Effects of Grassland Management on Breeding Birds at the Western Edge of the Tallgrass Prairie Ecosystem in Kansas

Authors: Powell, Alexis F.L.A., and Busby, William H.

•

Effects of Grassland Management on Breeding Birds at the Western Edge of the Tallgrass Prairie Ecosystem in Kansas

Alexis F.L.A. Powell[1,2,3]

[1]Kansas Biological Survey
2101 Constant Ave
University of Kansas
Lawrence, KS 66047, USA

William H. Busby[1]

•

[2] Corresponding author:
alveypowell@yahoo.com; (651) 308-0555

[3] Current address:
Department of Ecology, Evolution and Behavior; 100 Ecology Building, 1987 Upper Buford Circle, University of Minnesota, St. Paul MN 55108, USA

ABSTRACT: We studied responses of breeding birds to alternative regimes for managing tallgrass prairie at the Smoky Hill Air National Guard Range in central Kansas. Species richness, diversity, and evenness did not differ among treatments, but overall abundance was highest in unburned idle (i.e., not grazed or hayed) transects, and was lowest in idle transects burned that spring. However, no treatment was either superior or inferior to all others for attracting the highest numbers of every species. Dickcissels (*Spiza americana*) and Henslow's sparrows (*Ammodramus henslowii*) were most numerous in unburned idle units, grasshopper sparrows (*A. savannarum*) were most abundant in grazed units and hayed units, upland sandpipers (*Bartramia longicauda*) were most often found in burned units, whereas eastern meadowlarks (*Sturnella magna*) were less abundant in burned units than in all other treatments. We conclude that the recent switch to burning idle units every 3–4 years, rather than annually, has benefitted most grassland bird species. The variety of management regimes implemented at Smoky Hill Air National Guard Range fosters heterogeneity of vegetative structure across the landscape, and thereby allows the site to provide for differing needs of various species, thus enhancing its value for grassland bird conservation.

Index terms: grassland birds, grazing, haying, prescribed burning, rangeland, tallgrass prairie

INTRODUCTION

Declines of grassland bird populations have been more precipitous and widespread than seen in any other natural habitat-associated avian assemblage in North America (Samson et al. 1999). Grassland birds suffered tremendous habitat loss during the 19th and early 20th centuries when > 95% of tallgrass prairie was converted to row crops and non-native pasture, and they continue to lose ground due to ongoing destruction of grassland, intensification of land use, and successional transformation of native grasslands, often through underuse or overuse of prescribed fire (Askins et al. 2007; With et al. 2008). Since the inception of the North American Breeding Bird Survey in 1966, most grassland birds have declined, and in many cases these declines have occurred nearly range-wide (Sauer et al. 2011). Optimally managing remaining grasslands for the conservation of grassland birds will depend upon better understanding of the merits of management alternatives for providing, over both short and long terms, the habitats that they require. Fire and grazing played key roles in shaping the tallgrass prairie ecosystem, and great variability in their spatiotemporal distribution and intensity generated a dynamic shifting mosaic of diverse interconnected grassland habitats at multiple scales (Anderson 1990; Steinauer and Collins 1996; Knapp et al. 1999; Fuhlendorf and Engle 2001). Currently, the condition of native prairies depends upon the particulars of human-made decisions about how these forces are applied, often with little variability, to isolated remnants in a greatly altered landscape.

Smoky Hill Air National Guard Range (SHANGR), Saline County, Kansas, is one of the largest publicly-owned remnants of tallgrass prairie in North America. Located in the transition between tall and mixed-grass prairie biomes, the 13,708-ha property is mostly native grassland of the Dakota Hills Tallgrass type (Kindscher and Loring 2007). The large size (~259 ha) of management units at SHANGR, together with the constancy with which each has been treated over the past several decades, makes the property an excellent de facto experimental landscape. Each of the grassland management regimes historically implemented there - haying, frequent burning, and grazing in combination with infrequent burning - has been successful at preserving unplowed prairie and facilitating reversion of land cultivated prior to military acquisition in 1942, but significant differences in plant species composition, richness, and abundance exist among units according to their management. For example, hayed units have significantly higher species richness and abundances of disturbance-sensitive species and lower abundances of weedy and nonnative species than do grazed units (Kindscher and Loring 2007). Some differences in vegetation among treatments, such as amount of forb cover (highest in hayed units) or bare ground (highest in recently burned units), might be expected to directly influence their use by birds.

Our primary goal was to investigate whether breeding season densities of

grassland-obligate birds differ among units at SHANGR according to their land management. Besides comparing grazed, hayed, and idle (i.e., not grazed, hayed, or similarly disturbed or exploited) treatments, we wanted to investigate whether birds might have been affected by a policy (intended to reduce soil erosion) in recent years to reduce burn frequency of idle areas at SHANGR from annually to every 3–4 years. We aimed to explain patterns of bird abundance among treatments based on the correspondence between the birds' known habitat preferences and treatment effects on vegetative structure, and, therefore, we measured aspects of the latter. As background to our study and to inform its design, we did general avifaunal surveys at SHANGR to describe species richness, and we conducted spring roadside counts of birds to identify the most prominent breeding species and establish benchmarks for population monitoring in the future. Our study was implemented to inform management of SHANGR and other prairies near the western limit of the tallgrass ecosystem for the conservation of grassland birds.

METHODS

Our study area, SHANGR (Figure 1), lies at the western edge of the tallgrass prairie ecosystem and consists mainly of unplowed (10,121 ha) and go-back (i.e., reverted, formerly cultivated; 2429 ha) native grassland, the key contributors of vegetative cover being little bluestem (*Schizachyrium scoparium*, 38%), big bluestem (*Andropogon gerardii*, 24%) and rough dropseed (*Sporobolus asper*, 14%; Kindscher and Loring 2007). Military use of the property consists mainly of bombing and aerial gunnery practice from overflying aircraft, so physical disturbance is limited to localized areas around targets and there are few buildings, vehicles, and personnel at the site. Though closed to the general public, the outlying portions of SHANGR are leased to local ranchers and, like most other native prairie in the region, used for agriculture, primarily cattle (*Bos taurus*) grazing.

