

Grassland Bird Responses to Land Management in the Largest Remaining Tallgrass Prairie

CORINA J. RAHMIG,* WILLIAM E. JENSEN,*† AND KIMBERLY A. WITH,*‡

*Division of Biology, Kansas State University, Manhattan, KS 66506, U.S.A.

Abstract: Extensive habitat loss and changing agricultural practices have caused widespread declines in grassland birds throughout North America. The Flint Hills of Kansas and Oklahoma—the largest remaining tallgrass prairie—is important for grassland bird conservation despite supporting a major cattle industry. In 2004 and 2005, we assessed the community, population, and demographic responses of grassland birds to the predominant management practices (grazing, burning, and haying) of the region, including grasslands restored under the Conservation Reserve Program (CRP). We targeted 3 species at the core of this avian community: the Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus saviannarum*), and Eastern Meadowlark (*Sturnella magna*). Bird diversity was higher in native prairie hayfields and grazed pastures than CRP fields, which were dominated by Dickcissels. Although Dickcissel density was highest in CRP, their nest success was highest and nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) lowest in unburned hayfields (in 2004). Conversely, Grasshopper Sparrow density was highest in grazed pastures, but their nest success was lowest in these pastures and highest in burned hayfields, where cowbird parasitism was also lowest (in 2004). Management did not influence density and nest survival of Eastern Meadowlarks, which were uniformly low across the region. Nest success was extremely low (5–12%) for all 3 species in 2005, perhaps because of a record spring drought. Although the CRP has benefited grassland birds in agricultural landscapes, these areas may have lower habitat value in the context of native prairie. Hayfields may provide beneficial habitat for some grassland birds in the Flint Hills because they are mowed later in the breeding season than elsewhere in the Midwest. Widespread grazing and annual burning have homogenized habitat—and thus grassland-bird responses—across the Flint Hills. Diversification of management practices could increase habitat heterogeneity and enhance the conservation potential of the Flint Hills for grassland birds.

Keywords: brood parasitism, Conservation Reserve Program, density, diversity, grazing, nest survival, prescribed burning

Respuestas de Aves de Pastizal al Manejo de Tierra en el Remanente más Extenso de Tallgrass Prairie

Resumen: La pérdida de hábitat y el cambio de prácticas agrícolas han causado declinaciones generalizadas en las aves de pastizal en toda Norte América. Las Flint Hills en Kansas y Oklahoma—el remanente más extenso de tallgrass prairie—son importantes para la conservación de aves de pastizal no obstante que soporta una importante industria ganadera. En 2004 y 2005, evaluamos las respuestas de la comunidad, población y demografía de aves de pastizal a las prácticas de manejo predominantes (pastoreo, quema y almiar) en la región, incluyendo pastizales restaurados bajo el Programa de Conservación de Reservas (PCR). Nos centramos en tres especies en el núcleo de esta comunidad de aves: *Spiza americana*, *Ammodramus saviannarum* y *Sturnella magna*. La diversidad de aves fue mayor en las praderas nativas y en los pastizales pastoreados que en los campos del PCR, que fueron dominados por *S. americana*. Aunque la densidad de *S. americana* fue mayor en PCR, su éxito de nidación fue mayor y el parasitismo de nidos por *Molothrus ater* fue menor en las tierras no quemadas (en 2004). Por el contrario, la densidad de *A. saviannarum* fue mayor en los pastizales

†Current address: Department of Biological Sciences, Emporia State University, Emporia, KS 66801, U.S.A.

‡Address correspondence to K. A. With, email kwith@ksu.edu

Paper submitted December 27, 2007; revised manuscript accepted August 11, 2008.

pastoreados, pero su éxito de nidación fue menor en estos pastizales y mayor en los pastizales quemados, donde el parasitismo también fue menor (en 2004). El manejo no influyó en la densidad y supervivencia de nidos de *S. magna*, que fueron bajas en toda la región. El éxito de nidación fue extremadamente bajo (5–12%) en las tres especies en 2005, quizás debido a una sequía primaveral sin precedente. Aunque el PCR ha beneficiado a las aves en paisajes agrícolas, estas áreas pueden tener menor valor de hábitat en el contexto de la pradera nativa. Los terrenos con almiar pueden proporcionar hábitat benéfico a algunas aves de pastizal las Flint Hill porque son segados al final de la época reproductiva. El pastoreo extensivo y las quemas anuales han homogeneizado el hábitat—y por lo tanto las respuestas de las aves de pastizal—en las Flint Hills. La diversificación de las prácticas de manejo podría incrementar la heterogeneidad del hábitat y resaltar el potencial de conservación de las Flint Hills para las aves de pastizal.

Palabras Clave: densidad, diversidad, parasitismo de nido, pastoreo, Programa de Conservación de Reservas, quemas prescritas, supervivencia de nidos

Introduction

Nearly 80% of prairie in the United States has been converted to other land uses (Samson & Knopf 1994), which has precipitated widespread declines in grassland birds (Peterjohn & Sauer 1999). Where large remnants of prairie still occur, the predominant land-management practices of the region ultimately control habitat quality for grassland birds (Fuhlendorf & Engle 2001). For example, only 4% of tallgrass prairie remains (Samson & Knopf 1994), most of it located in the Flint Hills of Kansas and Oklahoma. The Flint Hills is thus considered important for grassland bird conservation. The American Bird Conservancy has designated 5 sites within the Flint Hills as globally important bird areas. The Flint Hills also support a major cattle industry, however. Season- or year-long stocking occurs on approximately 65% of managed grassland in the Flint Hills (With et al. 2008), where pastures are generally stocked with cow-calf units and burned every 2–3 years. Intensive-early stocking began in the 1980s and now occurs on 25% of managed grassland in the Flint Hills (With et al. 2008). Intensive-early stocked pastures are burned annually and “double stocked” for half the season (Smith & Owensby 1978). Population declines of Greater Prairie Chickens (*Tympanuchus cupido*) in Kansas coincide with the occurrence of intensive-early stocking (Robbins et al. 2002), but its effect on other grassland birds is unknown.

Recent changes in the intensity and distribution of cattle grazing in the Flint Hills may also contribute to higher brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) on grassland birds. Cowbirds lay their eggs in the nests of other songbirds, often removing host eggs in the process; brood parasitism thus has negative fitness consequences for the host (Lowther 1993). Cowbirds have always been abundant in the open grasslands of the Great Plains (Lowther 1993), where about half of grassland species experience moderate brood parasitism (10–30%, Koford et al. 2000), although much higher lev-

els occur in parts of the Flint Hills (>70%, Jensen & Cully 2005).

Native prairie is also hayed for livestock forage in the Flint Hills (approximately 7% of managed grassland; With et al. 2008). Mowing is done after or late in the nesting season of grassland birds in the region (mid-July), which contrasts with hayfields elsewhere in the United States, where mowing occurs earlier and repeatedly throughout the breeding season (Bollinger et al. 1990). Hayfields may thus afford high-quality habitat for grassland birds in the Flint Hills, but this has not been evaluated previously. Some grassland in the Flint Hills (approximately 3%) has been restored through the Conservation Reserve Program (CRP), a program under the U.S. Department of Agriculture that gives incentives to landowners to remove highly erodible cropland from production and manage it instead for soil, water, and wildlife conservation. The CRP is the largest conservation program on private lands in the United States, and populations of several grassland birds have benefited from the CRP (Reynolds et al. 1994; Herkert 1998, 2007; McCoy et al. 1999). Although CRP grasslands are an improvement over row crops, their benefit to grassland birds is less clear in landscapes where CRP fields are embedded within native prairie, such as in the Flint Hills.

