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Relative effects of litter and management on grassland bird abundance in Missouri, USA

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Summary

Transect bird surveys were conducted at 43 tallgrass prairies in southwestern Missouri, U.S.A. in mid-June each year from 1992 to 1999. Litter volume on and near the ground was estimated on a nine-point scale during 1994 to 1999. The relative importance of management type (rotational burning, rotational haying, or a combination of both) and litter volume on relative abundance was analysed for three declining grassland songbirds: Henslow's Sparrow *Ammodramus henslowii*, Grasshopper Sparrow *A. savannarum*, and Dickcissel *Spiza americana*. Haying resulted in significantly higher abundance than burning for all species except Dickcissel, for which few significant management effects were detected. Henslow's Sparrow increased in abundance from light to heavy litter, Grasshopper Sparrow peaked in low to intermediate litter, and Dickcissel showed little pattern relative to litter. Litter scores recorded in each management type increased with number of years since last treatment. Although litter profoundly affected bird abundance, independent and equally important was whether that litter was obtained via haying or burning. Greater consistency among years in hayed vegetation structure may help explain these birds' preference for haying over burning or haying + burning. Rotational haying should be employed more than burning in the management of these declining birds, especially for the sharply declining, fire-sensitive Henslow's and Grasshopper Sparrows.

Introduction

Tallgrass prairie has been almost entirely destroyed in most central North American states and provinces since European settlement (Samson and Knopf 1994). Grassland and ground-nesting birds in eastern and central North America have shown the greatest community-wide declines of any Nearctic biome and nesting guild, respectively (Peterjohn *et al.* 1994). The demise of North American grassland began 150 years ago with the replacement of millions of native grazing mammals by cattle, followed by conversion of most tallgrass prairie to tilled crops (Knopf 1994). In addition to the effects of habitat loss, grassland bird declines are compounded by area sensitivity of some of the rarer species (Herkert 1994a).

The North American Breeding Bird Survey (BBS) has revealed declines in the population of Henslow's Sparrow *Ammodramus henslowii* by 93%, of Grasshopper Sparrow *A. savannarum* by 66%, and of Dickcissel *Spiza americana* by 38%, survey-wide, between 1966 and 1998 (Sauer *et al.* 1999). Henslow's and Grasshopper Sparrows are among the fastest declining North American songbirds (Peterjohn *et al.* 1994).

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Table 1. Summary of study sites and survey effort for Henslow's and Grasshopper Sparrows and Dickcissels by management type in southwestern Missouri prairies in June during 1994 to 1999. Some sites contained multiple management types

	All	Hay	Hay + burn	Burn
Number of sites	43	24	27	7
Mean patch size per site (ha)	137	149	118	244
Median patch size per site (ha)	65	69	68	68
Minimum–maximum patch sizes (ha)	6 – 855	16 – 593	10 – 571	6 – 855
Total unit surveys	535	242	256	37
Total survey distance (km)	224.3	96.8	114.3	13.1
Mean (±SD) unit survey distance (m)	419±220	400±197	447±235	353±229
No. individuals recorded				
Henslow's Sparrow	1,874	1,192	627	55
Grasshopper Sparrow	678	375	285	18
Dickcissel	2,174	1,043	995	136

Vegetation structure and management of grasslands can strongly affect which species of birds live there, and at what abundance (e.g. Kahl *et al.* 1985, Zimmerman 1988, Bollinger *et al.* 1990, Herkert 1994a, Dale *et al.* 1997). However, relatively few studies (e.g. Owens and Myres 1973, Vickery *et al.* 1999) have analysed the effects of management and vegetation structure in a way that separates their effects on grassland birds. This paper therefore investigates the effects of two aspects of prairie management on three declining grassland songbirds. Specifically, the quantity of litter volume present, and the management practices that generated this vegetation structure. The results of such research can guide efforts to improve land management strategies for conserving grassland songbirds.

Study area

We selected 43 prairie preserves (Table 1) within 200 km south and east of Kansas City, Missouri (37°02′–38°55′N, 93°13′–95°93′W) (Swengel 1996, Figure 1). The area has hot summers, cool winters, and an average of 105 cm annual precipitation.

We classified sites, or units (subsites) within them, by management type observed on visits during 1991 to 1999 (Table 1). Twenty-four prairies were rotationally hayed (mowed, with baling and removal of clippings) in summer (late June–late July) every 1–4 years, with a mean of 45% of their area hayed per year (range 0–100%). Seven sites were rotationally burned on an approximately 1.5–4 year cycle, with a mean of 45% of their area burned per year (range 0–100%). Nearly all management fires occur in March or April (Solecki and Toney 1986). Twenty-seven sites were rotationally managed with both haying (mean 40% of their area hayed per year) and burning (mean 35–40% of their area burned per year), typically but not always having more intensive management (mean 75–80% of area burned and/or hayed per year) than either hayed or burned prairies. It was usual, even at the smallest sites, for only a portion of the site to be managed in a given year. At 15 prairies, different management types were practised in two different parts of the site.

