Topographic Patterns of Nest Placement and Habitat Quality for Grassland Birds in Tallgrass Prairie

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ABSTRACT.—Much of the tallgrass prairie remaining in North America occurs in hilly regions, such as the Flint Hills of Kansas and Oklahoma. Despite the conservation importance of these areas for grassland birds, little is known about how topographic variation in habitat affects the nesting ecology of these species. We examined topographic patterns of nest distribution, daily nest survival and nest-site selection for three species: Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus savannarum*) and Eastern Meadowlark (*Sturnella magna*). Dickcissels shifted from nesting more in lowlands to uplands as the season progressed. Grasshopper Sparrows and Eastern Meadowlarks generally nested in midland habitats, but seasonal differences were still evident in the relative proportions of nests found in lowlands vs. uplands. Topography did not affect nest survival of Dickcissels or Grasshopper Sparrows and had only a marginal effect on nest survival for Eastern Meadowlarks. Nest survival for Dickcissels and Grasshopper Sparrows was highly dependent on nest-site vegetation, however. Dickcissels and Eastern Meadowlarks both experienced greater daily nest survival with increasing vertical vegetation structure at nest sites, whereas daily nest survival for Grasshopper Sparrows increased with increasing cover of litter and grass. Although topography may not affect nest survival directly, it may have indirect effects mediated through nest-site vegetation because of selective nest placement. For example, Dickcissels and Eastern Meadowlarks selected sites with greater vertical vegetation structure than generally available, even in upland sites where vegetation structure was reduced. Conservation planning for grassland birds may thus need to consider how topographic variation affects habitat quality within hilly regions where much of the remaining tallgrass prairie occurs.

INTRODUCTION

Grassland bird populations have exhibited widespread declines in North America over the past 50 y, presumably because of the wholesale loss and degradation of their breeding habitat (Askins, 1993; Herkert, 1995; Peterjohn and Sauer, 1999). Less than 5% of tallgrass prairie remains (Samson and Knopf, 1994), and much of that is located in hilly regions such as the Flint Hills of Kansas and Oklahoma, the Sand Hills of Nebraska, and the Loess Hills of Iowa. Despite the presumed conservation importance of these areas for grassland birds, the effect of topography on habitat quality and the settlement patterns of nesting birds has rarely been considered. In the Flint Hills, for example, topographic position has been associated with variation in habitat quality for Dickcissels (*Spiza americana*). Males settled first in old agricultural fields with taller denser vegetation (*i.e.*, lowland sites) and had more females and nests per territory than males that arrived later and/or defended a territory in upland pastures (Zimmerman, 1971, 1982). In southwestern Wisconsin, greater densities of Bobolink (*Dolichonyx orvzivorus*) and Savannah Sparrow (*Passerculus sandwichensis*) were

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found in large upland pastures than in smaller lowland pastures (Renfrew and Ribic, 2002). Topography has also been identified as a factor increasing bird diversity on a tallgrass prairie preserve in west-central Iowa because of the increased vegetation diversity associated with variable topography (Laubach, 1984).

The Flint Hills contain the largest contiguous expanse of unplowed tallgrass prairie remaining in North America (Knapp and Seastedt, 1998); it was this hilly rocky terrain that allowed much of the region to remain unplowed. Topography may contribute to habitat heterogeneity in tallgrass prairie through effects on soils (Ransom *et al.*, 1998; Hook and Burke, 2000), plant productivity (Abrams *et al.*, 1986; Briggs and Knapp, 1995; Knapp *et al.*, 1998) and the composition and structure of vegetation communities (Abrams and Hulbert, 1987). These effects may be further modified by land-management practices. In the Flint Hills, grasslands are predominantly managed as rangeland for cattle, which involves annual spring burning to increase forage production and quality (Zimmerman, 1997). Topography influences the distribution and grazing patterns of cattle (Gillen *et al.*, 1984; Senft *et al.*, 1985; Pinchak *et al.*, 1991), which in turn interacts with fire to affect habitat structure and heterogeneity (Abrams and Hulbert, 1987). Grazing directly influences habitat structure by reducing litter depth and increasing the patchiness of litter (*i.e.*, dead, non-standing vegetation; Knapp *et al.*, 1999), as well as increasing the local diversity and abundance of preferred forage, such as forbs (Vinton *et al.*, 1993; Hartnett *et al.*, 1996; Towne *et al.*, 2005). Land-management practices geared toward cattle production should thus be influenced by topographic variation, thus, affecting the structure and quality of grassland bird habitat within the Flint Hills.

Our objectives in this study were, thus, to examine topographic effects on the nesting ecology of Dickcissel, Grasshopper Sparrows (*Ammodramus savannarum*) and Eastern Meadowlarks (*Sturnella magna*). These species represent the ''core'' of the avian community in the Flint Hills (Zimmerman, 1993). The specific questions we addressed were: (1) Does the distribution of nesting birds vary among topographic positions, and if so, are these patterns consistent throughout the breeding season?; (2) To what extent is nest-site selection (the non-random placement of nests with respect to available habitat) influenced by topography?; and (3) Does topographic position directly or indirectly (*e.g.*, through local nest-site vegetation) affect nest survival of these grassland birds?