Our objective was to evaluate how current land-management practices in the Flint Hills influence grassland birds at the community, population, and demographic level. Therefore, we assessed patterns of bird species richness and diversity related to management across the Flint Hills and differences in density, nest survival, and risk of brood parasitism among management treatments for the core species of this avian community (Zimmerman 1997). The Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus saviannarum*), and Eastern Meadowlark (*Sturnella magna*). Eastern Meadowlarks and Grasshopper Sparrows have declined by 72 and 65%, respectively, during the past 40 years (Butcher & Niven 2007), and Dickcissels are

considered a species of conservation concern (National Audubon Society 2004).

Methods

Study Region

The Flint Hills of Kansas and Oklahoma encompass over 50,000 km² of native tallgrass prairie. Although floristically diverse, it is dominated by 4 main grasses: big bluestem (*Andropogon gerardii*), Indian grass (*Panicum virgatum*), switchgrass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparium*). The structure and dynamics of the system are governed by the interaction of grazing, fire, and precipitation (Knapp et al. 1998). Precipitation averages about 855 mm annually, but is extremely variable among years. Rainfall was normal or above normal during the 2004 and 2005 breeding seasons (1 May–31 July; 2004, 43.5 cm; 2005, 39.4 cm; 1971–2005, $\bar{x} = 37.3 \pm 15.44$ cm, $n = 35$ years, Manhattan, Kansas). Nevertheless, precipitation was approximately 40% normal in spring 2005, making it the driest on record (1 March–31 May; 2004, 26.6 cm; 2005, 10.5 cm; 1971–2005, $\bar{x} = 26.5 \pm 10.11$ cm, $n = 35$ years).

In 2004 and 2005 we surveyed birds in 36, 10-ha plots (316 × 316 m) distributed among 7 management treatments as follows: burned ($n = 4$ plots) and unburned ($n = 4$) CRP fields (CRPB/U) planted to native grasses (CP2); burned ($n = 5$) and unburned ($n = 5$) native prairie hayfields (HAYB/U); burned ($n = 6$) and unburned ($n = 6$) season-long stocked cattle pastures (SLSB/U; approximately 0.6 cattle/ha grazed May–September); and burned ($n = 6$) intensive-early stocked cattle pastures (IESB; approximately 1.25 cattle/ha grazed May–mid July; Owensby et al. 1988). Burning in the Flint Hills is done in mid-April. Unburned sites were not burned that particular year. Most sites were on private land; thus, land-management decisions (i.e., burning) were made by landowners. We therefore needed to locate additional sites in 2005 to maintain our level of replication among burn treatments. We sampled 24 sites for 2 years and the other 24 sites in 1 year only (total = 48 sites surveyed over 2 years). Sites were also blocked by region (north, central, south) to encompass environmental variation in precipitation, productivity, and cowbird parasitism across the Flint Hills (Jensen & Cully 2005). We selected the location of study sites at random within pastures among several potential locations that exhibited representative topographic relief of the overall site, were within 0.8 km of the nearest vehicle access point, and were >100 m from a road, fence line, or gallery forest (i.e., edge). Random placement of plots was not possible in smaller fields (CRP, hayfields).

Vegetation Surveys

We surveyed vegetation on study sites at 40-m intervals along 4 transects spaced 40 m apart (280 × 120 m grid = 8 points/transect × 4 transects = 32 points/plot). At each sampling point, we visually estimated 6 vegetation cover types within a 0.25-m² sampling frame: percent standing cover of live grass, dead grass, forb, and woody growth; percent bare ground; and percent litter. We also estimated the mean litter depth as the average of measurements taken at the 4 corners of the sampling frame for each point. Finally, we estimated standing-crop biomass by taking visual obstruction readings (VOR; Robel et al. 1970) at a distance of 4 m from the center of the frame in each cardinal direction. We also calculated the standard deviation of the 4 VORs per point as an index of structural heterogeneity. Vegetation was sampled twice each season during the same 2-week intervals when bird surveys were conducted. To compare habitat among management treatments, we averaged vegetation measures across all sampling points and across both sampling periods for each plot.

Bird Surveys

We surveyed birds along a line transect (316 × 200 m = 6.3 ha) that bisected each study plot along the axis with the greatest elevation range. We conducted 2 bird surveys each year (24 May–10 June and 21 June–10 July 2004; 25 May–12 June and 20 June–2 July 2005). We estimated the perpendicular distance to each bird sighted or heard (excluding flyovers) along the transect within distance intervals of 0 m, 1–10 m, 11–20 m, 21–40 m, 41–70 m, and 71–100 m. We chose these intervals to minimize error in the estimation of greater distances and to standardize comparisons among observers. We began surveys approximately 15 min after sunrise and completed them within 3 h. Four observers conducted bird surveys each year, and all were experienced in distance estimation and grassland bird identification. Because of our site placement and the surrounding landscape context (grassland), our surveys emphasized the grass-dependent species of the Flint Hills.

Community Measures

We recorded species richness (S), the number of species present, at each site. For species diversity, we calculated the Shannon–Weiner index [$H' = -\sum(p_i \ln p_i)$], where p_i is the proportional abundance of species i . We also calculated Shannon's index of evenness ($E = H'/H_{\max}$), where $H_{\max} = \ln(S)$ and represents the maximum diversity possible at the site. Low evenness ($E \rightarrow 0$) means many individuals of only a few species were present.

Population Density

We estimated species-specific densities of singing males on each study site with Program Distance (Buckland et al. 2001; Thomas et al. 2004). Program Distance calculates densities (birds per hectare) on the basis of best-fit models of detection probability indicated by the lowest Akaike's information criterion (AIC) values. Because different observers conducted the bird surveys among regions (north, central, south) and could have differed in their ability to detect birds, we fitted separate detection-probability curves for each region and species, along with global detection-probability curves, to estimate the density of Dickcissels, Grasshopper Sparrows, and Eastern Meadowlarks on each site and year. These species were the only 3 in our study with sufficient numbers of detections ($n > 60$) to estimate detection functions (Buckland et al. 2001). We used AIC values corrected for small sample size (AIC_c) to choose the best detection function for each species and region (Table 1).

Nest Survival

We searched for nests every 7–10 days by rope dragging, which flushed incubating females. We rechecked nests every 3–4 days and recorded nest contents, including presence of cowbird eggs and nestlings. A nest was successful if it fledged at least one host nestling. Signs of failure included missing nest contents, egg-shell fragments, dead nestlings, feathers, or a disturbed nest cup. When the evidence was equivocal, we considered nests “successful” if nestlings were old enough to have fledged between visits. We assumed the total number of host or cowbirds fledged was the same as the number of nestlings present on our previous visit.

Table 1. Best-fit detection probability functions used to calculate density estimates for 3 grassland birds in the Flint Hills.

Year	Species	Region	Detections	Detection function/expansion
2004	DICK	south	97	uniform/cosine
		central	189	uniform/none
		north	89	uniform/none
	EAME GRSP	global	57	uniform/none
		south	45	uniform/simple polynomial
		central	95	hazard/cosine
2005	DICK	north	53	uniform/none
		south	183	uniform/cosine
		central	280	uniform/cosine
	EAME GRSP	north	138	uniform/none
		global	184	uniform/none
		global	354	hazard/none

Abbreviations: DICK, Dickcissel; EAME, Eastern Meadowlark; GRSP, Grasshopper Sparrow.