Though contiguous in extent, SHANGR is divided for administrative purposes into "fire grid" units (Figure 1), which generally
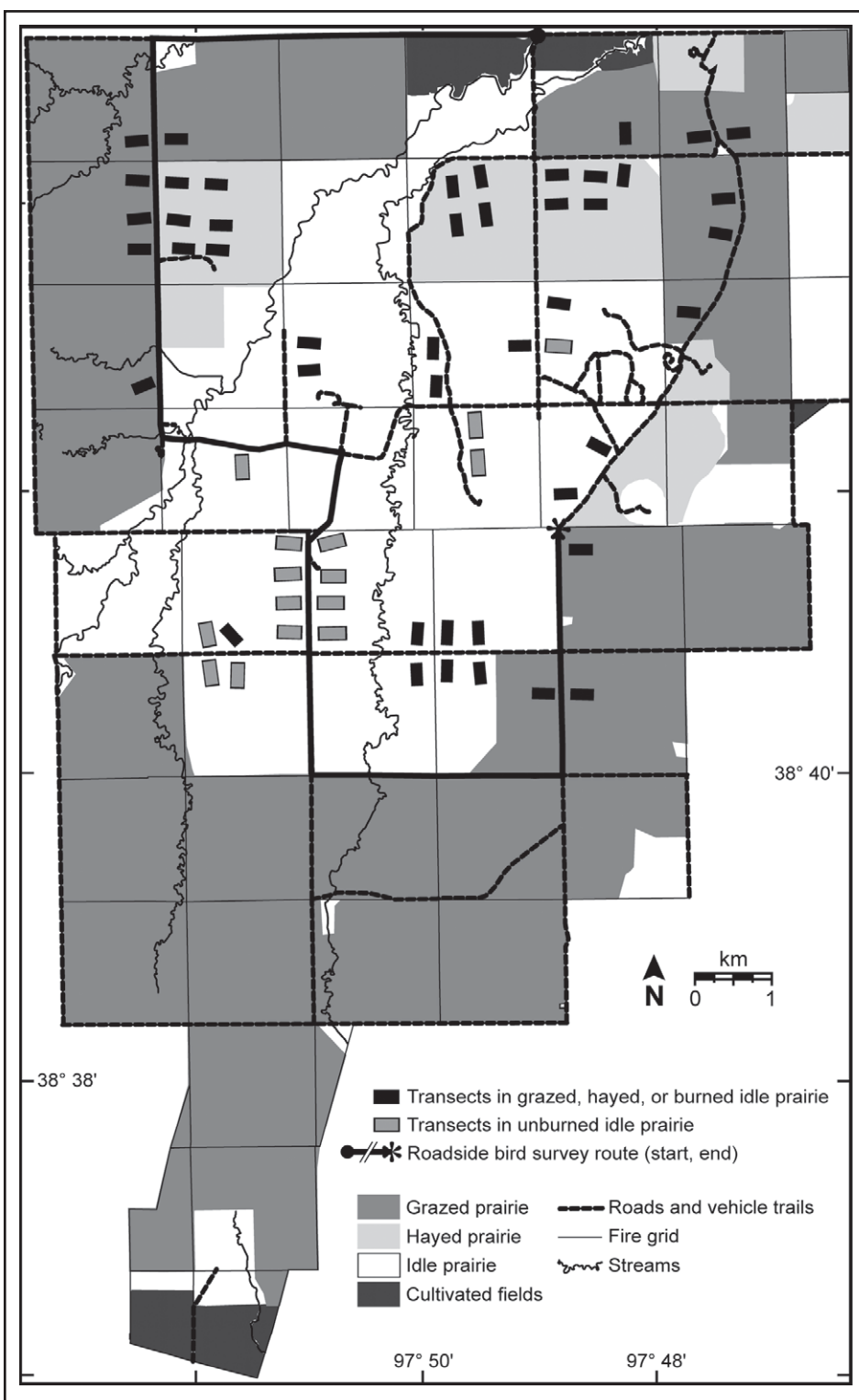
Figure 1. Smoky Hill Air National Guard Range, Saline County, Kansas, showing bird survey locations and land uses. The full extent of the northeastern part of the property, which is used by the Kansas Army National Guard, is not shown.

define the boundaries between unleased management areas and mostly coincide with the boundaries between leased parcels. Most fire grid units (51 of 59 total, and all the units we worked in) are ~259 ha in size and used in one of three ways: for (1) cattle grazing, (2) hay production, or (3) idle parts, managed with fire alone, of a

centrally-located 4091-ha "impact area," in which targets are placed for bombing practice. Grazed areas (6797 ha) are stocked with cattle 1 May – 31 October at a rate of 160 kg per ha, that being a moderate grazing intensity for the region. Some units are double-stocked (Smith and Owensby 1978), in which case grazing occurs 1 May – 30 July. Grazed units are managed with prescribed fire in April or early May every 3 – 8 years, but only those units not burned for the past year or more were used in our study. Hayed areas (1166 ha) are cut once annually in July. Prior to 1996, all idle units in the impact area (3314 ha) were burned annually to reduce the frequency and severity of wildfires resulting from military training activities, but current policy is to burn most of them approximately every 3 – 4 years. Fires are especially frequent in the impact area because wildfires can occur there at any time of year, and some portions are still burned annually due to wildfires or their risk. Prescribed burning is curtailed during droughts.