METHODS

STUDY AREA

We conducted this study in the Flint Hills of Kansas and northeastern Oklahoma during the 2004 breeding season (25 Apr.–27 Jul.). The Flint Hills comprises approximately 1.6 million ha of rangeland (Knapp and Seastedt, 1998). Dominant vegetation of the region consists of the warm-season grasses big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*) (Pieper, 2005). Some representative forb and woody species of the region include western ragweed (*Ambrosia psilostachya*), lead plant (*Amorpha canescens*), smooth sumac (*Rhus glabra*) and buckbrush (*Symphoricarpos orbiculatus*) (Abrams *et al.*, 1986; Hartnett *et al.*, 1996). Terrain of the Flint Hills is characterized by high local topographic relief, where distinct hilltops and steep sloping midlands commonly occur in areas outside the major river drainages (Fig. 1). In the Flint Hills, 85% of managed grasslands in Kansas (USDA, 2004a) and 98% of those in Oklahoma (Osage Co.; USDA, 2004b) were used for cattle production. Throughout the region, prescribed spring burns (mid-Apr.) are commonly implemented by ranchers to increase the productivity (Anderson *et al.*, 1970) and nutritional value of grass for cattle (Owensby *et al.*, 1995; Pieper, 2005).
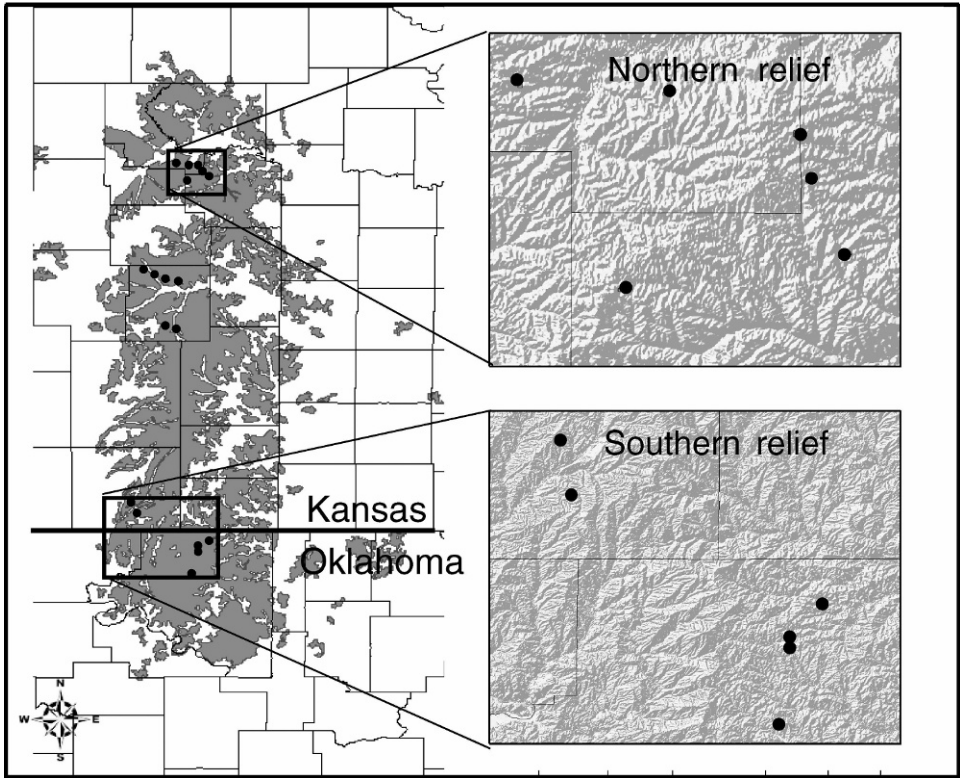
FIG. 1.—Unplowed tallgrass prairie (gray) in the Flint Hills of Kansas and Oklahoma, and shaded relief maps of northern and southern regions. Locations of study sites are indicated by black circles

We selected 18 sites that encompassed the major grazing practices within the Flint Hills, with six sites in each of the northern, central and southern regions (Fig. 1). Site treatments consisted of intensive early-stocking (grazed approximately Apr. 15–Jul. 15 at a stocking density of ~1.25 cattle/ha) and burned in Apr. just before the 2004 field season (IESB) or season long-stocking (grazed approximately Apr. 15–Oct. 15 at a stocking density of ~0.6 cattle/ha) and burned (SLSB) or not burned (SLSU) just before the 2004 field season (Owensby *et al.*, 1995). Within sites, we placed 5-ha plots (320 m × 160 m) so they incorporated the representative topographic relief of each pasture.

<div align="center">NEST SURVEYS</div>

We found nests by rope-dragging to flush incubating females and occasionally through observation of parents or incidental to other field activities. We actively searched for nests every 7–10 d, starting 26 Apr. in the southern region 10 May in the central region and 25 May in the northern region. To ensure a uniform search effort, the entire 5-ha plot was dragged during each nest search. We marked nests at a distance of 5 m (5 paces) with a flag and relocated them on subsequent visits using a hand-held Global Positioning System unit. We visited nests every 3–4 d (rarely 5 d) to determine nest contents and nest fate. Nests were considered successful if they fledged at least a single host young (*i.e.*, we excluded nests that

fledged only Brown-headed Cowbird [*Molothrus ater*] young) in the interval preceding the final visit, and there was no evidence of predation (broken egg shells, disturbed nest lining) or trampling by cattle.

VEGETATION SURVEYS

We measured vegetation structure at nest sites at the end of each nesting attempt. At each nest site, we quantified vertical vegetation structure by placing a Robel pole directly next to the nest and obtaining four visual obstruction readings (VOR; Robel *et al.*, 1970) taken from the four cardinal directions. To estimate horizontal cover of vegetation, a 0.25-m^2 square frame was centered on the nest in which we estimated proportion of cover for live grass, forbs (broad-leaved vegetation) and bare ground (exposed ground without litter). We estimated litter depth (dead, non-standing vegetation) by averaging four measurements of litter depth (cm) taken at the corners of the frame.

We also characterized vegetation within each study plot by surveying vegetation at 40-m intervals along four transects that were spaced 40-m apart (a 280 m $\times$ 120 m grid = 8 points/transect $\times$ 4 transects = 32 points/plot). We sampled vegetation points early (May 24–Jun. 4) and late (Jun. 21–Jul. 3) in the field season to capture seasonal variation in vegetation. We estimated vegetation structure at points using the same methodology as that for nest sites.

CATEGORIZATION OF TOPOGRAPHIC POSITION

To determine the topographic position of nests and site vegetation points, we downloaded Digital Elevation Models (30 m $\times$ 30 m grid cells) from the National Elevation Dataset (http://gisdasc.kgs.ku.edu/) and the USGS ''Seamless Data Distribution'' system (http://seamless.usgs.gov/wedsite/seamless). We used ArcInfo 9.1 (ESRI, Redding, California) to convert these into 2-m shaded contour maps to highlight terrain and elevation differences on sites. We projected locations of nests and vegetation points onto maps and categorized the topographic position of each using characteristics of the terrain. We used a generalized topographic model of the Flint Hills to conceptualize a lowland, midland and upland sequence (*see* Fig 4.1 in Ransom *et al.*, 1998). Lowlands were identified as relatively flat areas at the base of the hill and uplands were identified as the relatively flat hilltop areas. Midlands were identified as the steep side slopes (''breaks'') between upland and lowland areas, which were illustrated by narrow contour lines on the maps. Vegetation points and nests occurring on two of the sites were categorized as uplands because these sites were positioned entirely in flatter areas upslope of most of the surrounding landscape.