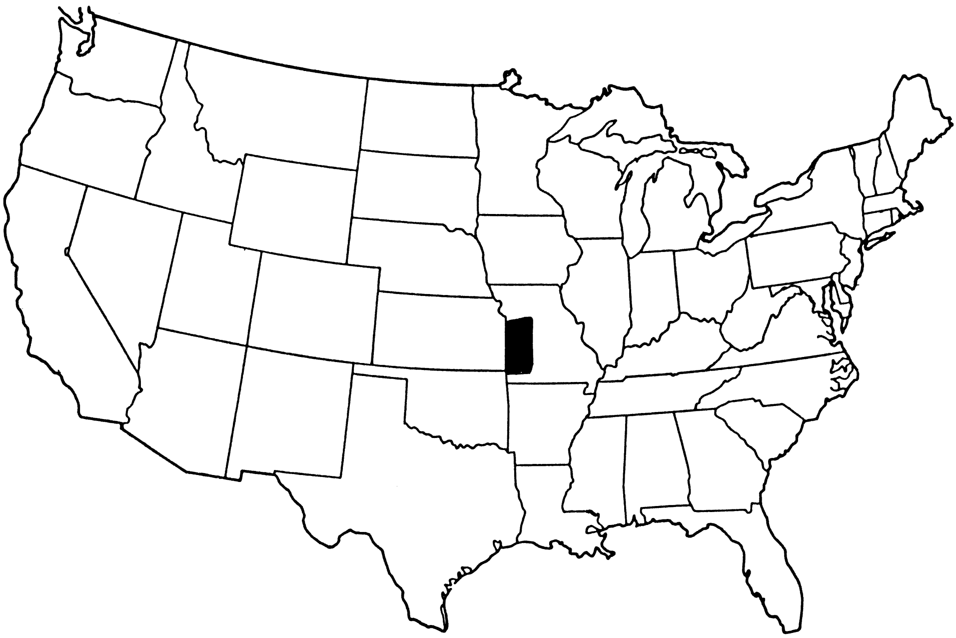

Figure 1. The study area (in black) for Henslow's Sparrow, Grasshopper Sparrow and Dickcissel in southwestern Missouri, central U.S.A., where the 43 study sites were located.

Methods

Transects

While walking about 1.5–2 km/hour, we counted all singing or visible Henslow's Sparrows once per year along the same unlimited width transects during 14–24 June in 1992 to 1999, and Grasshopper Sparrows and Dickcissels in 1993 to 1999 (Swengel 1996). Individuals outside the preserve were not counted. We surveyed at all times of day between 06h55 and 18h55 standard time, but randomized the time at which sites were surveyed among years. A new unit (subsite) began each time the prairie type, quality, management type, or treatment year changed along the transect route. Unit boundaries remained stable, except when a unit was divided into two because of a difference in management type or treatment year. Unit surveys averaged 419 m in length, with roughly similar mean lengths among management types (Table 1).

We classified prairie type (wet, 1; wet-mesic, 2; mesic, 3; dry-mesic, 4; dry, 5) and floristic quality (degraded, 1; semidegraded, 2; undegraded, 3; based on native plant diversity and extent of weeds and brush) after site descriptions by Skinner *et al.* (1984), The Nature Conservancy (1991), and Toney (1993). Prairies were "diverse" (graded 2) if they included prairie types both drier and wetter than mesic, or "uniform" (graded 1) if they did not. During surveys we recorded which units had been hayed or burned within the past year. Treatments occurring <1 year ago were classified as 0 years ago and were in their first growing season since treatment, treatments 1–1.99 years ago were called 1 year ago, and so on. Few units went unmanaged for more than 3 years. We determined management type and treatment year from site descriptions by Skinner *et al.* (1984), The Nature Conservancy (1991), Toney (1993), and conversations with, correspondence with, and newsletters by staff from the managing agencies; and from direct observation during survey visits in June in consecutive years and additional visits in April 1991, July 1994 and April 1999. If type or year of treatment could not be determined for a unit survey, it was excluded from analysis.

Beginning in 1994, while conducting surveys, the senior author estimated dead plant litter volume on and near the ground in each unit, with a nine-point scale: 0 (no litter), 2 (light litter), 4 (moderate), 6 (heavy), and 8 (very heavy), and the intermediate values between each pair of these categories. This approach is similar to methods used by Bollinger (1995) and Granfors *et al.* (1996). They visually estimated litter in quadrats, and categorized them on a five-point litter density scale. In this study, a single litter estimate was assigned to the entire transect corridor of a unit. These estimates required little additional time to make, as litter is easy to observe while listening to and looking at birds, and readily sensed while walking through it.

Data analysis

We used multivariate analysis of relative bird abundance (observation rates of individuals per kilometre) in prairies managed in different ways to analyse the relative importance of management type and litter volume. By studying populations of birds on Missouri preserves already undergoing conservation management, we ensured that management types being compared were those that were already in use. A manipulative experimental approach would preclude the study of habitat and management effects at such a large number of sites, and would not indicate the effects of management on the larger spatial scale typically applied (experimental plots would be inappropriately small for such vagile animals).

We analysed unweighted log-transformed relative abundance of each bird species in each unit survey [$\log_e(1 + \text{individuals/km})$], and of the three species summed (''combined birds''), in forward stepwise multiple linear regressions against 17 types of independent variables. Many papers in Sauer and Droege (1990) reviewed the methods and validity of log-transformation and linear regression for analyses of bird censuses. Fourteen non-management variables were tested: year, analysed two ways (all years 1994–99, to measure trend; and as six dichotomous variables: a 1994 survey was coded as 1 for the variable ''1994'' and 0 for variables ''1995'', ''1996'', ''1997'', ''1998'' and ''1999'', and so on for each year); Julian date; survey starting time (24 hour clock); crepuscularity (hours between survey starting time and noon standard time); wind speed (km/hour); percentage time the sun was shining; temperature (°C); latitude; longitude; prairie size (ha); prairie type; prairie diversity; and floristic quality. Management variables included management type (see next paragraph), litter, and years since most recent treatment.

