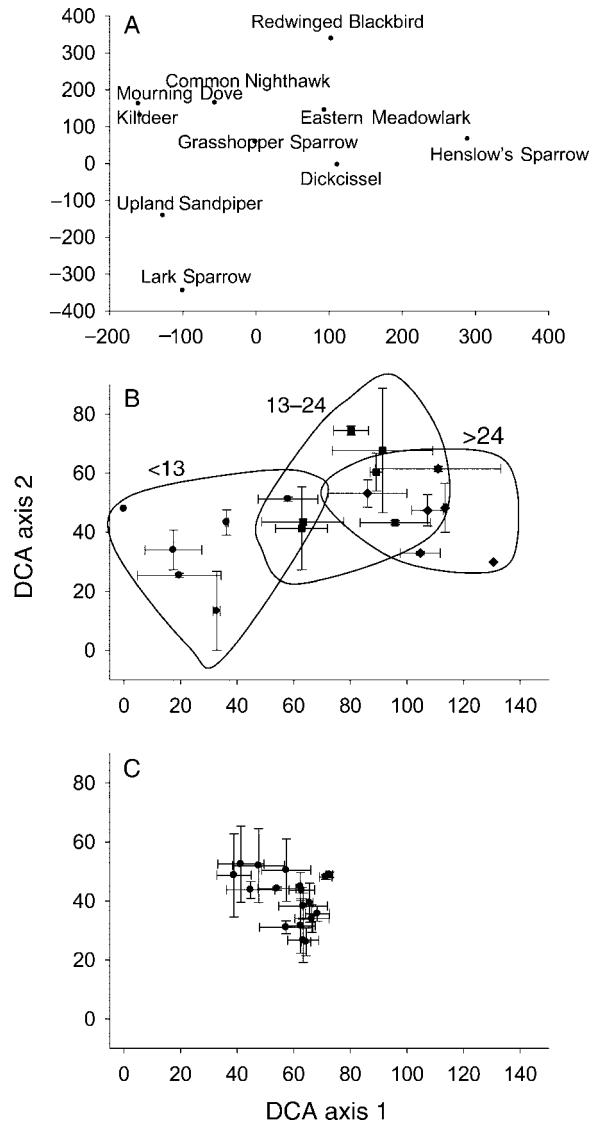


FIG. 3. Plots of the first two axes of the detrended correspondence analysis for the grassland bird abundance data. The plots represent (a) species scores for functional group and bare ground and litter; (b) site (patch) scores for the patch treatment; and (c) site (patch) scores for the traditional treatment. Envelopes encompassing site scores indicate months since focal disturbance (<13, 13–24, >24). Year symbols (diamond, 2001; square, 2002; and triangle, 2003) indicate the year of observation, not year of treatment.

Compared with the traditional treatment, the bird community in the patch treatment was more variable in space, and the Henslow's Sparrow was abundant in the patch treatment, but not encountered in the traditional treatment (Figs. 3 and 4). Several grassland bird species that occurred in peak abundance in patches with recent focal disturbance (<13 months) in the patch treatment, such as Upland Sandpiper and Killdeer, also increased heterogeneity of the bird community in the patch treatment compared with the traditional treatment.