To gain knowledge of the general composition of its avifauna, we conducted opportunistic surveys by car and foot in all seasons at SHANGR in 2003 – 2006. In those same years, to establish quantitative benchmarks (detection rates by species) for ongoing and future population monitoring, we conducted roadside bird surveys during two mornings each spring, in the periods 27 May – 8 June and 19 – 23 June. Each survey began 30 minutes before sunrise, and consisted of a series of 3-minute point counts of all individuals that were seen or heard, conducted at 805-m intervals along a fixed ~24.1-km route (Figure 1) designed to sample all major habitats.

To study effects of management on breeding bird abundances within grassland units, we established a set of 15 transects in each grassland treatment type (Figure 1), including two sets in the impact area, to allow comparison of idle areas that had burned following the previous growing season to those that had not. Transects in grazed, hayed, burned idle, and unburned idle treatments were located, respectively, within 11, 3, 7, and 6 different fire grid units. Issues of availability and access prevented locating transects randomly or

placing each transect in a separate unit, but the large size of units allowed transects within them to be placed distantly from one another and to vary in topographical and vegetative character as much as transects located within different units. Each of the 60 straight-line transects was 300 m long, marked every 50 m with survey flags or metal stakes, oriented perpendicular to and ≥ 100 m from the nearest vehicle trail, and was placed ≥ 250 m from any unit of a different treatment type parallel to the transect, ≥ 200 m from the nearest parallel transect, and ≥ 200 m from the nearest in-line transect. Each transect was surveyed once 23 May – 4 June (by the authors) and again 12 – 18 June (nearly always by a different observer than the first time, either by the authors or G. Pittman, Kansas Biological Survey) in 2005, a year with average precipitation (754 mm). Surveys took place between 0500 and 1100 CST, with winds ≤ 19 kph, temperatures of 8 – 30 °C, and during periods without significant precipitation. With only one or two exceptions, transects in impact area units were undisturbed during our study by dummy bombs or the heavy machinery used to recover them.

Surveys took ~20 min per transect, and were conducted by walking transects and counting birds seen ahead or to each side of the observer. We counted perched singing males in the cases of dickcissels (*Spiza americana*), grasshopper sparrows (*Ammodramus savannarum*), and Henslow's sparrows (*A. henslowii*). We separately counted perched singing and nonsinging eastern meadowlarks (*Sturnella magna*) and male and female brown-headed cowbirds (*Molothrus ater*). For the aforementioned species, we counted each individual seen ≤ 250 m from the transect, measured its distance from the observer with a laser rangefinder, and measured the angle between the sight line and transect direction with a sighting compass. We counted all upland sandpipers (*Bartramia longicauda*), including those scolding us in flight, seen ≤ 200 m from the transect. For species not described above, we simply counted perched individuals seen ≤ 80 m from the transect.

To compare the avian assemblages of each

treatment type, we calculated the number of species (S), total number of detections across species, Shannon's diversity index [$H'=-\sum p_i \ln(p_i)$, where p_i is the relative frequency of species i], and Shannon's index of evenness [$E = H' / \ln(S)$] for each transect. To compare abundances among treatments for each of the 10 most frequently encountered species, we calculated encounter rates (individuals per 1000 m of transect) for each transect by multiplying the average count across visits by 1000 m divided by the transect length. Using mean values for each transect, and treating transects as independent samples, we evaluated the effects of treatment on encounter rates with analysis of variance (ANOVA) in MINITAB, release 12.1 (Minitab, State College, Pennsylvania), and used the Tukey test to make pairwise post-hoc comparisons of multilevel factors. Prior to analysis, encounter rates were log-transformed [log(1 + individuals per 1000 m)] to improve homogeneity of variances, except with dickcissels and grasshopper sparrows, for which such transformation was counterproductive and thus the raw rates used. When residuals from ANOVA deviated from normality, we used the Kruskall-Wallis test to check for significant differences among treatments; those findings were equivalent to the ANOVA results in all cases so, for simplicity of presentation, are not reported.

We used DISTANCE, version 5.0, beta release 4 (Thomas et al. 2010), to estimate densities of species that we surveyed using distance sampling protocols. Program DISTANCE fits a model detection function to the frequency distribution of distances of individuals from the transect; then, by accounting for the proportion of individuals present but not detected, it estimates the density of individuals in the surveyed area. We followed guidelines detailed by Buckland et al. (2001) to iteratively determine data truncation distances, assess the need to bin data into intervals, and develop models. For each species, we created global models as well as models stratified by treatment, observer, survey round, and treatment × survey round, using all key functions available in DISTANCE combined with adjustment terms recommended for each. We used diagnostic tools in DISTANCE

to assess models - Akaike's Information Criterion (AIC) to select the most parsimonious models and the Kolmogorav-Smirnov test to check model fit to the data. We sometimes found that slightly different approaches yielded models with equally good fits to the data, similar AIC scores ($\leq$ 2 points difference were considered equal), and nearly identical density estimates, in which cases we selected the simplest model with the lowest AIC score. To evaluate whether pairwise comparisons between the density estimates by treatment were significantly different, we used Welch's approximate t-test for samples with unequal variances, and employed the Dunn-Šidák correction [$\alpha' = 1 - (1 - \alpha)^{1/k} = 1 - (1 - 0.05)^{1/6} = 0.009$] to adjust our threshold of significance for multiple comparisons (Sokal and Rohlf 1995).