Although these regressions treat all but dichotomous variables as linear, we, like Bollinger (1995), had little *a priori* reason to expect strongly non-linear bird responses to most variables. All variables except survey starting time and management type had obvious progressions from low to high. Crepuscularity corrected for a lack of a clear progression (in biological effect) in survey starting time. Management types were coded as four dichotomous variables for the four possible management types: haying, burning, combined management by haying + burning where the last treatment was haying (''hay + burn last hayed''), and haying + burning where the last treatment was burning (''hay + burn last burned''; coded 1 if unit survey was classified as that management type, and 0 if classified one of the other ways).

We used one-way analysis of variance (ANOVA) to test for effects of management type on log-transformed bird abundance when litter category was held constant, and vice versa. We grouped the nine litter codes into three categories (light, intermediate, heavy) with the mostly nearly equal samples of unit surveys to achieve adequate cell sizes.

These analyses included survey results for each year at each unit, instead of combining them into a single value to avoid pseudoreplication within site among years. Using a single value per unit would preclude analysis of effects of litter volume on bird abundance, since litter volume could vary dramatically in the same unit among years. Pseudoreplication within site among years is greatly counteracted by the much larger number of sites (43) and units (135) than years in this study. Many grassland bird studies have analysed patterns of bird abundance in multiple-year datasets from the same site(s) as if the data from each year were independent (e.g. Zimmerman 1992, Bollinger 1995, Herkert and Glass 1999, Vickery *et al.* 1999).

Statistically, this type of pseudoreplication (i.e. non-independence in number of birds observed in a site among years, perhaps due to site fidelity or habitat factors not analysed in this study) would serve to reduce the significance attributed to litter and management type (and the other factors). To counteract this, we reran the regressions separately for each year of the study, including all independent variables in the previous regressions except those related to year. Since non-management results in these ''annual'' regressions were consistent with the original ''overall'' regressions, we present just the management and litter results from the annual regressions.

We did not rerun the ANOVAs as repeated measures. In this type of analysis, a unit could be represented no more than once for each value in an independent variable. For example, a hayed unit surveyed each year from 1994 to 1999 could only be included in the litter analysis a maximum of three times (once for each litter category: light, intermediate and heavy). Repeated-measures ANOVA was possible for the half of the analysis testing for effects of litter category on bird abundance when management type was held constant, but the reverse analysis (testing for effects of management type when litter category was held constant) was not possible due to inadequate samples for several cells, since units were more likely to change in litter volume among years than in management type.

Tests were two-tailed with statistical significance of $P < 0.05$. Regressions used $P < 0.05$ to add/remove variables. ANOVAs used Duncan's post-hoc test to correct significance levels for multiple comparisons. All statistics were calculated using ABstat 7.20 (1994 Anderson-Bell Corporation, Parker, Co.). All analyses were restricted to data collected during 1994–1999.

Results

Non-management effects

Each of the primary habitat descriptors (diversity, patch size, prairie quality and prairie type) had significant effects on abundance of between two and four of the four bird species tested (Table 2). All birds were more abundant in higher quality prairie, and all but Grasshopper Sparrow were more abundant in larger prairies with uniform rather than diverse topography. Grasshopper Sparrow was more abundant in diverse prairies, and Henslow's and Grasshopper Sparrows more abundant in drier prairies. Dickcissels showed the strongest relationship with seasonal and annual timing (date, years), consistent with the dramatic inter-year fluctuations in regional abundance previously noted for this species (Fretwell 1973, Herkert 1994a). Only Henslow's Sparrow showed a significant

Table 2. Forward stepwise linear regressions of log-transformed relative bird abundance (individuals/km per unit survey) at southwestern Missouri prairies during June 1994–1999 versus environmental variables, with $P < 0.05$ to add/remove variables. Step (step-rank in regression) and standardized coefficients (r) are provided only for statistically significant litter and management results. From left to right columns, multiple r statistics: 0.616, 0.530, 0.442, and 0.567, $n = 519$ unit surveys and $P < 0.00005$ for each regression. 1995, 1999, crepuscularity, time of day, percent sunshine, and wind speed never had $P < 0.05$.

	Henslow's		Grasshopper		Dickcissel		Combined birds	
	Step	r	Step	r	Step	r	Step	r
Management								
Hay	2	+0.276****	5	+0.192****		10		
H + B last hay	5	+0.142**					10	−0.101*
H + B last burn			8	−0.152***			7	−0.213****
Burn	8	−0.100*			5	−0.150***	5	−0.295****
Years since treatment			1	−0.126*				
Litter	1	+0.367****	9	−0.207**			2	+0.183****
Habitat								
Diversity	6	−0.199****	6	+0.098*	6	−0.156***	6	−0.147***
Prairie size	4	+0.232****			4	+0.220****	4	+0.306****
Quality	7	+0.117**	7	+0.111**	9	+0.083*	3	+0.180****
Type	9	+0.082*	2	+0.167****				
Geography								
Latitude					3	−0.168****	8	−0.266****
Longitude			4	−0.226****			8	−0.209****
Timing								
Date in June					2	−0.222****		
Trend 1994–1999			3	−0.096*				
1994					8	+0.119*		
1996					1	+0.276****	1	+0.193****
1997					7	−0.100*		
1998			10	−0.128**				
Weather								
Temperature	3	−0.114**						

In all tables $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $^{****}P < 0.0001$.