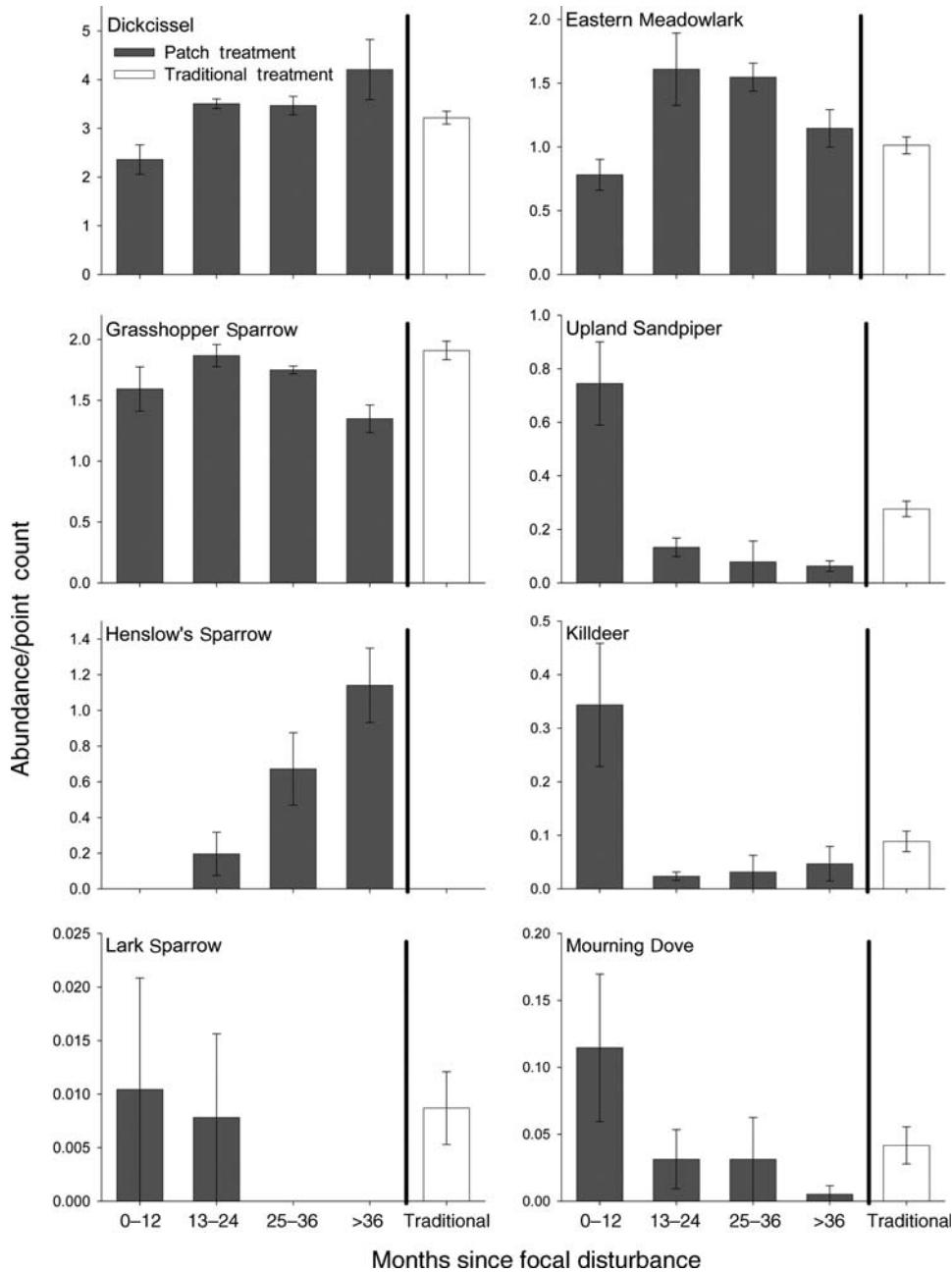


FIG. 4. Abundance of dominant birds observed in tallgrass prairie from 2001 to 2003 in the patches (grouped by months since focal disturbance) and traditional treatments. Error bars indicate standard errors across patch-by-year combinations.

Relationships between vegetation and the grassland bird community

The range of DCA axis 1 site scores was greater in the patch treatment than the traditional treatment in the vegetation and bird analyses, indicating that increased vegetation heterogeneity in the patch treatment led to increased heterogeneity of the grassland bird community. Variability in vegetation and grassland bird community on DCA axes 1 of the patch treatment was primarily driven by time since focal disturbance (Figs.