We surveyed the vegetative structure of transects during 16 – 26 June 2005. A meter stick was used to measure maximum heights of grass, forb, thatch (standing dead vegetation), and litter (matted dead vegetation) within a one meter radius of 10 – 20 locations at evenly spaced intervals along and random distances $\leq$ 80 m from each transect. At 5 – 20 randomly chosen locations in each transect, we stood a 4-mm diameter metal rod on end and counted the number of grass, forb, and litter plus thatch contacts in the intervals < 10, 10 – 20, 20 – 30, and 30+ cm from the ground. Litter contacts were difficult to interpret meaningfully when matted or degraded, so we counted no higher than 10 contacts in an interval (i.e., all counts over 10 were recorded as 10). A preliminary review of the means of each measure for each transect revealed that many were highly correlated, so the contact data were simplified for subsequent analyses to two intervals, < 20 and > 20 cm, for each vegetation type. Differences in vegetation parameters according to management type were analyzed in the same fashion as the encounter rates of birds, using mean values for each transect and treating transects as independent samples.

RESULTS

Altogether, during general surveys of birds at SHANGR, we encountered 150 of 164 species known from the site, 71 of which were detected in roadside surveys, and we documented 41 species as confirmed, 33 as probable, and 7 as possible breeders (for details, see Busby and Schmidt 2007). Rare habitats contributed disproportionately to species richness. Even though only ~2% of SHANGR is forested and < 1% is covered by ponds, woody vegetation-dependent birds made up 43% of the total species count and 58% of species in roadside surveys, whereas water-associated species likewise accounted for 28% and 7% of species. To compare, grassland specialists contributed only 21% and 25% of species recorded overall and on roadside surveys, respectively. On the other hand, of the five most numerous species ($\bar{x}$ number individuals per roadside survey), only the mourning dove (67.8, *Zenaida macroura*) was not a grassland obligate. The other four species - the dickcissel (71.5), eastern meadowlark (68.3), upland sandpiper (47.4), and the grasshopper sparrow (31.3) - comprised > 40% of all individuals counted.

During transect surveys, we recorded 1871 detections of 36 bird species (both survey rounds combined), of which 82% of detections and 39% of species were grassland specialists (but note that transect widths were not the same for all species). Eastern meadowlarks, dickcissels, and grasshopper sparrows were present in all, or nearly all, transects (they, plus upland sandpipers, accounted for 69% of all detections), accompanied by less regular to unique appearances by other grassland obligates, facultative inhabitants of grasslands, and species requiring more woody vegetation than generally present in our transects. Species richness was not significantly different among treatments, nor were indices of species diversity and species evenness (Table 1). However, bird abundance (across species) differed significantly by treatment overall (Table 1), largely due to the lower numbers of birds in burned as compared to unburned idle transects (Tukey value = -3.21, $P = 0.01$).

Encounter rates of the 10 most frequently detected species, five of which were grassland obligates, generally differed among treatments, and patterns of response differed among species (Table 2). For example, three grass-dependent species – the dickcissel, Henslow's sparrow, and the eastern meadowlark – had markedly lower abundances in burned as compared to unburned idle transects, whereas upland sandpipers were most abundant in burned idle transects. In contrast, none of the five most numerous facultative inhabitants of grassland differed significantly between burned and unburned idle transects. Mourning doves were most numerous in idle transects, Bell's vireos (*Vireo bellii*) more abundant in hayed and unburned idle transects, and brown-headed cowbirds were least abundant in hayed transects. Abundances of eastern kingbirds (*Tyrannus tyrannus*) and red-winged blackbirds (*Agelaius phoeniceus*) did not differ significantly among treatments; we observed that these species occurred within habitat features (isolated trees for the former, ponds and swales for the latter) that we did not formally measure and which were randomly distributed among treatments.

We had sufficient data to robustly model detection functions and estimate densities of dickcissels, grasshopper sparrows, and eastern meadowlarks according to treatment type with program DISTANCE. For the dickcissel data, histograms of the ungrouped detections, truncated to 150 m, revealed nearly ideal characteristics for simple and reliable density estimation: a "broad shoulder" near the transect line, very little heaping, and a similar distributional shape regardless of stratification scheme. Consequently, a simple global model (uniform key function with cosine adjustments of order 1) fit the data very well and had the best AIC score. In the case of the eastern meadowlark data, counts of singing males were considerably lower in the second round of surveys, whereas counts of all adults (singing or not) were very similar between rounds, so we used the latter for density estimation and other analyses. The distributional shape of the ungrouped data, truncated to 200 m, was excellent; but we found significant improvement in model fit (according to AIC scores) when differences in detection probability among observers were incorporated. After trying a number of approaches, all of which produced nearly identical density estimates,

Table 1. Diversity and abundance metrics ($\bar{x}$ ± SE per transect, $n = 15$, two rounds of surveys combined) by treatment of the bird species assemblages present along transects at Smoky Hill Air National Guard Range in May–June 2005, and ANOVA tests for significant differences.

	Management treatment type				$F_{3,56}$	P
	Burned Idle	Unburned Idle	Grazed	Hayed		
Species richness (*S*)	7.7 ± 0.49	8.8 ± 0.76	6.9 ± 0.35	8.3 ± 0.70	1.85	0.15
Shannon diversity (*H'*)	1.8 ± 0.05	1.8 ± 0.09	1.7 ± 0.05	1.8 ± 0.09	0.91	0.44
Shannon evenness (*E*)	0.9 ± 0.02	0.9 ± 0.01	0.9 ± 0.01	0.9 ± 0.01	0.78	0.51
Abundance (N detections)	27 ± 2.7	37 ± 2.7	30 ± 1.5	31 ± 1.6	3.47	0.02

we settled on a global model (half-normal key function without adjustments) with observer as a covariate. The distribution of the grasshopper sparrow data, truncated to 100 m, exhibited heaping around 35 m due to evasive movement by the subjects or observer detection bias; we chose a global model (hazard rate key function without adjustments) with observer as a covariate since it had a good fit and the lowest AIC score. For each of these three species, patterns of significant differences in density among treatments (Table 3) were the same as apparent from their encounter rates (Table 2). Dickcissels were 1.6 - 2× more numerous in unburned idle transects than in other treatments. Eastern meadowlarks were about half as numerous in burned idle transects than in other treatments. Grasshopper sparrows were 1.6 - 3× more numerous in grazed transects and hayed transects than in either burned or unburned idle transects. Detections of brown-headed cowbirds were too few, even after pooling data for males and females, to make stratified density estimates; density across all transects combined was 0.23 (± 0.036 SE) individuals per ha.