Statistical Analyses

We performed separate analyses for each year because not all plots could be surveyed both years and because of the marked difference in spring precipitation between years, which could interact with management to influence vegetation and thus grassland bird responses.

We used a randomized block design (PROC GLM; SAS Institute 2005) to compare species diversity and evenness among management practices. We performed separate analyses for densities of Dickcissels, Grasshopper Sparrows, and Eastern Meadowlarks across management types, again blocked by region. We used Fisher's least significant difference test to make pairwise comparisons among management regimes when F tests of overall differences in means were significant ($\alpha \leq 0.05$).

Daily nest-survival probabilities were analyzed with Mayfield logistic regression (Hazler 2004). This approach adjusts for the total number of nest-exposure days within a logistic-regression framework by treating each day as an individual Bernoulli trial in which the nest either survived (0) or failed (1), where failure was assumed to occur at the midpoint between visits. For each species we modeled daily nest survival as a function of management type (region as a fixed effect) with the logistic regression function in PROC GENMOD (SAS Institute 2005), which accommodates continuous and categorical (e.g., management type) variables. We excluded CRP in this analysis for Grasshopper Sparrows and Eastern Meadowlarks because they effectively did not nest in this habitat (<10 nests/CRP treatment).

We also tested for the effect of brood parasitism on nest-survival rates by modeling daily nest survival as a function of cowbird presence or absence in a nest. We used likelihood-ratio tests (type III sums of squares) to test for the significance of management effects.

We used logistic regression to model parasitism rates (nests parasitized/total nests) as a function of management (PROC GENMOD). We again excluded CRP from this analysis for Grasshopper Sparrows and Eastern Meadowlarks because few nests of either species were found in this habitat. We used a generalized linear model (PROC GENMOD) to model parasitism intensity (maximum number of cowbird eggs or nestlings in a nest) as a function of management; we assumed a Poisson distribution and used a log link to restrict estimates to positive values. We included region as a fixed effect in these analyses to account for the gradient in cowbird parasitism across the region (Jensen & Cully 2005). We used likelihood-ratio tests (type III sums of squares) to test for significance of management type on the probabilities and intensities of parasitism. Finally, we used a generalized linear model (PROC GENMOD) to investigate how brood parasitism affected the reproductive output of their hosts by comparing the number of host young fledged from successful

parasitized and nonparasitized nests. We again assumed a Poisson distribution and used a log link.

Results

Vegetation of Managed Grasslands

Burned areas had 3.2 times more bare ground and about one-third less standing crop biomass (assayed by VOR) than unburned grassland (bare ground: $\bar{X}_{\text{burned}} = 76.6\%$, $\bar{X}_{\text{unburned}} = 24.0\%$; VOR: $\bar{X}_{\text{burned}} = 19.4$, $\bar{X}_{\text{unburned}} = 26.8$; combined years; Supporting Information). Conversely, unburned areas had 5.7 times more dead grass and litter cover than burned grassland (dead grass: $\bar{X}_{\text{burned}} = 1.2\%$, $\bar{X}_{\text{unburned}} = 6.7\%$; litter depth: $\bar{X}_{\text{burned}} = 0.9$ cm, $\bar{X}_{\text{unburned}} = 4.8$ cm; combined years; Supporting Information). Live grass cover was 2 times greater on burned hayfields (highest) than on unburned CRP fields (lowest). Unburned CRP had higher biomass (2.4–2.8 times

more than the lowest, IESB), more dead grass (approximately 15 times greater than the lowest, CRPB), more litter (11.1–11.9 times more than the lowest, CRPB), and more forb cover (2.2–2.7 times more than the lowest, CRPB) than other managed grasslands (Supporting Information).

Community and Population Responses to Management

On average we encountered 4.4 species/site in 2004 (SD 1.05, range 2–7 species, $n = 36$ sites) and 5.3 species/site in 2005 (SD 1.56, range 3–9 species, $n = 36$ sites). The most common species, in order of decreasing abundance, were Dickcissels, Eastern Meadowlarks, Grasshopper Sparrows, and Brown-headed Cowbirds, all of which were detected in at least 50% of sites both years (Supporting Information). Species detected in at least 25% of the sites were Red-winged Blackbirds (*Agelaius phoeniceus*) and, in 2005, Henslow's Sparrows (*Am. henslowii*) and Northern Bobwhites (*Colinus*

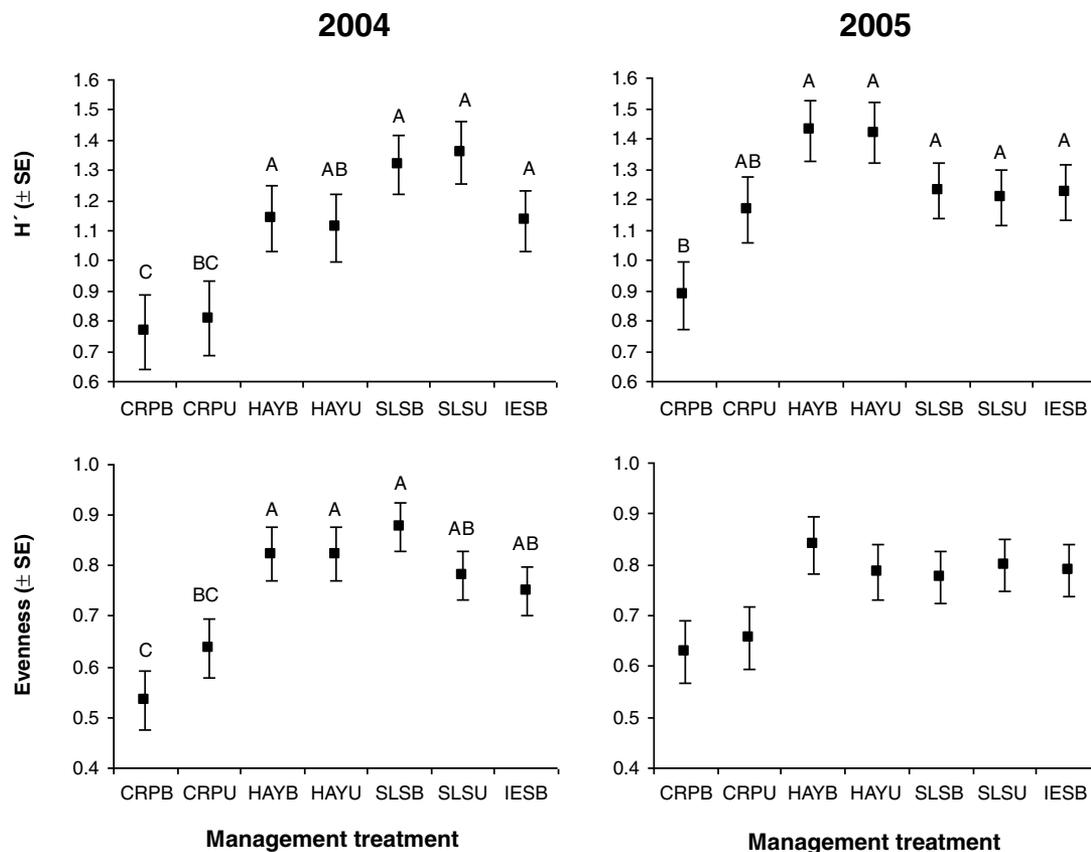


Figure 1. Grassland bird diversity (H') and evenness among different management practices of the Flint Hills. Means with the same letter are not significantly different ($\alpha = 0.05$) on the basis of Fisher's least significant difference tests. Management treatments: CRPB, burned Conservation Reserve Program field; CRPU, unburned Conservation Reserve Program field; HAYB, burned native hayfield; HAYU, unburned hayfield; SLSB, burned season-long grazed pasture; SLSU, unburned season-long grazed pasture; IESB, burned intensive-early season grazed pasture.

virginianus). Management had a significant effect on bird species diversity (H') in both years, which was lowest in CRP fields (2004: $F = 4.34$, $p = 0.005$; 2005: $F = 2.99$, $p = 0.023$; Fig. 1). Management also influenced community evenness in 2004 ($F = 4.56$, $p = 0.005$) but not in 2005 ($F = 1.76$, $p = 0.146$). In 2004 the

most even communities were in SLSB and hayfields, with the least even communities found in CRP fields, which were dominated by Dickcissels.