1b and 3b). DCA site scores from the vegetation analysis were strongly correlated with the DCA site scores from the grassland bird community analysis, indicating that changes in cover of vegetation functional groups associated with time since focal disturbance were correlated with changes in the grassland bird community. On axis 1 of the vegetation DCA, litter was the most important functional group variable, increasing from near 0% cover in patches with recent focal disturbance (<13 months) in the patch treatment and in the

traditional treatment to near 100% cover in patches with >24 months of recovery in the patch treatment (Figs. 1 and 2). Increases in litter cover over time in the patch treatment were highly correlated with changes in the grassland bird community. For example, Henslow's Sparrow was not present in patches with recent focal disturbance (<13 months) in the patch treatment or traditional treatment where litter cover was low (Fig. 2).

DISCUSSION

Patch-level spatial heterogeneity in tallgrass prairie can be increased by applying fire to discrete patches in the landscape and allowing grazing animals to select among burned and unburned patches. This type of ecosystem management is an attempt to more closely mimic the fire-grazing interaction that was important in the North American Great Plains before European settlement (Fuhlendorf and Engle 2001, 2004). Domestic and native grazing animals preferentially select most recently burned patches, increasing the amount of bare ground and the abundance of disturbance-dependent forbs. Meanwhile, unburned patches or patches that have not been burned in several years are avoided by grazing animals and accumulate litter and increase in tallgrass dominance. This spatial heterogeneity of vegetation structure provides greater breadth of habitat and increases the variety of grassland bird communities that can occur across the landscape over traditional approaches to management and conservation. The role of heterogeneity has been acknowledged in the maintenance of productivity and biodiversity in numerous ecosystems (Collins 1992, Adler et al. 2001, Fuhlendorf and Engle 2001, Benton et al. 2003), and our study supports the importance of heterogeneity for conservation of grassland ecosystems.

Fire and grazing have been identified as essential ecological processes in the maintenance of grassland ecosystems, but they have traditionally been viewed as separate disturbances (Collins 2000, Fuhlendorf and Engle 2001, Harrison et al. 2003). For conservation, our study indicates that spatial and temporal patterns associated with the interaction of fire and grazing may be more important than their individual effects when uniformly applied. Most studies that include grazing and fire are typically conducted on treatment units where these disturbances are uniformly applied across the entire experimental unit and they are not allowed to interact in a spatially variable landscape. Traditional management of grasslands is largely based on these studies and following the model of intermediate disturbance with the objective of moderate, uniform disturbance resulting in homogenous vegetation structure (termed "management toward the middle"; Fuhlendorf and Engle 2001, 2004). Species composition and diversity of native flora and fauna are expected to be most responsive to disturbance regimes that closely mimic evolutionary regimes (Hobbs and Hueneke 1992, Fuhlendorf and Engle 2001). Grasslands, with a

long history of fire and grazing, evolved under the interactive influence of fire and grazing where probabilities of fire and grazing are interlocked through a series of positive and negative feedbacks (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001). Our data suggest that bird communities in the tallgrass prairie region of North America respond to this fire-grazing interaction.

Grassland bird response to our treatments mirrored that of vegetation response, with four times greater avian heterogeneity (as measured by variation in DCA axis 1) in the patch treatment than the traditional treatment. Similarities in analyses of grassland birds and vegetation demonstrate a strong association across these trophic levels. Litter was the most heterogeneous vegetation variable in the patch treatment and correlated strongly with variability in the grassland bird community (DCA site scores). Henslow's Sparrows were absent in the traditional treatment and patches in the patch treatment with recent focal disturbance, due to lack of litter accumulation, but a codominant in patches that had not been burned in two years. Upland Sandpiper and Killdeer were more abundant in patches at the other end of the disturbance gradient, where litter was minimal and bare ground was high in the patch treatment. So, the patch treatment included species that require vegetation structure associated with undisturbed habitats and species that require vegetation structure associated with heavily disturbed habitats occurring within the same pasture. These species were either absent or less abundant under traditionally managed grasslands.