The vegetative structure of transects differed significantly among treatments (Table 4). Burned idle transects differed from the others in that they essentially lacked litter and thatch. The other treatments had a dense litter layer, at least near the ground (< 20 cm). Unburned idle transects had the tallest vegetation (both living and dead) and had higher overall vegetation density because of their much higher densities of grass and forbs > 20 cm. Grazed and hayed transects tended to be intermediate in character to the idle transects and to be similar to one another, except that hayed

areas had shorter thatch and less litter > 20 cm. One parameter, grass density < 20 cm, differed from most other measures in being highest in the burned treatment; it was inversely related to litter levels, so it was highest in burned, followed by hayed, grazed, and unburned idle transects, though the difference was not as great as with other measures.

DISCUSSION

We found that the methods by which grassland units at SHANGR were managed had significant impacts on the densities of birds that they harbored in the breeding season. The most common grassland species were present in nearly every transect, but their abundances were strongly affected by treatment. Patterns of abundance varied among species according to their differing habitat preferences. Overall avian abundance was highest in unburned idle transects and lowest in their burned idle counterparts, but because no single management type was either superior or inferior to all others for attracting the most species or highest numbers of every species, the treatments did not differ significantly with respect to species richness, diversity, or evenness. Nevertheless, differences in species composition among treatments were apparent in a few cases, as discussed below.

Judging from patterns of avian abundance overall, and of three of the five most frequently encountered grassland species, the decision to reduce the frequency of burning in the impact area from annually to every 3 - 4 years has likely been to the net benefit of grassland birds. Henslow's sparrows are low-density breeders at SHANGR

(detected in 11 of 15 unburned idle, and 3 of 15 grazed transects), and their presence is critically dependent on the existence of unburned units in the impact area, which provide the dense litter and standing dead vegetation that they require (Cully and Michaels 2000). In contrast, dickcissels were numerous throughout the property, yet were most abundant in unburned idle transects – an unsurprising finding since the species is known to prefer, and have its highest breeding success, in areas of tall dense grass with abundant tall forbs (Winter 1999; Frey et al. 2008). Eastern meadowlarks were also numerous throughout SHANGR, but were significantly less abundant in burned transects than in any other treatment, most likely because those areas lacked the litter or (at least early in the growing season when meadowlarks have their first brood) grassy cover that they require despite tolerating a wide range of other grassland characteristics (Lanyon 1995). Grasshopper sparrows were also least abundant in burned idle transects, though not significantly so in post hoc comparison to unburned idle transects. Mourning doves, which are facultative inhabitants of grasslands, were most abundant in unburned transects, significantly more so than in grazed and hayed, and nearly more so ($P = 0.06$) than in burned treatments, but we have no explanation for this pattern, which seems contrary to their typical habitat associations.

Despite the lower numbers of several species in burned idle units, prescribed fire is likely vital for conserving grassland birds at SHANGR. Burned units are themselves an important habitat component for upland sandpipers, which are not territorial and roam over large tracts, congregating in

Table 2. Encounter rates ($\bar{x}$ detections per 1000 m transect ± SE, $n = 15$) by treatment for the 10 most frequently encountered bird species along transects at Smoky Hill Air National Guard Range in May–June 2005, and ANOVA tests for significance of treatment effects on transformed [$\log_{10}$ (1 + individuals per 1000 m transect)] encounter rates. For each species, encounter rates not sharing a superscript letter are significantly different (Tukey test, P < 0.05). Encounter rates of dickcissels and grasshopper sparrows were not transformed for analysis. Counts (N) and encounter rates of dickcissels, grasshopper sparrows, and Henslow's sparrows were of singing males only.

Species	N	Transects Present (%)	Transect Width (m)	Management treatment type				$F_{3,56}$	P
				Burned Idle	Unburned Idle	Grazed	Hayed		
Grass-dependent:									
Upland sandpiper	142	80	400	6.8 ± 1.51[a]	2.1 ± 0.62[b]	4.2 ± 0.80[ab]	2.7 ± 0.69[b]	5.22	0.003
Dickcissel	395	98	300	10.3 ± 1.25[a]	16.2 ± 1.41[b]	8.1 ± 1.31[a]	9.2 ± 1.44[a]	7.01	<0.001
Grasshopper sparrow	340	95	200	4.6 ± 1.01[a]	7.4 ± 0.65[a]	12.3 ± 1.06[b]	13.4 ± 1.38[b]	15.53	<0.001
Henslow's sparrow	26	23	260	0[a]	2.3 ± 0.58[b]	0.6 ± 0.35[a]	0[a]	16.31	<0.001
Eastern meadowlark	415	100	400	6.3 ± 0.75[a]	13.7 ± 1.31[b]	14.2 ± 1.49[b]	11.9 ± 0.90[b]	13.07	<0.001
Grassland facultative:									
Mourning dove	58	33	160	1.4 ± 0.73[ab]	4.0 ± 1.06[a]	0.6 ± 0.39[b]	0.4 ± 0.26[b]	5.94	0.001
Eastern kingbird	86	73	160	2.9 ± 0.41[a]	1.8 ± 0.44[a]	2.1 ± 0.60[a]	2.8 ± 0.53[a]	1.61	0.200
Bell's vireo	35	25	160	0[a]	1.3 ± 0.61[ab]	0[a]	2.6 ± 0.71[b]	10.01	<0.001
Red-winged blackbird	69	20	160	4.8 ± 2.82[a]	1.4 ± 1.14[a]	0.2 ± 0.22[a]	1.2 ± 0.78[a]	1.89	0.140
Brown-headed cowbird	137	60	160	3.3 ± 1.26[ab]	6.0 ± 1.57[a]	4.4 ± 1.21[ab]	1.4 ± 0.56[b]	2.88	0.040