Management influenced densities of Dickcissels and Grasshopper Sparrows, but not Eastern Meadowlarks, in both years (Fig. 2). Dickcissel densities were up to 3

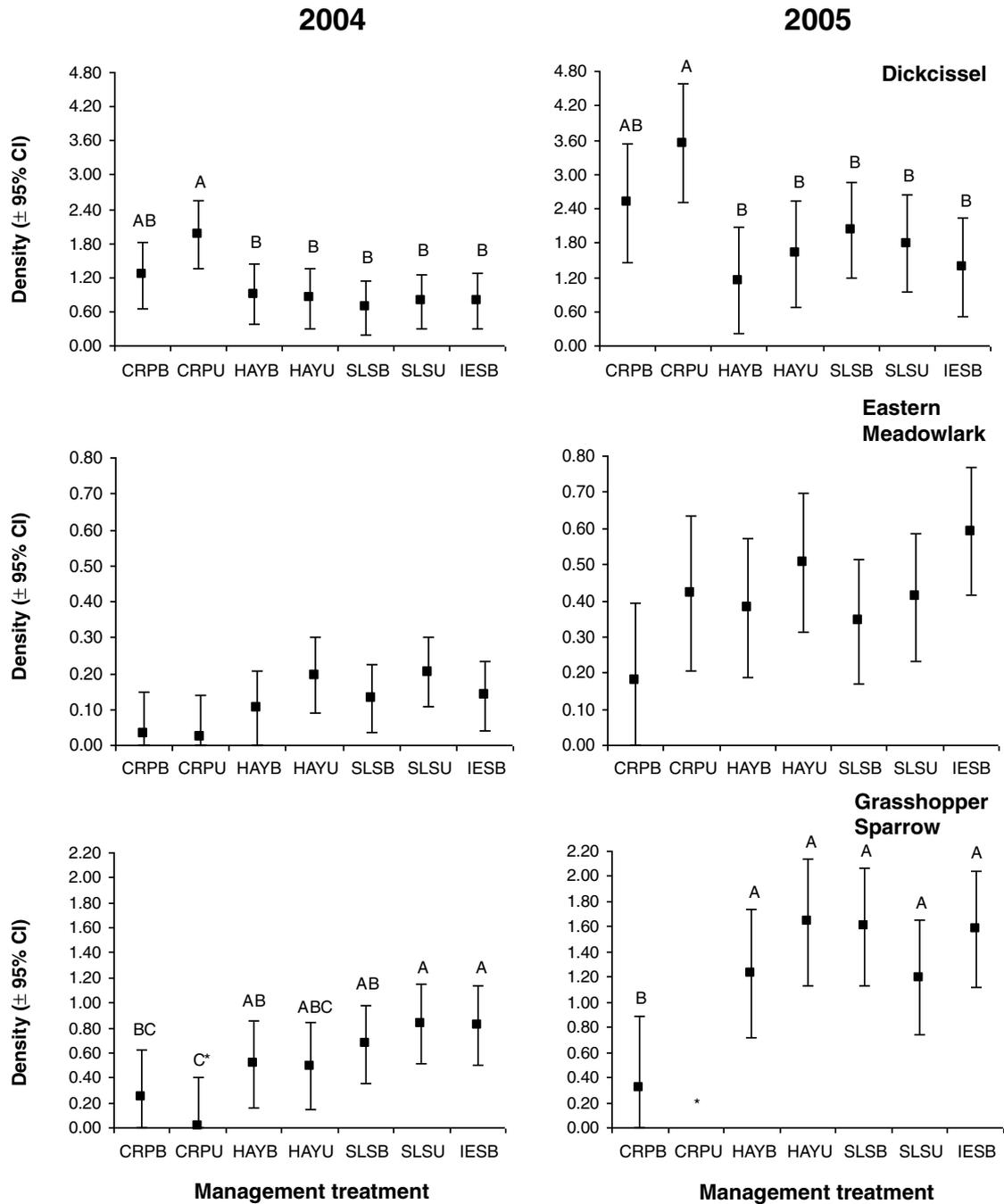


Figure 2. Densities (mean and 95% CI) of Dickcissels, Eastern Meadowlark, and Grasshopper Sparrows among management practices of the Flint Hills. The Conservation Reserve Program (CRPU) was not included in the analysis of Grasshopper Sparrow (GRSP) density in 2005, and the lower interval of GRSP density in CRPU was truncated at zero in 2004. Means with the same letter are not significantly different ($\alpha = 0.05$) on the basis of Fisher's least significant difference tests. Management treatment abbreviations are defined in Fig. 1.

times greater in unburned CRP than in other managed grasslands (2004: $F = 2.65$, $p = 0.037$; 2005: $F = 2.84$, $p = 0.028$). Conversely, densities of Grasshopper Sparrows were lowest in CRP both years—approximately 3–10 times greater in IESB and SLSU (2004: $F = 3.70$, $p = 0.013$; 2005: $F = 3.06$, $p = 0.020$).

Management Effects on Nest Survival

We found 531 Dickcissel, 166 Grasshopper Sparrow, and 119 Eastern Meadowlark nests in 2004 and 416 Dickcis-

sel, 164 Grasshopper Sparrow, and 149 Eastern Meadowlark nests in 2005 (1545 nests). Dickcissel daily nest survival was influenced by management in 2004 ($\chi^2[6] = 12.60$, $p = 0.050$; Fig. 3). Dickcissel nest success was significantly higher in HAYU (48.1%, assuming a 23-day nesting cycle) than in all other management types (16.4% SLSB–26.6% CRPU). Management also influenced daily nest survival in Grasshopper Sparrows in 2004 ($\chi^2[4] = 13.08$, $p = 0.011$; Fig. 3). Daily nest survival was significantly higher in HAYB (overall nest success of