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response to weather, with higher abundance in cooler conditions. Significant geographical patterns included higher abundance of Grasshopper Sparrow further east and Dickcissel further south, and of combined species both eastward and southward.

The habitat, geography, timing, and weather factors comprised 19 (76%) of 25 factors in the overall regressions (Table 2) and 12 of 18 (67%) in the annual regressions (Table 3). The percentages of significant results attributed to these factors were 50%, 60%, 89%, and 60% for Henslow's and Grasshopper Sparrow, Dickcissel, and combined sparrows, respectively, in the overall regressions, and 45%, 53%, 71%, and 48% in the annual regressions.

The two daily timing variables (crepuscularity, time of day) showed no significant effect for any species (Table 2). During 09h00–17h00 (when most surveys occurred), each management type was represented in each two-hour block in proportions similar as for all types combined (Table 4). However, in the earliest time block, hayed units were relatively under-represented and all management types with a burning component were over-represented then.

Management and litter

One or more management variables were significant in all four overall regressions, with the litter a significant variable in three (Table 2). Haying always had a positive effect on bird abundance when significant, and burning a negative effect. Hay + burn last hayed was positive for Henslow's Sparrow abundance and negative for combined bird abundance, while hay + burn last burned was negative for both Grasshopper Sparrow and combined bird abundance. Henslow's Sparrow and combined bird abundance covaried strongly with litter, while Grasshopper Sparrow abundance was negatively associated with litter, and Dickcissel showed no pattern. Significant results in the annual regressions were similar (Table 3), except that the single significant result of hay + burn last hayed was negative for Henslow's Sparrow abundance, and Dickcissel abundance showed a single positive significant result for litter.

In one-way ANOVA of bird abundance versus management type when litter category was controlled (Table 5), significantly higher bird abundance occurred with haying and lower abundance with burning, except for Dickcissel, which showed virtually no significant effects by management. Of 12 analyses, mean bird abundance was highest 11 times in hay, once in hay + burn last hayed (when hay had the second highest abundance), and never in hay + burn last burned and burn. Burn had the lowest bird abundance six times, hay + burn last burned three, hay + burn last hayed three, and hay never. Hay had significantly higher bird abundance than burn eight times, hay + burn last burned eight times, and hay + burn last hayed three times. In none of the analyses did other management types have significantly higher bird abundance than hay. Hay + burn last hayed and hay + burn last burned only differed significantly twice (each was higher once), but hay + burn last hayed had significantly greater bird abundance than burn six times, versus just twice for hay + burn last burned.

In one-way ANOVA of bird abundance versus litter category when management type was controlled (Table 5), significant results were similar to the regressions. Henslow's Sparrow had strong significant patterns of progressively higher

Table 3. Forward stepwise linear regressions of log-transformed relative bird abundance (individuals/km per unit survey), at southwestern Missouri prairies during June, 1994 to 1999) versus environmental variables, analysed separately for each year, with $P < 0.05$ to add/remove variables. Step (step-rank in regression), and standardized coefficients (*r*) are provided only for statistically significant litter and management results, as well as the number of significant steps in each regression.

	1994		1995		1996		1997		1998		1999	
	Step	*r*	Step	*r*	Step	*r*	Step	*r*	Step	*r*	Step	*r*
Henslow's Sparrow												
Hay	3	+0.270***	1	+0.265**								
H + B last hayed							3	−0.292**				
H + B last burned												
Burn			5	−0.355***			2	−0.255**	2	−0.380		
Years since treatment												
Litter	1	+0.570****	3	+0.489****	1	+0.466****	1	+0.397****	1	+0.601****	1	+0.443****
n steps	4		5		3		5		4		1	
Grasshopper Sparrow												
Hay			4	+0.285**	4	+0.226*	3	+0.444***				
H + B last hayed												
H + B last burned					2	−0.235*						
Burn												
Years since treatment			2	−0.429****	3	−0.358			1	−0.380***		
Litter							2	−0.422***				
n steps	1		5		4		4		2		1	
Dickcissel												
Hay							2	+0.273*				
H + B last hayed												
H + B												
Burn			3	−0.263**					1	−0.497***		
Years since treatment												
Litter									2	+0.275**		
n steps	3		5		0		2		3		1	

Table 3—continued

	1994		1995		1996		1997		1998		1999	
	Step	*r*	Step	*r*	Step	*r*	Step	*r*	Step	*r*	Step	*r*
Combined birds												
Hay			1	+0.303***			1	+0.338**				
H + B last hayed												
H + B last burned					2	−0.346						
Burn	3	−0.202*	3	−0.437****	3	−0.467***	2	−0.289**	1	−0.709***		
Years since treatment												
Litter	1	+0.435****					3	+0.240*	2	+0.525	1	+0.308**
n steps	3		5		5		3		6		1	

Multiple *r* statistics ranged from 0.468 to 0.782, 0.275 to 0.615, 0.219 to 0.574, and 0.308 to 0.748, for Henslow's Sparrow, Grasshopper, Sparrow, Dickcissel, and combined birds, respectively. $N = 96$, 91, 81, 82, 86, and 83 unit surveys for each year respectively. *P* values for the regressions ranged from 0.0000 to 0.0000, 0.000 to 0.009, 0.0000 to 0.046, and 0.0000 to 0.005 respectively.