recently burned areas where they prefer to forage (Houston and Bowen 2001), and where we most often encountered them (Note that because their home ranges are much larger than the area surveyed by each transect, and because nest locations may be far from shared foraging areas, the pattern of sandpiper abundance that we found more likely reflects frequency of habitat use than it does nesting densities). More salient for the grassland avifauna as a whole is that without periodic fire, which reverses successional processes by removing woody vegetation, litter, and thatch, the grasslands of SHANGR would be lost through conversion to woodland (Briggs et al. 2005). In 1859, the property had only 37 ha of woodland, but ecological processes, including natural patterns of fire, have since been altered, and it now has 243 ha of woods, mostly adjacent to creeks, plus many scattered trees and hedgerows in the uplands (Kindscher and Loring 2007). Burned and unburned idle units at SHANGR are not fixed treatments, but rather alternating outcomes of a rotational burning scheme. We cannot assess whether burning impact area units every 3 - 4 years will be frequent enough in the modern landscape to maintain their grassland character long term (see Briggs et al. 2005), but the outcomes of that burn regime should be monitored and adjustments made if necessary.

Both hayed and grazed transects had vegetation of similarly moderate height and density with intermediate litter levels, and they attracted similar numbers of birds. Grasshopper sparrows, which require both litter for nesting and open patches of ground for foraging (Vickery 1996), were especially abundant. Hayed and grazed treatments did, however, differ with respect to prevalence and distribution of woody vegetation. In grazed transects, woody vegetation was usually scarce and occurred as scattered trees or low and diffuse brush, whereas most hayed transects contained well-defined islands of tall and dense shrubs (e.g. *Cornus drummondii, Prunus* spp.), which have developed around small rock outcrops or eroded stream channels that deter hay cutting. Shrub patches in a grassy matrix typifies Bell's vireo habitat in the region (Zimmerman 1993);

Table 3. Density estimates (individuals per hectare ± SE) by treatment for the most frequently encountered bird species along transects at Smoky Hill Air National Guard Range in May–June 2005. For dickcissels and grasshopper sparrows, estimates are of singing males; for eastern meadowlarks they are of all adults. For each species, density estimates with different superscript letters are significantly different ($\alpha' = 0.009$).

Species	Burned Idle	Unburned Idle	Grazed	Hayed
Dickcissel	0.58 ± 0.073^a	0.92 ± 0.085^b	0.46 ± 0.076^a	0.52 ± 0.083^a
Grasshopper sparrow	0.29 ± 0.065^a	0.48 ± 0.044^a	0.79 ± 0.072^b	0.86 ± 0.092^b
Eastern meadowlark	0.28 ± 0.035^a	0.61 ± 0.062^b	0.63 ± 0.070^b	0.53 ± 0.044^b

and, indeed, the species was conspicuous in hayed transects and present to a lesser extent in unburned idle transects (which also, for lack of grazing and recent fire, contain some shrubby areas), but absent elsewhere. Its pattern of occurrence was representative of a suite of less frequently encountered shrub-dwelling species, including the house wren (*Troglodytes aedon*; 5 detections in 4 transects), gray catbird (*Dumetella carolinensis*; 13 in 9), brown thrasher (*Toxostoma rufum*; 25 in 16), yellow warbler (*Setophaga petechia*; 10 in 7), and the common yellowthroat (*Geothlypis trichas*; 15 in 11). Provided that the shrubby areas of hayed transects do not expand and undergo further succession into woodland, they contribute a valuable habitat component and resemble those less-frequently burned areas that occurred naturally within prairie landscapes around some creeks and ravines. We note that other studies have found higher numbers and rates of brood parasitism by brown-headed cowbirds in association with woody vegetation (Patten et al. 2006), but for reasons unknown and perhaps spurious, we found cowbirds least abundant in hayed transects.

Study strengths and limitations

Although we primarily used encounter rates to describe patterns of avian abundance, distance sampling was an invaluable means of testing for counting biases. Because we found no significant differences in detection functions by treatment for the several species that we could evaluate, and observer biases were distributed fairly evenly among treatments, we are confident that encounter rates for each species in our study accurately reflect differences in its relative abundance among treatments. Distance sampling also allowed us to make absolute density estimates for four species (three of those by treatment), which can be directly compared to results of future population surveys at SHANGR or studies elsewhere.

Our methods were not well suited to gathering enough, or the appropriate, data to evaluate effects of treatment on several species of conservation significance that occur at SHANGR at low densities or that are wide-ranging. Transect surveys, at least as implemented here (with respect to transect size, number, and perhaps placement away from habitat edges), were an inefficient or ineffective means of encountering these species, which included the greater prairie-chicken (*Tympanuchus cupido*; 19 detections in 10 transects), northern

Table 4. Vegetation measures ($\overline{x} \pm SE$, $n = 15$) by treatment along transects at Smoky Hill Air National Guard Range in June 2005, and ANOVA tests for significant differences. Means within each measurement category not sharing a superscript letter are significantly different (Tukey test, $P < 0.05$).