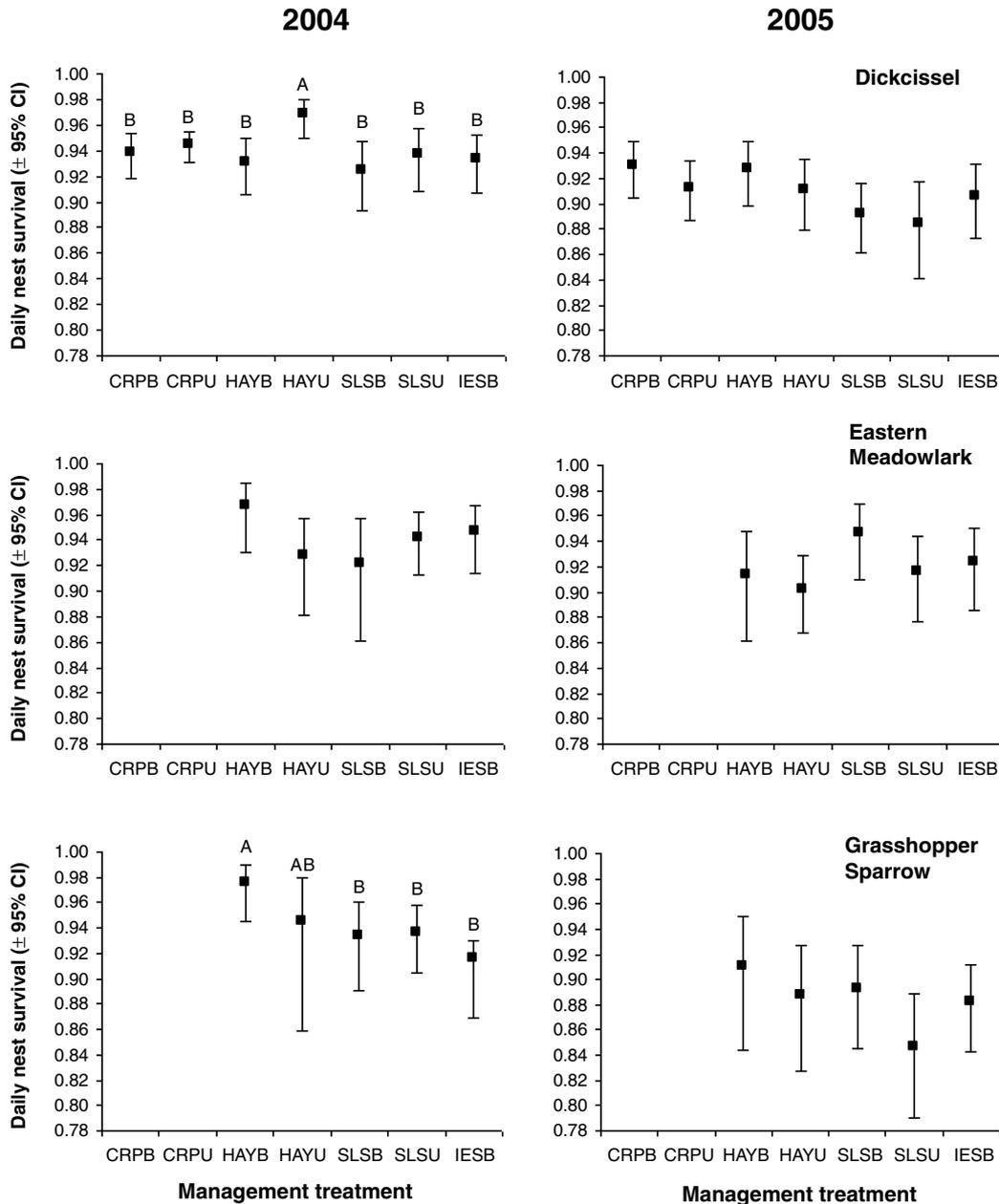


Figure 3. Daily nest survival of 3 grassland birds among management practices of the Flint Hills. Means with the same letter are not significantly different ($\alpha = 0.05$) on the basis of least significant difference tests. Management treatment abbreviations are defined in Fig. 1.

55.7%, assuming a 24-day nesting cycle) than in pastures (12.3% IESB–20.9% SLSU).

In 2005 daily nest survival for Dickcissels and Grasshopper Sparrows was low across all sites and did not differ significantly among management types ($\chi^2[6] = 3.58, p = 0.47$ and $\chi^2[4] = 8.59, p = 0.20$, respectively). Mean daily nest survival rates were 0.912 (95% CI: 0.902, 0.921) for Dickcissels and 0.884 (95% CI: 0.864, 0.901) for Grasshopper Sparrows. These rates translate into an overall nest success of 12.0% for Dickcissels and 5.1% for Grasshopper Sparrows. Daily nest survival for Eastern Meadowlarks was not influenced by management in either year (2004: $\chi^2[4] = 4.37, p = 0.36$; 2005: $\chi^2[4] = 4.14, p = 0.39$). Mean daily nest survival rates were 0.940 (95% CI: 0.925, 0.952) in 2004 and 0.919 (95% CI: 0.904, 0.933) in 2005. These rates translate into an overall nest success of 17.6 and 9.5% in 2004 and 2005, respectively (assuming a 28-day nesting cycle).

The presence of cowbird eggs or nestlings had no significant effect on daily nest survival in either year (2004: $\chi^2[1] = 0.01, p = 0.915$; 2005: $\chi^2[1] = 1.08, p = 0.300$). Predation was the main cause of nest failure (2004: 79%; 2005: 83%). Desertion also contributed to nest failure, accounting for 15% (2004) and 12% (2005) of failed nests.

Management Effects on Brood Parasitism

Parasitism rates differed significantly by host species (2004: $\chi^2[2] = 13.48, p = 0.001$; 2005: $\chi^2[2] = 33.82, p < 0.001$), and were highest for Dickcissels (2004: 43%; 2005: 47%) and Grasshopper Sparrows (2004: 42%; 2005: 45%) and lowest for Eastern Meadowlarks (2004: 25%; 2005: 24%). Management influenced the probability of a Dickcissel nest being parasitized (2004: $\chi^2[6] = 26.77, p < 0.001$; 2005: $\chi^2[6] = 29.86, p < 0.001$). In 2004 Dickcissels were at lowest risk in HAYU, whereas in 2005 they were also at low risk in CRPB (Fig. 4). The probability of a Grasshopper Sparrow nest being parasitized also differed among management types (2004: $\chi^2[4] = 21.38, p < 0.001$; 2005: $\chi^2[4] = 11.15, p = 0.025$). Nests were least likely to be parasitized in HAYB in 2004, but in 2005 nests were at lowest risk of parasitism in SLSU and HAYU (Fig. 4). Eastern Meadowlark nests had a lower probability of being parasitized in HAYU than any other management type in 2004 ($\chi^2[4] = 18.05, p = 0.001$), but differences were not significant in 2005 ($\chi^2[4] = 1.87, p = 0.760$). Management had a marginal effect on the intensity of brood parasitism in 2004 ($\chi^2[6] = 10.83, p = 0.094$), but not in 2005 ($\chi^2[6] = 6.21, p = 0.400$). There were also significant regional effects in parasitism across all species in both years, where nests were parasitized by cowbirds more often, and with greater intensity, in the northern part of the Flint Hills (all species, 2004: $\chi^2[2] = 13.89, p < 0.001$; 2005: $\chi^2[2] = 7.99, p = 0.018$). For example, 2.1–4.7 times more Dickcissel nests, 2.9–4.7 times more Eastern Meadowlark, and 3.6–4.4 times

more Grasshopper Sparrow nests were parasitized in the northern than southern Flint Hills (Table 2).

Parasitism influenced the number of host nestlings fledged from successful nests in both years (2004: $\chi^2[1] = 36.13, p < 0.001$; 2005: $\chi^2[1] = 21.11, p < 0.001$). In 2004 successful unparasitized nests ($n = 129$) fledged an average of 3.59 (95% CI: 3.31, 3.90) host nestlings, whereas successful parasitized nests ($n = 161$) fledged an average of 2.36 (95% CI: 2.11, 2.65) host nestlings. Nests that had been parasitized thus fledged 1.23 fewer young than nests that had not been parasitized. In 2005 successful unparasitized nests ($n = 91$) fledged an average of 3.32 (95% CI: 2.96, 3.72) host nestlings, whereas successful parasitized nests ($n = 58$) fledged an average of 1.76 (95% CI: 1.45, 2.14) host nestlings. This translates into 1.56 fewer young fledged in parasitized than in unparasitized nests.