Table 4. Percentage of unit surveys for Henslow's and Grasshopper Sparrows and Dickcissels in June, 1994 to 1999 which began in each of six time periods (Central Standard Time), by management type. The earliest survey began at 07h07 and the latest ended at 18h25.

	Hay ($n = 242$)	Hay + burn last hayed ($n = 130$)	Hay + burn last burned ($n = 126$)	Burn ($n = 37$)	Total
07h00 to < 09h00	5.8	23.8	19.8	32.4	15.3
09h00 to < 11h00	23.1	26.9	22.2	21.6	23.7
11h00 to < 13h00	24.0	13.1	19.0	18.9	19.8
13h00 to < 15h00	21.0	16.9	22.2	10.8	19.6
15h00 to < 17h00	20.2	16.9	12.7	13.5	17.2
17h00 to < 19h00	5.8	2.3	4.0	2.7	4.3

abundance with increasing litter, while Grasshopper Sparrow showed the reverse. Dickcissel usually showed no significant relationship with litter. In these ANOVA, management type had significant results relatively more often than litter (9 of 12 versus 8 of 16 tests, respectively).

Litter and years since last treatment

Years since last treatment had only one significant effect in the four overall regressions (Table 2) and three significant effects in 24 annual regressions (Table 3), in spite of its vital role in explaining bird abundance in a previous study where litter data were insufficient for analysis (Swengel 1996). To test whether litter was capturing effects previously attributed to years since last treatment, we reran all regressions excluding litter but retaining years since last treatment as an independent variable. Years since last treatment had a significant effect on bird abundance in the same overall regressions that litter had, and in all but four of the same annual regressions, with the same sign as litter in all cases, but a lower r in all except two overall and four annual regressions. All the new overall regressions, and all but five of the new annual regressions, had lower multiple r values than the original regressions including litter. In almost all cases, mean litter score recorded on unit surveys in each management type increased with years since last treatment (Figure 2).

Discussion

Time of day versus grassland bird detection

Walk *et al.* (2000) reported significantly higher singing rates of some grassland birds, including Henslow's Sparrow, during the night compared with sunrise and shortly after sunset. This is consistent with Robins (1971), who recorded Henslow's Sparrow singing rates for the entire 24–hour period. However, Robins (1971) reported calling throughout the day, when there was relatively less vari-

Table 5. Mean ±SD) relative bird abundance (individuals/km per unit survey) at southwestern Missouri prairies during June 1994 to 1999, by individual species and all species combined, for each management type and litter category. N = number of unit surveys in each sample. Means within a litter × species cell (testing for differences among management types, down a column) not followed by any similar capital letters are significantly different (Duncan's post-hoc test of log-transformed abundances, $P < 0.05$). Means within a management type × species cell (testing for differences among litter categories, across a line) not followed by any similar lower case letters are significantly different (Duncan's post-hoc test of log-transformed abundances, $P < 0.05$).

	Light litter[a]				Medium litter[b]				Heavy litter[c]			
	n	mean ± SD			*n*	mean ± SD			*n*	mean ± SD		
Henslow's Sparrow												
Hay[d]	17	6.82 ±6.59	A	b	126	10.74 ±11.87	A	b	99	15.78 ±10.58	A	a
Hay + burn												
Last hay[e]	20	2.14 ±2.81	B	c	90	7.62 ±10.60	AB	b	20	13.35 ±9.20	A	a
Last burn[f]	84	1.04 ±2.31	B	c	15	2.77 ±2.69	BC	b	27	13.88 ±8.82	A	a
Burn[g]	13	2.49 ±3.28	B	a	15	2.72 ±4.94	C	a	9	4.27 ±8.93	B	a
Grasshopper Sparrow												
Hay	17	4.98 ±5.33	A	a	126	5.46 ±5.59	A	a	99	1.56 ±2.60	A	b
Hay+burn												
Last hay	20	2.74 ±2.73	AB	a	90	3.73 ±5.46	AB	a	20	3.03 ±4.62	A	a
Last burn	84	1.75 ±2.31	B	a	15	1.40 ±2.36	BC	a	27	1.36 ±2.37	A	a
Burn	13	2.02 ±2.06	AB	a	15	0.21 ±0.80	C	b	9	0.00 ±0.00	A	b
Dickcissel												
Hay	17	12.64 ±6.59	A	a	126	10.48 ±7.44	A	a	99	11.55 ±7.16	A	a
Hay + burn												
Last hay	20	5.96 ±5.49	B	b	90	9.44 ±6.66	A	a	20	8.58 ±6.27	A	ab
Last burn	84	9.16 ±4.99	A	a	15	6.63 ±4.13	A	a	27	9.94 ±7.04	A	a
Burn	13	11.58 ±5.00	A	a	15	7.68 ±7.11	A	a	9	9.83 ±6.39	A	a
Combined birds												
Hay	17	24.44 ±10.10	AB	a	126	26.67 ±15.63	A	a	99	28.89 ±13.53	A	a
Hay + Burn												
Last hay	20	10.84 ±7.88	C	b	90	20.80 ±15.62	A	a	20	24.97 ±12.20	A	a
Last burn	84	11.95 ±6.35	C	b	15	10.80 ±5.38	B	b	27	25.07 ±13.16	A	a
Burn	13	16.08 ±8.49	BC	a	15	10.60 ±8.47	B	a	9	11.99 ±11.19	B	a

[a] F tests for light litter × species cells: 11.61, 3.41, 6.47 and 5.98 for Henslow's Sparrow, Grasshopper Sparrow, Dickcissel, and combined birds, respectively, with P (rounded to the fourth decimal place) = 0.0000, 0.0195, 0.0004, and 0.0008.