STATISTICAL ANALYSES

Nest distribution.—We used Cochran-Mantel-Hanzel statistics within a contingency table analysis to explore the distribution of nests relative to topographic position (lowland, midland, upland), season (early, late) and management treatment (SLSU, SLSB, IESB). We treated topographic position as an ordinal variable, and only included data from sites with all three topographic positions present for this analysis (16 of our 18 sites). To define early- and late-season groups of nests, we categorized individual nests as ''early'' or ''late'' season based on the date the nest was located and by identifying a midpoint in the nesting season for each species. Most nests were found during incubation, so nest-location dates provide a reasonable approximation of initiation date within season. For these analyses, we used 6 Jun. as the seasonal midpoint for Eastern Meadowlark, 16 Jun. as the midpoint for Grasshopper Sparrow and 3 Jul. as the midpoint for Dickcissel. Our analyses addressed both three-factor (topographic position, season and management treatment) and two-factor (topographic

position and season or topographic position and management treatment) contingency tables. Alpha (α) was set at 0.10 for all statistical analyses. Unless otherwise noted, all analyses were conducted using SAS 9.1 (SAS Institute Inc., 2004).

Vegetation.—We estimated vertical vegetation structure by calculating the median of the four VOR values (Robel *et al.*, 1970). We used median rather than mean VOR because the former is less affected by extreme values (*i.e.*, presence or absence of vegetation at a given height). We derived composite variables describing vegetation structure using Principal Components Analysis (PCA) performed on the mean scores for each of the other four variables we measured at each point: proportion of live grass, live forb, bare ground and litter depth. Components were estimated from the correlation matrix and were retained if eigenvalues were ≥ 1. We viewed component loadings greater than 0.30 or less than -0.30 as ''significant'' and loadings greater than 0.50 or less than -0.50 as ''very significant'' in terms of the variation in the distribution explained by the eigenvector (McGarigal *et al.*, 2000).

We performed analysis of covariance to examine how site vegetation varied with topographic position, management and time of season. In the site vegetation analysis, vertical vegetation structure (VOR) and principal components from the vegetation analysis were modeled as a function of topographic position (lowland, midland, upland), management treatment (IESB, SLSU, SLSB) and time of season (early vs. late). We obtained a single model using a backward selection procedure (with $P > 0.10$ as the removal criterion); topographic position was always retained as a predictor to test for topographic effects on vegetation. We computed mean vegetation values from the final model and compared these using two-sample *t*-tests. All *F*-tests and *t*-tests were made using Type III sums of squares, α of 0.10, and Satterthwaite degrees of freedom.

Daily nest survival.—For each species, we modeled variation in daily nest survival (DNS) using the Nest Survival Model in Program MARK (White and Burnham, 1999). Our nest survival model included the effects of nest topographic position, management treatment, time within season and nest-site variables such as VOR and nest vegetation principal components identified by PCA (*see* below). These factors were selected because topographic position and management treatment influence vegetation and grazing activity on sites, time is associated with seasonal changes in vegetation (biomass increases during the season) and nest-site vegetation may affect microclimate and predation risk. In MARK, we fit models using a logit link and by incorporating management as a group covariate with topographic position, VOR and principal components as individual covariates. Topographic position was included as an ordinal covariate in this analysis and time of season was included as a linear effect.

The candidate set of models included the global model, which we defined as the model with the management treatment by topographic position interaction, an additive time effect and nest-site vegetation covariates (topo * mng + time + nest vegetation). We considered all combinations of these factors during model comparisons, including the constant model. We compared models using Akaike's Information Criterion adjusted for small sample size (AIC$_c$; Burnham and Anderson, 1998). To account for uncertainty in model selection, we used Akaike Weights (AIC$_c$ w_i) to obtain model-averaged estimates of DNS. If the addition of a parameter to the model did not result in a reduction in the deviance, the model was removed from the candidate set before model averaging (Guthery *et al.*, 2005). Final estimates of DNS for each species were calculated based on the top models with a cumulative AIC$_c$ $w_i \geq 0.80$. Daily nest survival estimates and unconditional standard errors were obtained across a range of covariate values for important nest-site covariates and topographic position and/or time if they were present in the top models.

TABLE 1.—Summary of contingency table analysis (Cochran-Mantel-Hanzel correlation statistic, X^2) of factors affecting the distribution of nests for three grassland birds in the Flint Hills

Species	n	Factors[a]	X^2	df	P
Dickcissel	105	Topo*Season*Mng	3.36	1	0.05
		Topo*Season	2.74	1	0.10
		Topo*Mng	0.86[b]	2	0.65
Grasshopper Sparrow	102	Topo*Season*Mng	2.66	1	0.10
		Topo*Season	2.58	1	0.11
		Topo*Mng	4.92[b]	2	0.09
Eastern Meadowlark	42	Topo*Season*Mng	2.50	1	0.11
		Topo*Season	3.09	1	0.08
		Topo*Mng	10.36[b]	2	0.01

[a] Topo = topographic position (lowland, midland, upland), Season = early vs. late, Mng = management treatment (IESB, SLSB, SLSU)

[b] Row mean scores statistic

Nest-site selection.—To explore what vegetation features were important in nest-site selection, we selected response variables that were meaningful indicators of nest-site quality from the DNS analysis (*see* RESULTS, DAILY NEST SURVIVAL) by identifying which model containing a vegetation covariate had the lowest AIC_c. We used DNS as an index of habitat quality, consistent with the expectation that demographic rates such as fecundity (a function of DNS) will be higher in good-quality than poor-quality habitat. If a principal component describing nest-site vegetation was identified as a meaningful indicator of nest-site quality, we performed PCA on site and nest vegetation data simultaneously to ensure component scores were comparable. The effect of topography on nest-site selection was examined by conducting an analysis similar to that of the site vegetation analysis, except that for this analysis we limited our inferences to statistical tests of slope parameters and comparisons between nest and site vegetation at each topographic position in each management treatment. Averages of the early- and late-season vegetation surveys were calculated for each site vegetation point before this analysis. A predictor named ''point type'' (nest or site) was created in order to compare nest and site-wide vegetation. The full factorial model was fit with the interaction between topographic position, management treatment and point type. Mean models were fit to obtain slope estimates and statistical tests for regression lines and two sample *t*-tests were used to compare nest and site vegetation. Throughout the results, we report means ± SE.