	Management treatment type				$F_{3,56}$	P
	Burned Idle	Unburned Idle	Grazed	Hayed		
Maximum height (cm):						
Grass	52.1 ± 1.75^{ab}	59.2 ± 1.08^c	55.7 ± 1.68^{ac}	47.7 ± 1.37^b	10.86	< 0.001
Forbs	47.3 ± 2.36^a	60.7 ± 1.20^b	51.4 ± 2.11^a	50.1 ± 1.29^a	9.92	< 0.001
Thatch	38.1 ± 4.41^a	93.0 ± 3.20^b	74.0 ± 2.49^c	42.9 ± 2.93^a	61.02	< 0.001
Litter	0.3 ± 0.14^a	12.5 ± 1.21^b	9.4 ± 1.05^c	6.5 ± 0.42^c	39.42	< 0.001
Density (number of contacts with a vertical 4 mm-diameter rod):						
Grass > 20 cm	1.8 ± 0.21^a	5.1 ± 0.39^b	2.8 ± 0.30^a	2.6 ± 0.38^a	18.49	< 0.001
Grass < 20 cm	3.9 ± 0.34^a	2.4 ± 0.21^b	3.2 ± 0.30^{ab}	3.5 ± 0.33^{ab}	4.33	0.008
Forbs > 20 cm	0.3 ± 0.09^a	0.9 ± 0.12^b	0.3 ± 0.09^a	0.3 ± 0.09^a	9.56	< 0.001
Forbs < 20 cm	0.4 ± 0.09^a	0.4 ± 0.08^a	0.3 ± 0.06^a	0.3 ± 0.08^a	0.80	0.500
Thatch & litter > 20 cm	0.2 ± 0.08^a	1.9 ± 0.30^b	1.3 ± 0.27^b	0.4 ± 0.09^a	14.61	< 0.001
Litter & thatch < 20 cm	1.5 ± 0.27^a	10.6 ± 0.51^b	9.4 ± 0.58^{bc}	8.1 ± 0.42^c	77.79	< 0.001

bobwhite (*Colinus virginianus*; 3 in 2), common nighthawk (*Chordeiles minor*; 13 in 11), and the loggerhead shrike (*Lanius ludovicianus*; 3 in 2).

Bird abundance is not always indicative of habitat quality (Van Horne 1983), though the two are usually correlated (Bock and Jones 2004). Our judgments about the merits of management regimes may not be accurate if nesting success differs among treatments. For example, hayed transects attract high densities of grassland birds, and reproductive success in them can be high when cutting occurs late in the growing season (Rahmig et al. 2009); however, if cutting occurs before young have fledged, hayed units could be population sinks. Because most birds fledge their first (or only) brood by late June or early July at SHANGR, and prairie condition declines if cutting is consistently delayed until August (and late-cut hay is low in quality; Towne and Ohlenbusch 1992), we recommend hay be cut during the second half of July. The value of hayed areas for birds also depends upon the extent to which they are used (e.g., for second broods) subsequent to cutting, but on that matter we have no information. Another example of where the relationship between abundance and nesting productivity might not be straightforward concerns the pattern of migratory arrival and settlement of dickcissels. Numbers and nesting effort of that species are known not to peak in Kansas until mid July (Zimmerman 1971; Temple 2002); and indeed, we found abundance substantially higher in all treatments in the second round of surveys as compared to the first, especially in grazed and in burned idle transects, where it doubled (but remained lower than in unburned transects). It may be that grazed and burned areas improve in quality as the growing season progresses, becoming as suitable for nesting as unburned areas (Zimmerman 1997), but another possibility is that as available habitat fills, less competitive males are forced into marginal areas (Zimmerman 1971). Male dickcissels in preferred habitat attract 2 - 6 mates, whereas others may have none (Zimmerman 1966, 1982; Temple 2002), so differences in male density may underestimate disparities in nesting activity among treatments (e.g., Robel et al. 1998).

Conservation value of SHANGR

We found that SHANGR harbors high densities of grassland birds, most of which are declining nationally and some of them regionally (Sauer et al. 2011), and believe that it constitutes an area of exceptionally high value for their conservation. Among the special features of the site are its native tallgrass prairie flora, its large overall size, the large size of its management units, its low fragmentation, and its high ratio of interior to edge habitat (i.e., low perimeter to area ratio of management units and the property as a whole). The variety of management regimes implemented at SHANGR further enhance its value by fostering vegetative structural heterogeneity in the landscape, and thus the ability of the site to provide for differing and complex habitat requirements of various species. Switching from the current system of geographically-fixed treatment types to some form of mixed management (e.g., alternating between haying, grazing, or leaving a unit idle in different years) might further enhance habitat quality by changing the scale of heterogeneity and generating novel combinations of environmental variables, and is an alternative worth investigating. Also significant is that some regimes valuable to the prairie biota and present at SHANGR are rare in the modern landscape. Examples include the large hayed units, the fairly long interval between prescribed burns of grazed units, and the existence of effectively idle prairie, especially that which is subject to rotational prescribed burning and seasonally-variable wildfire. Over recent decades, the trend has been toward more intensive use of native rangeland than is current practice at SHANGR. For example, spring burning of tallgrass prairie in the Flint Hills, which lie just east of the Smoky Hills, has become extraordinarily widespread (e.g., 67.4% of total area in 2004; With et al. 2008) because many pastures are burned annually, often to promote higher beef yields in conjunction with early-season double-stocking; grassland bird abundances and nest success are depressed in such areas (Zimmerman 1997; Patten et al. 2006; Powell 2008). Apart from helping inform future policy at SHANGR and bringing attention to its conservation significance, we hope our findings are of general value for informing management of tallgrass prairie along its western limit.

Alexis Powell is a natural history enthusiast with diverse interests in organismal, evolutionary, and conservation biology. Currently, he is a postdoctoral associate in the BioTechnology Institute at the University of Minnesota, where he studies evolution through experiments with synthetic microbial assemblages. He also investigates avian phylogenetics and evolution of plumage color patterning in collaboration with his former doctoral advisors in the UMN's Ecology, Evolution, and Behavior program and Bell Museum of Natural History.