[b] F tests for medium litter × species cells: 7.48, 10.96, 1.97 and 15.22, respectively, with P = 0.0000, 0.0000, 0.1193, and 0.0000.

[c] F tests for heavy litter × species cells: 8.58, 2.27, 1.80 and 8.66, respectively, with P = 0.0000, 0.0825, 0.1493, and 0.0000.

[d] F tests for hay × species cells: 9.35, 22,42, 1.31 and 1.51, respectively, with P = 0.0001, 0.0000, 0.2729, and 0.2220, respectively.

[e] F tests for hay + burn last hay × species cells: 7.95, 0.18, 3.90, and 7.50, respectively, with P = 0.006, 0.8315, 0.0227, and 0.0000, respectively.

[f] F tests for hay + burn last burn × species cells: 70.28, 0.64, 1.81, and 10.36, respectively, with P = 0.000, 0.5283, 0.1682, and 0.0000, respectively.

[g] F tests for burn × species cells: 0.19, 10.42, 2.35, and 1.78, respectively, with P = 0.8281, 0.0003, 0.1106, and 0.1850, respectively.

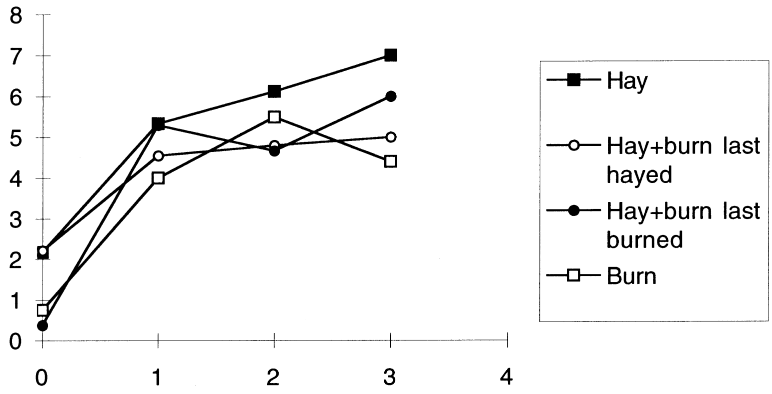

Figure 2. Mean litter scores in June surveys at southwestern Missouri prairies during 1994–1999, for each year since last treatment, by management type.

ation than between the nocturnal/crepuscular period and daytime. Kantrud (1981) and Bollinger (1995) reported relatively little variation in calling by grassland birds during the day, consistent with our previous and current analyses (Swengel 1996, Table 2). A bias toward increased grassland bird singing earlier than later in the day was not apparent in our study, but even if there were, this would not have contributed to the higher bird abundance recorded under haying (Tables 2, 3, 5). Surveys in that management type were relatively underrepresented in the earliest time period, while all management types with a burning component were over-represented then (Table 4).

Adult density versus breeding success

Concerns have been raised over whether adult density reliably relates to nesting success (Van Horne 1983, Vickery *et al.* 1992, Winter and Faaborg 1999). However, grassland bird studies that have measured both have typically found similar results, or at least no significant conflict. Of the four species analysed by Winter and Faaborg (1999) for area sensitivity, abundance of adult Henslow's Sparrows increased significantly with increasing patch size, while a slight but non-significant increase was shown in nesting success. Dickcissel nesting success was significantly greater in larger patches while no significant relationship for adult density was shown. The other two species, including Grasshopper Sparrow, showed no significant patterns for either measure. Of the three species analysed by Vickery *et al.* (1992), only two to six nests were found for two species, including Grasshopper Sparrow. The third species showed no significant pattern between nesting success and category of territory density. Skinner (1975) described a general similarity in Grasshopper Sparrow adult and nest densities, with greater values for both in sites grazed moderately, and lower values in idled sites. Differences between adult and breeding measures therefore appear to be a matter not of direction (opposite patterns) but of degree (a significant pattern for one and a non-significant pattern of similar direction, or no pattern, for the other). A true conflict between adult abundance and breeding success can only be tested when both nest success and density (total breeding productivity) are assessed.

Litter versus management

Litter and management both greatly influence grassland bird abundance (e.g. Kahl *et al.* 1985, Bollinger *et al.* 1990, Herkert 1994a, Dale *et al.* 1997), but relatively few studies (e.g. Owens and Myres 1973, Vickery *et al.* 1999) have analysed the effects of both litter and management simultaneously. Our results on management and litter preferences were consistent with the literature, but perhaps showed a stronger negative effect by burning and positive effect by rotational haying on the species tested due to our large sample size of each management type in similar prairies. For example, Winter (1998) did not find a significant difference in Henslow's Sparrow abundance between haying and burning during 1995 to 1997 at 13 study sites (all of which were surveyed in our study). Nonetheless, her and our results are not statistically contradictory, as she did not find significantly higher Henslow's Sparrow abundance with burning.