RESULTS

NEST DISTRIBUTION

Topographic position had a significant effect on nest distribution, although the distribution shifted during the season for some species (topo*season; Table 1). Early in the season a greater proportion of Dickcissel nests were found in lowlands, whereas later in the season proportionately more nests were placed in uplands than lowlands (Fig. 2a). In contrast, most Grasshopper Sparrow nests were found in midlands regardless of time of season (Fig. 2b). However, a greater proportion of nests were placed in uplands early in the season compared to later in the season (Fig. 2b). Eastern Meadowlarks also nested predominantly in midlands, but they shifted in their use of lowlands relative to uplands over the course of the season. Proportionately more nests were placed in lowlands early in the
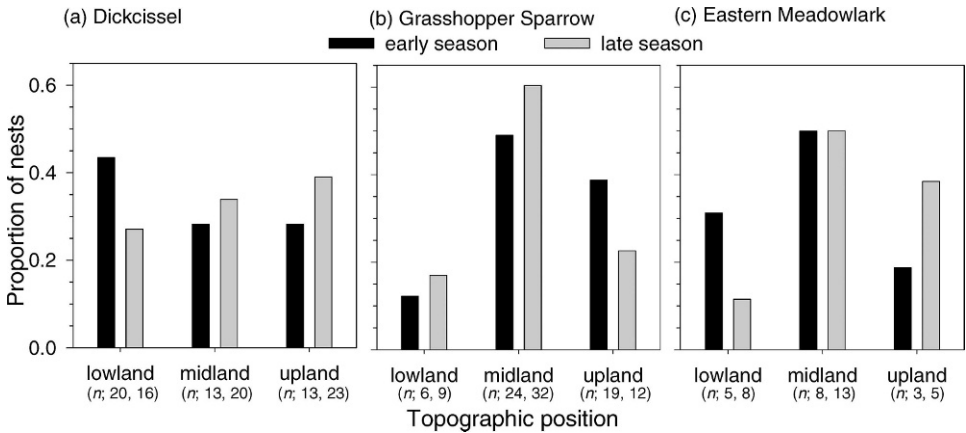
FIG. 2.—Topographic patterns of nest placement within early and late season time periods for (a) Dickcissel, (b) Grasshopper Sparrow and (c) Eastern Meadowlark at each topographic position. Values are calculated from the raw data from each time period. Sample sizes are presented under each category

season, whereas later in the season a greater proportion of nests were placed in uplands (Fig. 2c).

SITE AND NEST VEGETATION

Topographic position did not have a significant effect on vertical vegetation structure (VOR; Table 2). Instead, management interacted significantly with season to influence VOR, which was most evident in season-long grazed pastures ($P < 0.01$, Fig. 3a). The four measures of vegetation cover (grass, forb, litter and bare ground) on sites could be described by the first and second components retained from PCA (Table 3). The first component (PC1) described a gradient from litter and grass cover to bare ground, in which larger scores primarily represented greater litter and (to a lesser extent) grass cover. The second component (PC2) described forb cover exclusively, with larger component scores associated with greater forb cover (Table 3).
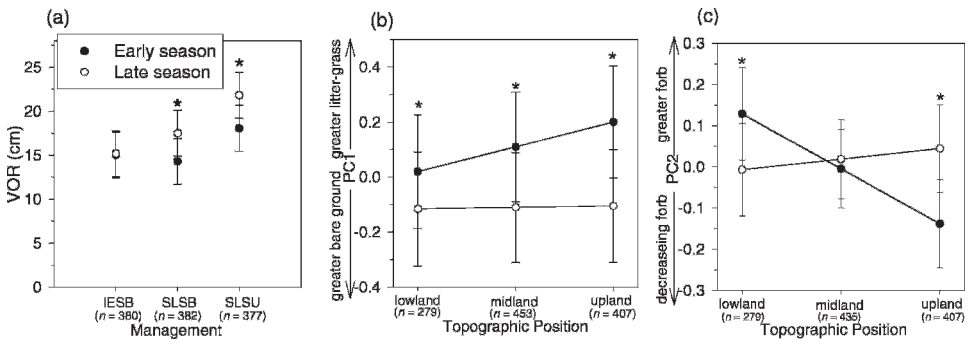

FIG. 3.—Site vegetation characteristics for (a) vegetation biomass, (b) PC1: live grass, litter depth and bare ground, and (c) PC2: cover of live forb. Points identify means and error bars represent 1 SE. Lines in (b) and (c) depict natural ordering of ordinal topographic categories. Asterisks denote pairs of means that are significantly different

TABLE 2.—Summary of factors affecting site vegetation on grazed grasslands in the Flint Hills

Habitat characteristic	Model[a]	Factors[b]	F	df[c]	P
VOR (cm)	Factorial	Topo*Mng*Season	0.77	2, 581	0.46
	Final	Topo	2.14	1, 598	0.14
		Mng*Season	9.85	2, 577	<0.01
Grass-Litter (PC1)	Factorial	Topo*Mng*Season	0.92	2, 561	0.40
	Final	Topo*Season	2.79	1, 563	0.10
		Mng	5.34	2, 15	0.02
Forb (PC2)	Factorial	Topo*Mng*Season	1.82	2, 529	0.16
	Final	Topo*Season	7.77	1, 529	<0.01
		Mng	4.97	2, 15	0.02

[a] All models were fit with all lower-level interactions and main effects; only tests for higher-order effects are shown

[b] Topo = topographic position (lowland, midland, upland); Mng = management treatment (IESB, SLSB, SLSU); Season = early vs. late season

[c] df = Satterthwaite degrees of freedom (numerator, denominator)

Litter and grass cover (PC1) were significantly affected by both management and the interaction between topographic position and time (Table 2). In terms of management effects, litter and grass cover were greatest in season-long stocked pastures that were unburned (SLSU; 0.91 ± 0.34), intermediate in season-long stocked pastures that were burned (SLSB; -0.37 ± 0.34) and least in intensive-early stocked pastures that were burned (IESB; -0.54 ± 0.34). Comparisons among management types indicate that grass and litter cover was significantly lower in IESB and SLSB than in SLSU (IESB vs. SLSB: $t_{s15} = -2.98$, P = 0.01; IESB vs. SLSU: $t_{s15} = -2.65$, P = 0.02). The interactive effect of topography and time is explained by the apparent increase in litter and grass cover with increasing elevation during the early part of the season (Fig. 3b), which was most pronounced in midlands and uplands (lowland: $t_{s559} = 1.97$, P = 0.05; midland: $t_{s558} = 5.58$, P = 0.01; upland: $t_{s564} = 5.11$, P = 0.01; Fig. 3b).