Discussion

Because it is unrealistic to expect the restoration of millions of hectares of agricultural and grazing lands (Peterjohn 2003), understanding how grassland birds respond to current management practices is essential for their conservation within the context of these human-dominated landscapes. By simultaneously assessing community, population, and demographic responses to the predominant management regimes of the Flint Hills, we gained a more comprehensive understanding of what constitutes high-quality habitat for grassland birds within this highly managed system. Avian diversity and density are generally lower in grasslands than most other habitats, typically having <10 species and species densities of 0.5–2 pairs/ha (Wiens 1973; Cody 1985). Although we observed up to 9 species/site, only 4–5 species were encountered routinely (>50% plots). The most abundant were Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows, followed by Brown-headed Cowbirds and Red-winged Blackbirds or Henslow's Sparrows. This is consistent with other studies in the Flint Hills, which likewise report 4–5 grass-dependent ("grassland obligate") species as common (Zimmerman 1997; Coppedge et al. 2008). Although low, this is comparable to bird diversity in some other Great Plains grasslands. For example, of some 15 grass-dependent species in mixed-grass prairie in North Dakota, only 5 commonly occur (>50%) in cattle-grazed pastures, similar to our system (Lueders et al. 2006).

Grazed pastures and native prairie hayfields generally supported a more diverse and even assemblage of grassland birds than CRP fields (especially burned CRP). Although seeded with the dominant grasses of the tall-grass prairie, CRP fields differed structurally from native prairie hayfields or grazed pasture. Unburned CRP fields have higher standing crop biomass, more litter, more

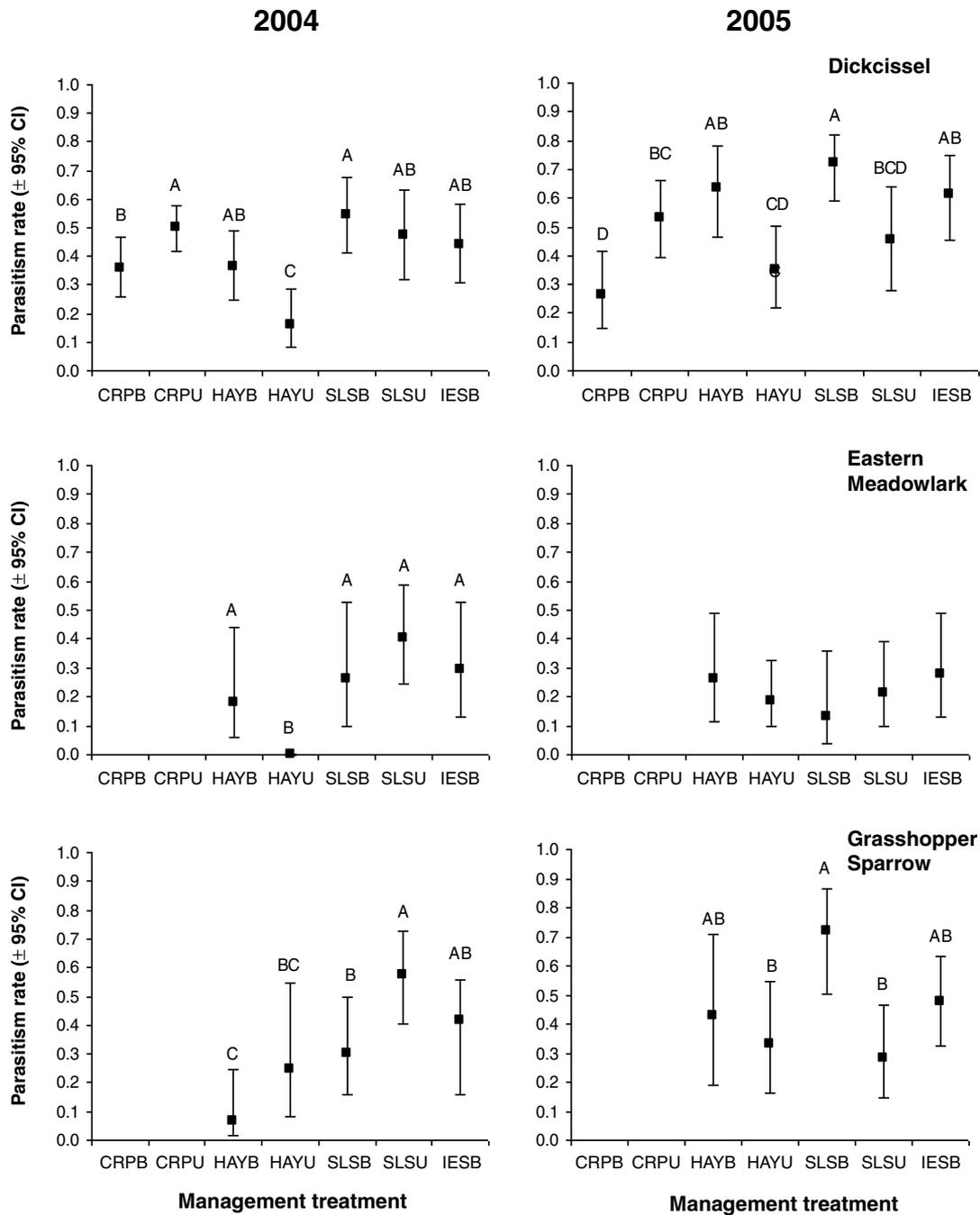


Figure 4. Rates of brood parasitism by Brown-headed Cowbirds for 3 grassland birds in different management practices common to the Flint Hills. Means with the same letter are not significantly different ($\alpha = 0.05$) on the basis of least significant difference tests. Management treatment abbreviations are defined in Fig. 1.

dead grass cover, more forb cover, and greater structural heterogeneity than other (especially unburned) management treatments (Supporting Information). Although bird species richness in CRP fields was similar to that of other managed grasslands in the Flint Hills ($\bar{x} = 4.6$ species, [SD 1.63], $n = 16$ site-years), they were dominated by Dickcissels. High Dickcissel density in CRP has been reported consistently (Best et al. 1997; Delisle & Savidge

1997; Robel et al. 1998), which is in keeping with this species' habitat preference for dense, tall vegetation and high forb cover (Temple 2002). Nevertheless, density is not an indication of habitat quality (Van Horne 1983), which is better assayed by reproductive success (Vickery et al. 1992). Daily nest survival for Dickcissels was actually highest in unburned hayfields (at least in 2004), where densities were about half that found in unburned

Table 2. Regional variation in brood parasitism rate (% nests parasitized) and intensity (cowbird eggs per parasitized nest) by Brown-headed Cowbirds on 3 grassland birds in the Flint Hills.