Although litter affected bird abundance profoundly in this study, even more important was how that litter was obtained: given a certain litter quantity, the management type used had a powerful and independent effect on bird abundance. Haying nearly always resulted in the highest bird abundance, and burning the lowest, within each litter category (Table 5). Greater consistency among years in vegetation structure may help explain this preference for hayed sites over burned or hayed + burned ones. Knick and Rotenberry (2000) found a significant positive effect of long-term consistency in vegetative cover type on abundance of scrub and grassland birds, while hayed areas have been shown to remain more consistent in vegetation height and litter from year to year than burned areas (Curtis and Partch 1950, Skinner *et al.* 1984, pers. obs.).

The higher average litter scores in the first year after treatment for haying versus burning, and hay + burn last hayed versus last burned (Figure 2) corresponds to Henslow's Sparrow's preference for haying over burning (Tables 2, 3, 5). However, while Grasshopper Sparrow preferred lighter litter, and litter scores averaged the highest in haying, the abundance of this species was significantly higher in haying. Thus, managing for consistently light/medium litter is less important for Grasshopper Sparrow than using a favourable management type. A haying regime designed to accommodate Henslow's Sparrow (i.e. by allowing one year of heavy litter in the rotation) is more favourable for Grasshopper Sparrow than fire regimes specifically designed for Grasshopper Sparrow by avoiding any years with heavy litter. However, ideal hay regimes for Grasshopper Sparrow would prevent litter from becoming heavier than medium.

Considerable concern has been expressed over the destruction of nests and nestlings from summer haying (e.g. Bollinger *et al.* 1990, Winter 1998). The midsummer haying we studied as conservation management occurs after the primary breeding season for grassland birds in that area (Winter 1999), in contrast to the earlier first hay cutting in the farm landscape. Nonetheless, some nests and pre-fledglings were doubtless destroyed when our study sites were hayed. However, fewer nests occur in the first year after cool-season fire due to sparse litter and live vegetation cover during the primary nesting period. Thus, cool-season burning reduces nest density more than midsummer haying.

Vegetation measurement in grassland bird studies

Although, from 1992 to 1993, no vegetation measurements were taken in this study, significant effects of management type and years since last treatment on bird abundance were still obtained (Swengel 1996). In 1994 we began a visual estimate of litter volume, requiring <30 seconds per unit survey to obtain, to include one measure of vegetation structure while still maximising time available for bird surveys. Although other vegetation measures also have important effects on grassland birds (e.g. Skinner 1975, Skinner *et al.* 1984), there is a trade-off in efficiency between bird surveying and vegetation sampling. When litter (a simple index that can be assessed rapidly) was significant in our analyses, it was at least as robust in accounting for variability in grassland bird abundance as the vegetation measures in other studies of the same species, using data which required more effort to collect (e.g. Herkert 1994a, Bollinger 1995).

Litter increased progressively with years since last treatment in this study of units managed about once every two years (maximum four years) (Figure 2). This colinearity made litter and treatment year almost interchangeable, but litter was nearly always more important. However, because of the rapid initial regrowth of tallgrass prairie after burning or cutting and its asymptotic approach to a high litter level (Kucera and Ehrenreich 1962, Figure 2), the relationship between litter and years since last treatment observed here could be weaker in sites with longer intervals between management treatments than in our study prairies. The value of years since last treatment as a surrogate for capturing litter effects should not be assumed, but tested. Either measure (litter score or years since last management) can be more rapidly obtained than quantitative vegetative measurements, which are valuable but more time-consuming to gather. When time and resources for monitoring birds are very limited, a reduction in time spent on vegetative measures can translate directly into an increased number of bird surveys conducted.

Management implications

Steep declines in populations of Henslow's and Grasshopper Sparrows (Sauer *et al.* 1999) should influence management of dry Missouri prairies preferentially over more secure species of animals and plants. Low or declining grassland bird populations in association with burning have been documented in numerous studies, with *Ammodramus* sparrows faring particularly poorly with fire (e.g. Zimmerman 1988, 1992, Herkert 1994b, Swengel 1996). Thus, rotational haying should be employed more than burning in the management of Henslow's and Grasshopper Sparrows populations. Henslow's Sparrow benefits from longer intervals between treatments (⩾2 years) while Grasshopper Sparrow favours annual to biennial haying, but all birds surveyed thrived with biennial midsummer haying. Management treatments for these birds should be less frequent in more northerly or sparser prairies, where litter accumulates more slowly.

The conservation benefits of non-intensive agricultural techniques such as haying, grazing and idling are well documented (Owens and Myres 1973, Skinner 1975, Dale *et al.* 1997), but this knowledge is inadequately applied in North American grassland conservation. Studies of these treatments often underestimate their potential for conservation by documenting the incidental effects on biota of agricultural practices designed for economic purposes. These techniques could realize their true conservation potential if unshackled from the economic restraints of the farm economy and applied scientifically for conservation purposes on reserves.

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References

Bollinger, E. K. (1995) Successional changes and habitat selection in hayfield bird communities. *Auk* 112: 720–730.

Bollinger, E. K., Bollinger, P. B. and Gavin, T. A. (1990) Effects of hay-cropping on eastern populations of the Bobolink. *Wildl. Soc. Bull.* 18: 142–150.

Curtis, J. T. and Partch, M. L. (1950) Some factors affecting flower production in *Andropogon gerardi*. *Ecology* 31: 488–489.