Forb cover (PC2) was likewise affected by management and the interaction between topographic position and time (Table 2). In terms of management, forb cover was greatest in IESB (0.41 ± 0.16), intermediate in SLSB (-0.12 ± 0.16) and least in SLSU (-0.27 ± 0.16). Comparisons among management types revealed that forb cover was significantly different in IESB compared to SLSB ($t_{s15.1} = 2.36$, P = 0.03) and SLSU ($t_{s15} = 2.99$, P =

TABLE 3.—Principal Component Analysis of site vegetation and nest vegetation data for grassland birds nesting in the Flint Hills. DICK = Dickcissel nests, GRSP = Grasshopper Sparrow nests, EAME = Eastern Meadowlark nests. Only retained components (PC1 and/or PC2) are displayed. Bold values indicate significant loadings

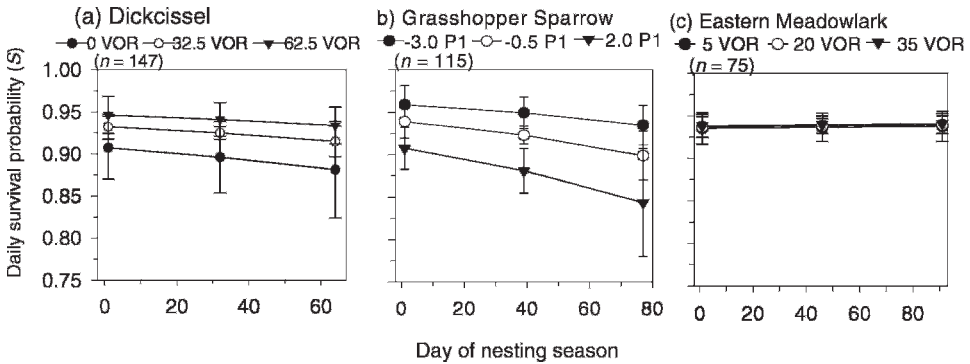|	Site ($n = 1139$)		DICK ($n = 147$)	GRSP ($n = 115$)		EAME ($n = 75$)	
Vegetation measure	PC1	PC2	PC1	PC1	PC2	PC1	PC2
Grass	**0.40**	0.13	**−0.41**	−0.06	**0.77**	0.06	**0.82**
Forb	0.05	**0.99**	**0.48**	0.23	**0.62**	0.37	**0.50**
Litter	**0.64**	0.09	**−0.55**	**−0.69**	−0.05	**−0.68**	0.08
Ground	**−0.66**	−0.07	**0.55**	**0.69**	−0.17	**0.64**	−0.29
Eigenvalue	1.71	1.00	2.15	1.60	1.11	1.70	1.08
Proportion variation explained	0.43	0.25	0.54	0.40	0.28	0.43	0.27

FIG. 4.—Model-averaged estimates of daily nest survival for (a) Dickcissel, (b) Grasshopper Sparrow and (c) Eastern Meadowlark, with unconditional SE (error bars = 1 SE). Estimates were calculated across time of season at minimum, intermediate and maximum values for the corresponding vegetation covariate, holding all other covariates at their mean

0.01). Topographic effects on forb cover changed over the season, with higher forb cover in lowlands early in the season ($t_{s525} = 1.76$, P = 0.08), but higher forb cover in uplands later in the season ($t_{s530} = -2.72$, P = 0.01; Fig. 3c).

Nest vegetation at Dickcissel nests was best described by the first principal component (PC1), which described an inverse relationship between grass/litter cover and forb/bare ground cover (Table 3). The first two principal components were retained to describe nest-site characteristics of Grasshopper Sparrows and Eastern Meadowlarks (Table 3). For these two species, components had a similar interpretation. For PC1, litter cover increased as bare ground decreased, and as PC2 increased, cover of grass and forb increased (Table 3).

DAILY NEST SURVIVAL

Topographic position was of little importance to Dickcissel DNS in the models we examined relative to VOR at nests and time of season (Table 4). Dickcissel DNS was described well by a constant survival rate, but there were several models that were equally parsimonious (Δ AIC$_c$ $\leq$ 2.0) and the model with VOR had only a slightly smaller Akaike weight (AIC$_c$ w_i) than the constant model (Table 5). Daily nest survival was predicted to decrease 4–6%/day across all VOR values after model averaging (Fig. 4a). This translates to a 6.5% vs. 22% overall nest success between nests that had the lowest observed VOR (0 cm) vs. those with the highest observed VOR (62.5 cm), respectively.

Topographic position also had a minimal effect on Grasshopper Sparrow DNS compared to the effect of litter and bare ground cover (PC1) at nests and time of season (Table 4). Litter and bare ground cover (PC1) occurred in all three of the top models indicating that it was an important variable in this analysis (Table 4). The top two models also included additive effects for time of season (Table 4). Model-averaged estimates indicated an increase of 6–11% in DNS between the observed extremes in litter and grass cover (Fig. 4b). There is a 4% vs. 27% probability of nest success when observed cover of litter (PC1) was low (2.0) vs. high (−3.0), respectively. Daily nest survival for Grasshopper Sparrows also declined throughout the season, and this effect was more pronounced than that observed for Dickcissels (Fig. 4b).

Topographic position was the most important covariate considered for Eastern Meadowlarks; however, the best description of DNS was the constant rate (Table 4).