William Busby is an Associate Scientist with the Kansas Biological Survey in Lawrence and serves as zoologist with the Kansas Natural Heritage Inventory. His research interests include vertebrate habitat use and its relationship to land management.

LITERATURE CITED

Anderson, R.C. 1990. The historic role of fire in the North American grassland. Pp. 8-18 *in* S.L. Collins and L.L. Wallace, eds., Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman.

Askins, R.A., F. Chávez-Ramírez, B.C. Dale, C.A. Haas, J.R. Herkert, F.L. Knopf, and P.D. Vickery. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Ornithological Monographs 64:1-46.

Bock, C.E., and Z.F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403-410.

Briggs, J.M., A.K. Knapp, J.M. Blair, J.L. Heisler, G.A. Hoch, M.S. Lett, and J.K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243–254.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundances of biological populations. Oxford University Press, New York.

Busby, W.H., and C.J. Schmidt. 2007. Animal surveys. Pp. 58–150 in W.H. Busby, J.M. Delisle, C.C. Freeman, K. Kindscher, H. Loring, D.E. Nimz, and C.J. Schmidt, A natural features inventory of the Smoky Hill ANG Range, Kansas. Open-file Report No. 137, Kansas Biological Survey, Lawrence.

Cully, J.F., Jr., and H.L. Michaels. 2000. Henslow's sparrow habitat associations on Kansas tallgrass prairie. Wilson Bulletin 112:115-123.

Fuhlendorf, S.D., and D.M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625-632.

Frey, C.M., W.E. Jensen, and K.A. With. 2008. Topographic patterns of nest placement and habitat quality for grassland birds in tallgrass prairie. American Midland Naturalist 160:220-234.

Houston, C.S., and D.E. Bowen, Jr. 2001. Upland Sandpiper (*Bartramia longicauda*). The Birds of North America No. 580, The Birds of North America, Inc., Philadelphia, Pa.

Kindscher, K., and H. Loring. 2007. Plant communities and landscape features. Pp. 11-34 in W.H. Busby, J.M. Delisle, C.C. Freeman, K. Kindscher, H. Loring, D.E. Nimz, and C.J. Schmidt. A natural features inventory of the Smoky Hill ANG Range, Kansas. Open-file Report No. 137, Kansas Biological Survey, Lawrence.

Knapp, A.K., J.M. Blair, J.M. Briggs, S.M. Collins, D.C. Hartnett, L.C. Johnson, and E.G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39-50.

Lanyon, W. E. 1995. Eastern Meadowlark (*Sturnella magna*). The Birds of North America No. 160, The Birds of North America, Inc., Philadelphia, Pa.

Patten, M.A., E. Shochat, D.L. Reinking, D.H. Wolfe, and S.K. Sherrod. 2006. Habitat edge, land management, and rates of brood parasitism in tallgrass prairie. Ecological Applications 16:687-695.

Powell, A.F.L.A. 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. Journal of Field Ornithology 79:41-52.

Rahmig, C.J., W.E. Jensen, and K.A. With. 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. Conservation Biology 23:420-423.

Robel, R.J., J.P. Hughes, S.D. Hull, K.E. Kemp, and D.S. Klute. 1998. Spring burning: resulting avian abundance and nesting in Kansas CRP. Journal of Range Management 51:132-138.

Samson, F.B., F.L. Knopf, and W.R. Ostlie. 1999. Grasslands. Pp. 437-445 *in* M.J. Mac, P.A. Opler, C.E. Puckett Haecker, and P.D. Doran, eds., Status and Trends of the Nation's Biological Resources. Biological Resources Division, U. S. Geological Survey, Reston, Va.

Sauer, J.R., J.E. Hines, J.E. Fallon, K.L. Pardieck, D.J. Ziolkowski, Jr., and W.A. Link. 2011. The North American Breeding Bird Survey, results and analysis 1966-2009. Version 3.23.2011 USGS Patuxent Wildlife Research Center, Laurel, Md.

Smith, E.F., and C.E. Owensby. 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills range. Journal of Range Management 31:14-17.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman, New York.

Steinauer, E.M., and S.L. Collins. 1996. Prairie ecology – the tallgrass prairie. Pp. 39-52 *in* F.B. Samson and F.L. Knopf, eds., Prairie Conservation: Preserving North America's Most Endangered Ecosystem. Island Press, Washington D.C.

Temple, S.A. 2002. Dickcissel (*Spiza americana*). The Birds of North America No. 703, The Birds of North America, Inc., Philadelphia, Pa.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5-14.

Towne, G. and P.D. Ohlenbusch. 1992. Native hay meadow management. MF-1042, Kansas State University Agricultural Experiment Station and Cooperative Extension Service, [Manhatten].

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Vickery, P.D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*). The Birds of North America No. 239, The Birds of North America No. 703. The Birds of North America, Inc., Philadelphia, Pa.

With, K.A., A.W. King, and W.E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152-3167.

Winter, M.A. 1999. Nesting biology of dickcissels and Henslow's sparrows in southwestern Missouri prairie fragments. Wilson Bulletin 111:515-527.

Zimmerman, J. L. 1966. Polygyny in the dickcissel. Auk 83:534-546.

Zimmerman, J. L. 1971. The territory and its density dependent effect in *Spiza americana*. Auk 88:591-612.

Zimmerman, J. L. 1982. Nesting success of dickcissels (*Spiza americana*) in preferred and less preferred habitats. Auk 99:292-298.

Zimmerman, J.L. 1993. The Birds of Konza: the Avian Ecology of the Tallgrass Prairie. University of Kansas Press, Lawrence.

Zimmerman, J.L. 1997. Avian community responses to fire, grazing, and drought in the tallgrass prairie. Pp. 167–180 *in* F.L. Knopf and F.B. Samson, eds., Ecology and Conservation of Great Plains Vertebrates. Ecological Studies 125, Springer-Verlag, New York.