Species	Year	Region	Nests (n)	Percent parasitized* (χ^2 , p)	Parasitism intensity
Dickcissel	2004	north	170	57.6 (23.74, <0.001)	1.79
		central	213		1.47
		south	157		1.39
	2005	north	61	83.6 (89.67, <0.001)	2.16
		central	238		1.52
		south	118		1.48
Eastern Meadowlark	2004	north	46	34.8 (4.59, = 0.101)	1.89
		central	25		1.75
		south	49		1.00
	2005	north	52	36.5 (13.97, <0.001)	1.68
		central	45		2.00
		south	52		1.20
Grasshopper Sparrow	2004	north	62	62.9 (16.10, <0.001)	2.17
		central	73		1.68
		south	40		1.29
	2005	north	46	67.4 (30.37, <0.001)	1.66
		central	63		2.00
		south	55		1.11

*Logistic regression results by host species are presented for parasitism rate.

CRP. Whether this reflects density-dependent effects on reproduction or habitat-specific differences in predation pressure is unknown.

Although Dickcissels were most abundant in CRP (especially CRPU), Grasshopper Sparrows and Eastern Meadowlarks had their lowest abundance within CRP (especially CRPB) and nested infrequently within these habitats. In contrast, CRP is source habitat for Grasshopper Sparrows and Eastern Meadowlarks in Missouri (McCoy et al. 1999), perhaps because they are seeded to cool-season grasses (CP1), which may create more attractive habitat for these species than the warm-season grass (CP2) plantings of the Flint Hills. Eastern Meadowlarks prefer moderately tall grasslands with abundant litter cover, high grass cover, and some forbs (Lanyon 1995). Although CRP fields in the Flint Hills appear to afford suitable habitat for meadowlarks, it may be that these fields are simply too small (approximately 12 ha) to satisfy this species' area requirements (5 ha; Herkert 1994), especially given the availability of much larger grasslands in the surrounding landscape. Conversely, Grasshopper Sparrows prefer more open grassland of intermediate height with some bare ground (Vickery 1996), which contrasts with the tall, dense vegetation of CRP fields. Thus, although CRP is better than row-crop agriculture (Best et al. 1997), it may not provide high-quality habitat for some grassland birds in the Flint Hills, especially given that it comprises a minor (<3%) portion of the landscape and is embedded within a much larger grassland as opposed to agricultural matrix.

Although current grazing practices, such as intensive-early stocking, have been implicated in the decline of some local grassland bird populations (Robbins et al.

2002), we found no significant effect of grazing system (season long vs. intensive-early stocking) on bird diversity or on the density or nest survival of the 3 core species. Relative to other management treatments, pastures generally supported lower densities of Dickcissels, moderately high densities of Eastern Meadowlarks, higher densities of Grasshopper Sparrows, and moderate-to-low reproductive success for all 3 species. This does not suggest that grazing has no effect on grassland birds, however. Grazing—and the burning that accompanies it—is so widespread across the Flint Hills that it has likely homogenized habitat and thus grassland bird responses to grazing effects. Almost all the grassland in the Flint Hills is grazed and up to two-thirds is burned annually in the spring (With et al. 2008). Historically, neither grazing nor burning was as widespread or uniform as in the modern landscape. The historical fire regime averaged 2–3 fires every 5 years (Collins & Gibson 1990), and native ungulates roamed large areas and effectively applied rest-rotational grazing to the landscape (Fuhlendorf & Engle 2001). Grazing is now so tightly coupled with burning in the Flint Hills that it is impossible to determine whether fire or grazing has the greater effect on grassland birds.

Rest-rotational grazing is not commonly practiced in the Flint Hills. Native prairie hayfields are thus often the only “ungrazed” prairie available. Although bird densities were similar in hayfields and grazed pastures, nest success for Dickcissels and Grasshopper Sparrows was approximately 2–4.5 times higher and brood parasitism 3.5–7 times lower in hayfields than other managed grasslands (at least in 2004). Because they are mowed late in the season in the Flint Hills, hayfields may simulate “rested” prairie in the larger grazed landscape. Thus,

native prairie hayfields contribute to broader-scale heterogeneity, which provides beneficial habitat for grassland birds, particularly species, such as Henslow's Sparrows, that are otherwise absent from burned, grazed prairie. This contrasts with elsewhere in the Midwest, where hayfields may function as "ecological traps" for grassland birds because of earlier and more frequent cutting throughout the breeding season (Bollinger et al. 1990).

Management may also indirectly affect grassland birds by increasing cowbird abundance. Cattle grazing (and potentially the burning associated with it) increases rates of brood parasitism in the southern Flint Hills (Patten et al. 2006). Although we observed a high incidence of brood parasitism in grazed pastures, there was considerable overlap with CRP fields and even hayfields (in 2005). Rates of brood parasitism may therefore be related more to regional cowbird abundance than land management or other landscape effects (Herkert et al. 2003; Jensen & Cully 2005). There is a strong regional gradient in cowbird abundance across the Flint Hills; cowbirds are up to 6.5 times more abundant in the northern than southern Flint Hills, although the reason for this is unclear (Jensen & Cully 2005). For all 3 species, nearly 2–5 times more nests were parasitized, and with greater intensity, in the northern Flint Hills. Although parasitism is heavy in some parts of the Flint Hills and has a fitness cost (approximately one fewer host young are fledged from parasitized nests), parasitism had no effect on nest survival and rarely if ever caused complete reproductive failure in the host. In contrast, predation accounted for the complete failure of 80% of nests and thus had a much greater impact than brood parasites on grassland bird productivity. Nevertheless, the reduced productivity of parasitized nests may exacerbate predation and other management effects on populations, especially for Dickcissels and Grasshopper Sparrows, which are heavily parasitized by cowbirds.

Management effects must always be assessed in the context of climate in the tallgrass prairie, given that it is the interaction of grazing, fire, and precipitation that governs the structure and dynamics of this system (Knapp et al. 1998). Grasslands are characterized by extreme climatic variability and periodic drought, which may explain the low diversity and density of grassland bird communities (Wiens 1973; Cody 1985). For grassland birds, climatic effects may therefore be reflected less in the presence or abundance of species than in productivity. Nest success for the 3 core species was extremely low across all management types (5–12% success) in the breeding season following a record spring drought (2005), a critical period for the development of grassland productivity (Briggs & Knapp 1995). In contrast, nest success varied across management treatments (except for Eastern Meadowlarks) in 2004. Low productivity in response to extreme drought is also observed in Vesper Sparrows (*Pooecetes gramineus*) in mixed-grass prairie (George

et al. 1992) and among birds in the California coastal sage scrub (Bolger et al. 2005). Bottom-up controls (prey availability) may become more important than top-down controls (management or predation effects) on avian productivity in drought years. Subsequently, climatic effects can exceed or swamp management effects on grassland birds in some years, thus complicating the assessment and management of grassland bird populations.

Despite being heavily managed for cattle production, the Flint Hills still maintains a full complement of tallgrass prairie birds. Nevertheless, current management practices are influencing the distribution and nest success of even the most common grassland birds, and some less common species are rarely found in the burned, grazed rangeland that now characterizes much of the Flint Hills (e.g., Henslow's Sparrows). From a conservation perspective, it is important to maintain a diverse landscape capable of meeting the habitat needs of different species. Alternative management practices capable of increasing heterogeneity are unlikely to be adopted, however, unless they are profitable and easily implemented. For example, increasing native prairie hay production might prove beneficial for some grassland birds in the Flint Hills, but this is unlikely to happen when market forces favor cattle production over hay production. Nevertheless, rising costs of livestock forage, owing to shifts in agricultural production toward biofuel crops, may soon make hay a more profitable commodity and thus land use. In the meantime patch burning, in which only a portion of the pasture is burned in a given year, can create diverse habitat within individual management units (Fuhlendorf & Engle 2001). Grassland bird diversity is 4 times greater in patch-burned than traditionally managed pastures, and several species are most abundant or only occur in patch-burned pastures (Fuhlendorf et al. 2006). Cattle production is similar between patch-burned and traditionally managed pastures, which demonstrates how alternative management approaches might provide economically feasible and practical solutions to the problem of balancing conservation with agribusiness, at least in the Flint Hills.