TABLE 4.—Top daily nest survival models for Dickcissels, Grasshopper Sparrows and Eastern Meadowlarks nesting in grazed grasslands of the Flint Hills

Species	Model structure[b]	Model statistics[a]			
		k	Dev	Δ AIC$_c$	w_i
Dickcissel (n = 147)	Constant	1	430.9	0.0	0.30
	VOR	2	429.0	0.1	0.28
	VOR + Time	3	427.2	0.4	0.25
	Time	2	430.0	1.2	0.17
Grasshopper Sparrow (n = 115)	Time + PC1	3	313.1	0.0	0.47
	Time + PC1 + Topo	4	312.1	1.0	0.29
	PC1	2	316.5	1.3	0.24
Eastern Meadowlark (n = 75)	Constant	1	254.8	0.0	0.39
	Topo	2	253.5	0.7	0.27
	Time	2	254.4	1.7	0.17
	VOR	2	254.5	1.7	0.17

[a] Dev = deviance, k = number of parameters, Topo = topographic position (lowland, midland, upland)

[b] Time = linear time trend; VOR = visual obstruction reading (cm), a measure of vertical vegetation structure; PC1 = Principal Component 1 from analysis of nest data; Constant = point estimate from all data pooled

Model-averaged estimates showed little change from the constant rate for any of the covariates considered likely due to the relatively high AIC$_c$ weight (w_i) for the constant model (Table 4; Fig. 4c).

NEST-SITE SELECTION

Vertical vegetation structure (VOR) was the most important nest-site vegetation characteristic influencing DNS for Dickcissels (*see* RESULTS, DAILY NEST SURVIVAL). We, therefore, included VOR as the response variable in this analysis because it represents an important habitat feature likely to affect nest-site selection in this species. Topographic position, management and type of point (nest or site vegetation) had a significant interactive effect on nest-site selection for Dickcissels (three-way interaction: $F_{2,715} = 3.07$, P = 0.05). Nest and site VOR were different across all topographic positions for each management treatment (Table 6). Dickcissels selected nest sites with greater VOR than was typically available within sites (Fig. 5a). The mean model revealed that there was a significant decline in VOR with increasing topographic position at nest locations of Dickcissels (slope = −3.62, $t_{s715} = −3.03$, P < 0.01) in season-long stocked pastures that were unburned (SLSU; Fig. 5a).

Cover of litter and bareground (PC1) was the most important nest-site vegetation feature associated with nest survival for Grasshopper Sparrows (*see* RESULTS, DAILY NEST SURVIVAL). These features were also represented by the first principal component (PC1) derived from the combined Grasshopper Sparrow nest and site data (Table 6). In season-long stocked pastures (SLSB and SLSU), nests had greater litter cover than site averages, and these differences increased with increasing elevation (Table 5; Fig. 5b).

Although nest-site vegetation did not have much influence on model-averaged estimates of DNS for Eastern Meadowlarks, model selection indicated VOR was still the vegetation characteristic with the greatest association with DNS (Table 4). For nearly all comparisons within topographic positions, VOR at nests was greater than site averages (Table 5), which indicates that Eastern Meadowlarks were selecting sites with greater VOR than was typically

TABLE 5.—Comparison of nest vegetation and site vegetation at different topographic positions in the Flint Hills for three grassland birds. IESB = intensive early-stocked burned, SLSB = season-long stocked burned, SLSU = season-long stocked unburned pasture. DICK = Dickcissel, GRSP = Grasshopper Sparrow, EAME = Eastern Meadowlark. P-values are *ns* if >0.10, * ≤0.10, ** ≤0.05, and *** ≤0.005

| | | IESB | | | | | SLSB | | | | | SLSU | | | | |
| | | Veg measure[a] | | Statistics | | | Veg measure[a] | | Statistics | | | Veg measure[a] | | Statistics | | |
Species	Topo[b]	Nest	Site	*t*	df[c]	P	Nest	Site	*t*	df[c]	P	Nest	Site	*t*	df[c]	P
DICK	low	25.0 (3.1)	15.2 (2.6)	5.6	716	***	26.6 (3.7)	15.5 (2.7)	4.6	714	***	39.3 (3.1)	20.6 (2.7)	10.9	715	***
	mid	26.0 (2.8)	15.1 (2.7)	10.1	718	***	27.9 (2.9)	15.8 (2.6)	9.2	716	***	35.7 (2.8)	20.0 (2.7)	13.6	717	***
	up	27.0 (3.1)	14.9 (2.6)	6.7	716	***	29.2 (2.8)	16.1 (2.6)	10.3	722	***	32.1 (3.2)	19.4 (2.6)	7.0	717	***
GRSP	low	−0.5 (0.4)	−0.7 (0.4)	1.1	692	*ns*	−0.1 (0.6)	−0.5 (0.4)	0.9	693	*ns*	1.0 (0.4)	0.9 (0.4)	0.1	693	*ns*
	mid	−0.5 (0.4)	−0.6 (0.3)	1.2	692	*ns*	0.1 (0.4)	−0.5 (0.4)	2.4	694	**	1.2 (0.4)	1.0 (0.4)	1.7	694	*
	up	−0.5 (0.4)	−0.6 (0.4)	0.3	692	*ns*	0.3 (0.4)	−0.4 (0.4)	3.8	694	***	1.4 (0.4)	1.0 (0.4)	1.8	694	*
EAME	low	23.8 (3.2)	15.4 (2.6)	4.5	643	***	29.3 (6.5)	16.4 (2.6)	2.6	642	**	25.2 (3.7)	20.7 (2.6)	1.9	642	*
	mid	22.8 (2.9)	15.1 (2.5)	5.8	644	***	24.7 (3.9)	16.0 (2.5)	3.4	643	***	25.3 (2.8)	20.0 (2.5)	4.4	642	***
	up	21.7 (3.4)	14.7 (2.6)	3.4	643	***	20.1 (3.1)	15.6 (2.5)	2.7	645	**	25.3 (3.2)	19.3 (2.6)	3.3	642	***

[a] Vegetation measures are means (SE) and vary by species: DICK = vertical vegetation structure (VOR), GRSP = grass-litter cover (PC1, Table 6), EAME = VOR

[b] Topo = topographic position (low = lowland, mid = midland, up = upland)

[c] df = Satterthwaite degrees of freedom

TABLE 6.—Principal Component Analysis of pooled site and Grasshopper Sparrow nest vegetation data (n = 1245). Boldface values indicate significant loadings

Vegetation measure	PC1	PC2
Grass	**0.39**	0.24
Forb	0.05	**0.96**
Litter	**0.64**	−0.11
Ground	**−0.66**	0.10
Eigenvalue	1.67	1.01
Proportion variation explained	0.42	0.25

available within sites. Differences between nests and sites decreased with increasing elevation (Fig. 5c), although this trend was significant only in SLSB pastures (slope = −4.62, t_{s644} = −1.73, P = 0.08; Fig. 5c).