Dale, B. C., Martin, P. A. and Taylor, P. S. (1997) Effects of hay management on grassland songbirds in Saskatchewan. *Wildl. Soc. Bull.* 25: 616–626.

Fretwell, S. (1973) The regulation of bird populations on Konza Prairie: the effects of events off the prairie. Pp. 71–76 in L. C. Hulbert, ed. *Third midwest prairie conference proceedings.* Manhattan, KS: Kansas State University.

Granfors, D. A., Church, K. E. and Smith, L. M. (1996) Eastern Meadowlarks nesting in rangelands and conservation reserve program fields in Kansas. *J. Field. Orn.* 67: 222–235.

Herkert, J. R. (1994a) The effects of habitat fragmentation on midwestern grassland bird communities. *Ecol. Appl.* 4: 461–471.

Herkert, J. R. (1994b) Status and habitat selection of the Henslow's Sparrow in Illinois. *Wilson Bull.* 106: 35–45.

Herkert, J. R. and Glass, W. D. (1999) Henslow's Sparrow response to prescribed fire in an Illinois prairie remnant. *Stud. in Avian Biol.* 19: 160–164.

Kahl, R. B., Baskett, T. S., Ellis, J. A. and J. N. Burroughs. (1985) Characteristics of summer habitats of selected nongame birds in Missouri. *Missouri Agric. Exp. Sta. Res. Bull.* 1056.

Kantrud, H. A. (1981) Grazing intensity effects on the breeding avifauna of North Dakota native grasslands. *Can. Field-Nat.* 94: 404–417.

Knick, S. T. and Rotenberry, J. T. (2000) Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. *Ecology 81*: 220–227.

Klute, D. S. and Robel, R. J. (1997). Will conversion of Conversation Reserve Program (CRP) lands to pasture be detrimental to grassland birds in Kansas? *Am. Midl. Nat.* 137:202–212.

Knopf, F. L. (1994) Avian assemblages on altered grasslands. *Stud. in Avian Biol.* 15: 247–257.

Kucera, C. L. and Ehrenreich, J. H. (1962) Some effects of annual burning on central Missouri prairie. *Ecology* 43: 334–336.

Owens, R. A. and Myres, M. T. (1973) Effects of agriculture upon populations of native grassland birds of an Alberta fescue grassland. *Can. J. Zool.* 51: 697–713.

Peterjohn, B. G., Sauer, J. R. and Link, W. A. (1994) The 1992 and 1993 summary of the North American breeding bird survey. *Bird Popul.* 2: 46–61.

Robins, J. 1971. A study of Henslow's Sparrow in Michigan. *Wilson Bull.* 83: 39–48.

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

Sauer, J. R. and Droege, S. (eds.) (1990) *Survey designs and statistical methods for the estimation of bird population trends.* Washington, D.C.: U.S. Fish and Wildlife Service, Biol. Rep. 90(1).

Sauer, J. R., Hines, J. E., Thomas, I., Fallow, J. and Gough, G. (1999) *The North American Breeding Bird Survey, results and analysis 1966–1998*, version 98.1. Laurel, MD.: USGS Patuxent Wildl. Res. Ctr. (3 Dec 1999).

Skinner, R. M. (1975) Grassland use patterns and prairie bird populations in Missouri. Pp. 171–180 in M. K. Wali, ed. *Prairie: a multiple view.* Grand Forks, ND.: University of North Dakota.

Skinner, R. M., Baskett, T. S. and Blenden, M. D. (1984) *Bird habitat on Missouri prairies*. Jefferson City, MO: Missouri Department of Conservation (Terrestrial series 14).

Solecki, M. K. and Toney, T. (1986) Characteristics and management of Missouri's public prairies. Pp. 168–171 in G. K. Clambey and R. H. Pemble, eds. *Proceedings of the Ninth North American Prairie Conference.* Fargo, ND.: Tricollege University Center for Environmental Studies.

Swengel, S. R. (1996) Management responses of three species of declining sparrows in tallgrass prairies. *Bird Conserv. Internatl.* 6: 241–253.

The Nature Conservancy (1991) *Discover natural Missouri.* St Louis, MO: The Nature Conservancy.

Toney, T. E. (1993) *Public prairies of Missouri*. Jefferson City, MO: Missouri Department of Conservation.

Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *J. Wildl. Manag.* 47: 893–901.

Vickery, P. D., Hunter, M. L. and Wells, J. V. (1992) Is density an indicator of breeding success? *Auk* 109: 706–710.

Vickery, P. D., Hunter, M. L. and Wells, J. V. (1999) Effects of fire and herbicide treatment on habitat selection in grassland birds in southern Maine. *Stud. in Avian Biol.* 19: 149–159.

Walk, J. W., Kershner, E. L. and Warner, R. E. (2000) Nocturnal singing in grassland birds. *Wilson Bull.* 112: 289–292.

Winter, M. (1998) Effects of habitat fragmentation on grassland-nesting birds in southwestern Missouri. Ph.D. thesis, University of Missouri, Columbia.

Winter, M. (1999) Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri. *Wilson Bull.* 111: 515–527.

Winter, M. and Faaborg, J. (1999) Patterns of area sensitivity in grassland-nesting birds. *Conserv. Biol.* 13: 1424–1436.

Zimmerman, J. L. (1988) Breeding season habitat selection by the Henslow's Sparrow (Ammodramus henslowii). *Wilson Bull.* 100: 17–24.

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

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