Application of the intermediate disturbance hypothesis to grasslands (described by Collins et al. 1995), as well as traditional conservation of grassland ecosystems, usually focuses management toward a single ecological state that is based on variable values and land management objectives (Holechek et al. 2003, Fuhlendorf and Engle 2001). Rarely are concepts of spatial and temporal heterogeneity incorporated into applications of ecological theory. For example, conservation and management of grasslands for agricultural production focus on minimizing heavy disturbances and minimizing the amount of land that is not disturbed. This is best illustrated by the fact that of the four principles of rangeland management, one is to maintain proper distribution. "Proper" is almost always considered uniform (Fuls 1992, Bailey et al. 1998, Holechek et al. 2003, Bailey 2005, Vavra 2005), and these data suggest that this management model is incapable of maintaining grassland bird diversity. As an alternative, we could focus on a preservationist approach to ecosystem conservation. From this perspective, some would suggest removal or protection from disturbance within the protected area. This can be effective in certain landscape contexts or on small refuges, but in general, it lowers the heterogeneity on large grassland landscapes. We suggest that, in historical grasslands,

there was a high degree of heterogeneity where most of the landscape was either heavily disturbed or undisturbed by the fire–grazing interaction (as well as other factors such as prairie dogs, *Cynomys* spp.). The positive feedback, where grazing animals select recently burned areas and the negative feedback that reduces the probability of fire on recently grazed areas assured that moderate, uniform disturbances were not evident in grassland ecosystems.

MANAGEMENT IMPLICATIONS

Shifts in abundance of dominant species, decreased spatial heterogeneity, and lowered species richness have been associated with uniform applications of disturbance in tallgrass prairie ecosystems (Collins et al. 1995, Collins 2000, Fuhlendorf and Engle 2001). For example, management for cattle production on private lands surrounding our study area uses annual, dormant-season fires combined with a short, intensive grazing period in an attempt to maximize livestock production while minimizing long-term site degradation (our traditional treatment) (Launchbaugh and Owensby 1978). This management model has been used in this region for >20 years, and declines in native biota such as Prairie Grouse have been associated with the practice (Applegate et al. 2002, Robbins and Ortega-Huerta 2002). Other studies in tallgrass prairie have noted a loss of characteristic prairie forbs under annual spring fire regimes (Kucera and Koelling 1964, Collins 1987). Studies from other continents also have noted incidents of declines in biodiversity associated with annual uniform fire regimes in grasslands (Jansen et al. 1999, Peet et al. 1999). It is clear that uniformly applied annual fires and associated grazing practices that promote uniformity are not conducive to the maintenance of biodiversity within grassland ecosystems.

It is critical that we understand fire and grazing in the context of their spatially controlled interactions rather than the traditional focus on grazing vs. no grazing and fire vs. no fire. We argue that because of the long evolutionary history of fire and grazing in grassland ecosystems of the North American Great Plains, conservation research should focus on the interaction of fire and grazing and the resulting shifting mosaic in the landscape that results from such interaction. While our replicated approach increased habitat heterogeneity, we recognize that it is much less complex in spatial and temporal pattern than pre-European disturbance patterns. However, it does indicate that heterogeneity is critical to biodiversity in grassland ecosystems and the fire–grazing interaction produces a shifting mosaic landscape.

Previous analysis of vegetation and livestock performance (Fuhlendorf and Engle 2004) found that a similar increase in heterogeneity of plant functional-group composition and structure from a fire grazing interaction, but resulted in no difference in livestock production compared to traditional uniform management. Our work reinforces their conclusions related to

the importance of heterogeneity to conservation by demonstrating that this type of management not only increases vegetation heterogeneity and maintains livestock production, but also increases grassland bird community heterogeneity. Collectively, these studies suggest that a heterogeneous approach to grassland conservation is capable of maintaining biodiversity and agricultural productivity simultaneously and serves as a model for an alternative paradigm in rangeland management and conservation.

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