DISCUSSION

In the Flint Hills, topography differentially influenced the nesting ecology of Dickcissels, Grasshopper Sparrows and Eastern Meadowlarks. A greater proportion of Dickcissel nests were placed in lowlands than either midlands or uplands early in the season. This is consistent with previous work that suggested that Dickcissels settled earlier on lowland sites because these areas had taller vegetation and more forb cover, which are preferred nesting habitat for Dickcissels (Zimmerman, 1971). When considering this preference for forbs, the seasonal shift in Dickcissel nest placement corresponded well with the seasonal changes in the distribution of forbs among topographic positions that we observed, where forb cover was higher in lowlands early in the season but was greater in uplands later in the season (compare Fig. 2a and 3c).

For Grasshopper Sparrows and Eastern Meadowlarks, nest placement was greatest in midlands. However, proportionately more Grasshopper Sparrow nests were found in uplands early in the season compared to later, which was the opposite of what was observed for Eastern Meadowlarks. Like Dickcissels, Eastern Meadowlarks nested more frequently in lowlands early in the season (albeit secondary to midlands), but shifted to higher use of
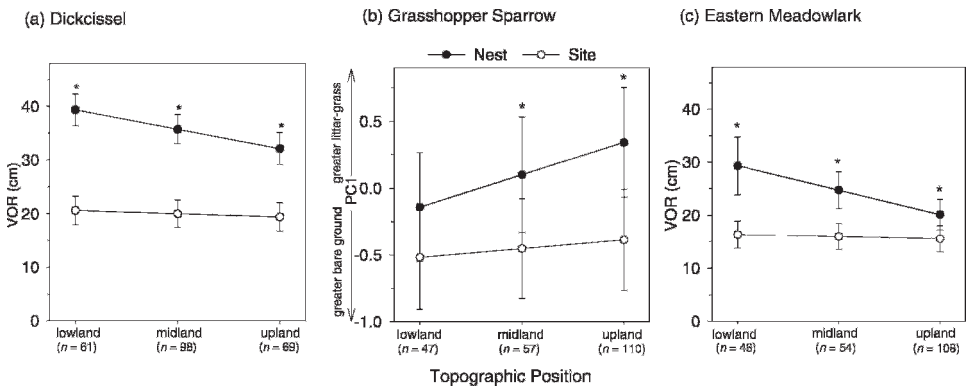

FIG. 5.—Nest-site selection patterns of (a) Dickcissel in SLSU, (b) Grasshopper Sparrow in SLSB and (c) Eastern Meadowlark in SLSB. Points identify means (error bars = 1 SE) and asterisks denote pairs of means that are significantly different

uplands as the season progressed (Fig. 2c). In contrast to Dickcissels, Grasshopper Sparrows generally occupy areas with moderate litter cover and depth (Wiens, 1973), which may explain their greater use of uplands early in the season in our study, where litter cover was greatest at that time (Fig. 4b).

Although topographic position in the Flint Hills has been identified as an important factor influencing vegetation density and productivity (Abrams *et al.*, 1986), we did not find a significant effect of topography on vertical vegetation structure (VOR). This could be due to the frequent rainfall that occurred throughout the region in late spring and early summer of the 2004 growing season. Stronger topographic effects might be expected in years of lower rainfall, when runoff from infrequent rains has little chance to infiltrate shallow soils of uplands (Ransom *et al.*, 1988), but can collect in lowlands, increasing the difference in soil moisture levels and productivity between lowlands and uplands. Thus, in years of frequent rains, water stress should be less of an issue in uplands, resulting in similar productivity across topographic positions. Stocking intensity could also have a substantial influence on vegetation patterns across topographic positions because cattle tend to concentrate activity at lower topographic positions and on gradual slopes (Gillen *et al.*, 1984; Senft *et al.*, 1985; Pinchak *et al.*, 1991). Therefore, concentrated grazing in lowlands could also lessen the effect of topographic position on vegetation biomass.

Our results suggest that variation in nest survival cannot be attributed to topographic position for Dickcissels and Grasshopper Sparrows, but nest survival may be marginally influenced by topographic position for Eastern Meadowlarks. For Dickcissels and especially Grasshopper Sparrows, DNS was highly dependent on specific nest-site characteristics. Vegetation structure near nests provides visual concealment (Davis, 2005), and shelter from wind and sun (With and Webb, 1993), and may explain why vegetation at nests is so important for nest survival. Dickcissels build their nests off the ground and increased vertical vegetation density around the nest probably reduces exposure to visual predators. In contrast, Grasshopper Sparrows often build domed nests on the ground, and thus exposure is probably lowest in areas with high litter cover. Grasshopper Sparrows selected sites with greater litter and grass cover in midlands and uplands of season-long stocked sites (Table 5). When considering how DNS was associated with greater vertical vegetation structure and litter cover in this species, there thus appears to be at least an indirect link between topographic position and nest survival.

In summary, topographic position may be an important factor influencing habitat quality of these grassland birds in the Flint Hills because of how it influences temporal patterns in vegetative cover, particularly of forbs, litter and grass. The distribution of nests within sites corresponded with seasonal shifts in the topographic variation of vegetation. Although topography may not have a direct effect on DNS, it may have indirect effects mediated through nest-site vegetation as a consequence of selective nest placement. Accounting for topographic variation in habitat is particularly relevant in the Flint Hills because this is one of the last great expanses of native tallgrass prairie remaining, and thus it offers perhaps the best opportunity for the management and conservation of grassland birds in this region. Many of the prairie remnants in North America are hilly areas that are poor cropland (*e.g.*, Loess Hills of Iowa, Sand Hills of Nebraska), so understanding how topographic variation affects habitat quality may also be important for grassland management and the conservation of grassland birds beyond the Flint Hills, especially where management actions might be principally directed at a given topographic position (*e.g.*, lowlands or slopes).