Acknowledgments

This study was supported by U.S. Department of Agriculture CSREES-NRI Managed Ecosystems Program grant 2003-35101-13714 to K.A.W. We appreciate the cooperation of the Nature Conservancy's Tallgrass Prairie Preserve, U.S. National Park Service's Tallgrass Prairie National Preserve, Emporia State University's Ross Natural History Reservation, and numerous private landowners for allowing us to work on their property. We thank our over 24 field assistants who helped collect data and J. J. Higgins and J. S. Pontius for statistical assistance.

Comments from T. Donovan and 2 anonymous reviewers improved the manuscript. We dedicate this paper to the memory of J. S. Pontius, colleague and advisor, who inspired many an ecologist to become better statisticians.

Supporting Information

Vegetation measures (Appendix S1) and relative bird densities (Appendix S2) within managed grasslands of the Flint Hills are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Best, L. B., H. Campa III, K. E. Kemp, R. J. Robel, M. R. Ryan, J. A. Savidge, H. P. Weeks Jr., and S. R. Winterstein. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. *Wildlife Society Bulletin* **25**:864–877.
- Bolger, D. T., M. A. Patten, and D. C. Bostock. 2005. Avian reproductive failure in response to an extreme climatic event. *Oecologia* **142**:398–406.
- Bollinger, E. K., P. B. Bollinger, and T. A. Gavin. 1990. Effects of hay-cropping on eastern populations of Bobolink. *Wildlife Society Bulletin* **18**:142–150.
- Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. *American Journal of Botany* **82**:1024–1030.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York.
- Butcher, G. S., and D. K. Niven. 2007. Combining data from the Christmas Bird Count and the Breeding Bird Survey to determine the continental status and trends of North America birds. National Audubon Society, New York. Available from <http://www.audubon.org/bird/stateofthebirds/CBID/content/Report.pdf> (accessed July 2008).
- Cody, M. L. 1985. Habitat selection in open-country birds. Pages 191–226 in M. L. Cody, editor. *Habitat selection in birds*. Academic Press, Orlando, Florida.
- Collins, S. L., and D. J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. Pages 81–98 in S. L. Collins and L. L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman, Oklahoma.
- Coppedge, B. R., S. D. Fuhlendorf, W. C. Harrell, and D. M. Engle. 2008. Avian community response to vegetation and structural features in grasslands managed with fire and grazing. *Biological Conservation* **141**:1196–1203.
- Delisle, J. M., and J. A. Savidge. 1997. Avian use and vegetation characteristics of Conservation Reserve Program fields. *Journal of Wildlife Management* **61**:318–325.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* **51**:625–632.
- Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* **16**:1706–1716.
- George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. *Ecological Applications* **2**:275–284.
- Hazler, K. R. 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. *Auk* **121**:707–716.
- Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecological Applications* **4**:461–471.
- Herkert, J. R. 1998. The influence of the CRP on Grasshopper Sparrow population trends in the mid-continental United States. *Wildlife Society Bulletin* **26**:227–231.
- Herkert, J. R. 2007. Conservation Reserve Program benefits on Henslow's Sparrows within the United States. *Journal of Wildlife Management* **71**:2749–2751.
- Herkert, J. R., et al. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the Midcontinental United States. *Conservation Biology* **17**:587–594.
- Jensen, W. E., and J. F. Cully Jr. 2005. Geographic variation in Brown-headed Cowbird (*Molothrus ater*) parasitism on Dickcissels (*Spiza americana*) in Great Plains tallgrass prairie. *Auk* **122**:648–660.
- Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. 1998. *Grassland dynamics: long-term research in tallgrass prairie*. Oxford University Press, New York.
- Koford, R. R., B. S. Bowen, J. T. Lokemoen, and A. D. Kruse. 2000. Cowbird parasitism in grassland and cropland in the northern Great Plains. Pages 229–235 in J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *Ecology and management of cowbirds*. University of Texas Press, Austin, Texas.
- Lanyon, W. E. 1995. Eastern Meadowlark (*Sturnella magna*). Number 160 in A. Poole and F. Gill, editors. *The birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.
- Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). Number 047 in A. Poole, editor. *The birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.
- Lueders, A. S., P. L. Kennedy, and D. H. Johnson. 2006. Influences of management regimes on breeding bird densities and habitat in mixed-grass prairie: an example from North Dakota. *Journal of Wildlife Management* **70**:600–606.
- McCoy, T. D., M. R. Ryan, E. W. Kurzejeski, and L. W. Burger Jr. 1999. Conservation Reserve Program: source of sink habitat for grassland birds in Missouri? *Journal of Wildlife Management* **63**:530–538.
- National Audubon Society. 2004. State of the birds, watch list. National Audubon Society, New York. Available from <http://www.audubon.org/bird/stateofthebirds/grasslands.html> (accessed September 2008).
- Owensby, C. E., R. Cochran, and E. F. Smith. 1988. Stocking rate effects on intensive-early stocked Flint Hills. *Journal of Range Management* **41**:483–487.
- 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.
- Peterjohn, B. G. 2003. Agricultural landscapes: can they support healthy bird populations as well as farm products? *Auk* **120**:14–19.
- Peterjohn, B. G., and J. R. Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966–1996. *Studies in Avian Biology* **19**:27–44.
- Reynolds, R. E., T. L. Shaffer, J. R. Sauer, and B. G. Peterjohn. 1994. Conservation Reserve Program: benefit for grassland birds in the northern plains. *Transactions of the North American Wildlife and Natural Resources Conference* **59**:328–336.
- Robbins, M. B., A. T. Peterson, and M. A. Ortega-Huerta. 2002. Major negative impacts of intensive-early cattle stocking on tallgrass prairies: the case of the Greater Prairie-Chicken. *North American Birds* **56**:239–244.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight

- of grassland vegetation. *Journal of Range Management* **23**:295-297.
- 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., and F. L. Knopf. 1994. Prairie conservation in North America. *BioScience* **44**:418-421.
- SAS Institute. 2005. SAS OnlineDoc, version 9. SAS Institute, Cary, North Carolina. Available from <http://support.sas.com/onlinedoc/913/docMainpage.jsp> (accessed September 2008).
- 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.
- Temple, S. A., 2002. Dickcissel. Number 703 in A. Poole editor. *The birds of North America*. Academy Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.
- Thomas, L., et al. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, Scotland. Available from <http://www.ruwpa.st-and.ac.uk/distance/> (accessed September 2008).
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Biology* **47**:893-901.
- Vickery, P. D. 1996. Grasshopper Sparrow. Number 239 in A. Poole, editor. *The birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.
- Vicerky, P. D., M. L. Hunter Jr., and J. V. Wells. 1992. Is density an indicator of breeding success? *Auk* **109**:706-710.
- Wiens, J. A. 1973. Pattern and process in grassland bird communities. *Ecological Monographs* **43**:237-270.
- 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* **41**:3152-3167.
- Zimmerman, J. L. 1997. Avian community responses to fire, grazing, and drought in the tallgrass prairie. Pages 167-180 in F. Knopf and F. B. Samson, editors. *Ecology and conservation of Great Plains vertebrates*. Springer-Verlag, New York.