L ITERATURE C ITED

A BRAMS, M. D., A. K. K NAPP AND L. C. H ULBERT. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie. *Am. J. Bot.*, **73**:1509–1515.

——— AND L. C. H ULBERT. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in Northeast Kansas. *Am. Midl. Nat.*, **117**:442–445.

A NDERSON, M. D., E. F. S MITH AND C. E. O WENSBY. 1970. Burning bluestem range. *J. Range Manage.*, **23**:81–92.

A SKINS, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Curr. Ornithol.*, **11**:1–34.

B RIGGS, J. M. AND A. K. K NAPP. 1995. Interannual variability in primary production in Tallgrass Prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *Am. J. Bot.*, **82**:1024–1030.

B URNHAM, K. P. AND D. R. A NDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York. 488 p.

D AVIS, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor*, **107**:605–616.

G ILLEN, R. L., W. C. K RUEGER AND R. F. M ILLER. 1984. Cattle distribution on mountain rangeland in northeastern Oregon. *J. Range Manage.*, **37**:549–553.

G UTHERY, F. S., L. A. B RENNAN, M. J. P ETERSON AND J. J. L USK. 2005. Information theory in wildlife science: critique and viewpoint. *J. Wildlife Manage.*, **69**:457–465.

H ARTNETT, D. C., K. R. H ICKMAN AND L. E. F ISHER-W ALTER. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *J. Range Manage.*, **49**:413–420.

H ERKERT, J. R. 1995. An analysis of Midwestern breeding bird population trends: 1966–1993. *Am. Midl. Nat.*, **134**:41–50.

H OOK, P. B. AND I. C. B URKE. 2000. Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate. *Ecology*, **81**:2686–2703.

K NAPP, A. K. AND T. R. S EASTEDT. 1998. Grasslands, Konza prairie, and long-term ecological research, p. 3–15. *In:* A. K. Knapp, J. M. Briggs, D. C. Hartnett and S. L. Collins (eds.). Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford University Press, New York. 364 p.

———, J. M. B RIGGS, J. M. B LAIR AND C. L. T URNER. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie, p. 193–221. *In:* A. K. Knapp, J. M. Briggs, D. C. Hartnett and S. L. Collins (eds.). Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford University Press, New York. 364 p.

———, J. M. B LAIR, J. M. B RIGGS, S. L. C OLLINS, D. C. H ARTNETT, L. C. J OHNSON AND E. G. T OWNE. 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience*, **49**:39–50.

L AUBACH, R. 1984. Breeding birds of Sheeder Prairie Preserve, west-central Iowa. *Proc. Iowa Acad. Sci.*, **91**:153–163.

M C G ARIGAL, K., S. C USHMAN AND S. S TAFFORD. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York. 283 p.

O WENSBY, C., R. C OCHRAN, K. A NDERSON, E. S MITH AND E. V ANZANT. 1995. 50-years of range research revisited. Cooperative Extension Service, Kansas State University, Manhattan, Kansas. 57 p. Available online: http://www.oznet.ksu.edu/library/crpsl2/138_1.pdf (6 Dec. 2007).

PETERJOHN, B. G. AND J. R. SAUER. 1999. Population status of North American grassland birds from the North America Breeding Bird Survey, 1966–1996. *Stud. Avian Biol.*, **19**:27–44.

PIEPER, R. D. 2005. Grasslands of central North America, p. 221–263. *In:* J. M. Suttie, S. G. Reynolds and C. Batello (eds.). Grasslands of the world. Food and Agricultural Organization of the United Nations, Rome, Italy. 514 p.

PINCHAK, W. E., M. A. SMITH, R. H. HART AND J. W. WAGGONER, JR. 1991. Beef cattle distribution patterns on foothill range. *J. Range Manage.*, **44**:267–275.

RANSOM, M. D., C. W. RICE, T. C. TODD AND W. A. WEHMUELLER. 1998. Soils and soil biota, p. 48–66. *In:* A. K. Knapp, J. M. Briggs, D. C. Hartnett and S. L. Collins (eds.). Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford University Press, New York. 364 p.

RENFREW, R. B. AND C. A. RIBIC. 2002. Influence of topography on density of grassland passerines in pastures. *Am. Midl. Nat.*, **147**:315–325.

ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *J. Range Manage.*, **23**:295–297.

SAMSON, F. AND F. KNOPF. 1994. Prairie conservation in North America. *BioScience*, **44**:418–421.

SENFT, R. L., L. R. RITTENHOUSE AND R. G. WOODMANSEE. 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. *J. Range Manage.*, **38**:82–87.

TOWNE, E. G., D. C. HARTNETT AND R. C. COCHRAN. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecol. Appl.*, **15**:1550–1559.

U.S. DEPARTMENT OF AGRICULTURE. 2004a. 2002 Census of agriculture. Kansas State and County Data. Vol. 1, Geographic Area Series Part 16. USDA, National Agricultural Statistics Service, Washington, D.C. 711 p. Available online: http://www.nass.usda.gov/census/census02/volume1/ks/KSVolume104.pdf (6 Dec. 2007).

———. 2004b. 2002 Census of agriculture. Oklahoma State and County Data, Volume 1, Geographic Area Series Part 36. USDA, National Agricultural Statistics Center, Washington, D.C.Available online: http://www.nass.usda.gov/census/census02/volume1/ok/OKVolume104.pdf (6 Dec. 2007).

VINTON, M. A., D. C. HARTNETT, E. J. FINCK AND J. M. BRIGGS. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *Am. Midl. Nat.*, **129**:10–18.

WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**(Suppl.):S120–S139.

WIENS, J. A. 1973. Pattern and process in grassland bird communities. *Ecol. Monogr.*, **43**:237–270.

WITH, K. A. AND D. R. WEBB. 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. *Condor*, **91**:401–413.

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

———. 1982. Nesting success of Dickcissels in preferred and less preferred habitats. *Auk*, **99**:292–298.

———. 1993. The birds of Konza: The avian ecology of the tallgrass prairie. University of Kansas Press, Kansas. 198 p.

———. 1997. Avian community responses to fire, grazing and drought in the tallgrass prairie, p. 167–180. *In:* F. L. Knopf and F. B. Samson (eds.). Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York. 320 p.