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GEOGRAPHIC VARIATION IN BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) PARASITISM ON DICKCISSELS (*SPIZA AMERICANA*) IN GREAT PLAINS TALLGRASS PRAIRIE

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ABSTRACT.—The incidence of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter “cowbirds”) within host species typically reflects the continental pattern in cowbird abundance across North America, where parasitism is heaviest in the Great Plains. However, we found considerable variation in cowbird parasitism on Dickcissel (*Spiza americana*) nests within a subregion of the Great Plains (the Flint Hills), where the highest levels of cowbird parasitism on grassland bird nests had been previously reported. Local parasitism frequencies on Dickcissel nests varied latitudinally across the Flint Hills, ranging from 0% to 92% of nests parasitized. Interestingly, we found no obvious patterns in habitat or host attributes that were associated with this steep geographic gradient in brood parasitism. Cowbird parasitism on Dickcissel nests was not correlated with the vertical density of local prairie vegetation, mean nest distance to edge, proportion of forest to grassland habitat surrounding study sites (≤ 5 to 10 km), geographic variation in host abundance, or Dickcissel density or nest initiation dates. Parasitism frequencies and intensities (number of cowbird eggs per parasitized nest) on Dickcissel nests were only significantly related to variation in local female cowbird density. Dickcissel clutch size and apparent fledging success were negatively correlated with local cowbird parasitism levels. Geographic patterns in cowbird abundance within and among regions should be considered when establishing conservation areas for grassland birds or other cowbird hosts of concern. Received 24 October 2003, accepted 18 November 2004.

Key words: brood parasitism, Brown-headed Cowbird, Dickcissel, geographic variation, *Molothrus ater*, *Spiza americana*.

Variación Geográfica en el Parasitismo de Nidos de *Spiza americana* por *Molothrus ater* en Praderas de Pastos Altos de la Gran Planicie

RESUMEN.—La incidencia del parasitismo de cría por parte de *Molothrus ater* en sus especies hospederas típicamente refleja el patrón continental de abundancia de este parásito a través de América del Norte, donde el parasitismo es más intenso en la región de la gran planicie. Sin embargo, encontramos variación considerable en el parasitismo de los nidos de *Spiza americana* dentro de una subregión de la gran planicie (las colinas de Flint), en donde los niveles máximos de parasitismo de cría por parte de *M. ater* sobre aves de pastizal habían sido documentados

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previamente. Las frecuencias locales de parasitismo sobre los nidos de *S. americana* variaron latitudinalmente a través de las colinas de Flint, en un rango entre 0% y 92% de nidos parasitados. Resulta interesante que no encontramos patrones obvios en atributos del hábitat o del hospedero asociados con este marcado gradiente geográfico en el parasitismo de cría. El parasitismo de los nidos de *S. americana* no estuvo correlacionado con la densidad vertical de la vegetación local de pradera, la distancia media al borde, la proporción de bosque-pastizal en el ambiente que rodeaba los sitios de estudio (5 a 10 km), la variación geográfica en la abundancia del hospedero, la densidad poblacional de *S. americana* o la fecha de iniciación de la nidificación. Las frecuencias e intensidades (número de huevos de *M. ater* por nido parasitado) de parasitismo sólo estuvieron relacionadas significativamente con la variación en la densidad local de hembras de *M. ater*. El tamaño de la nidada y el éxito de emplumamiento aparente de *S. americana* estuvieron correlacionados negativamente con los niveles locales de parasitismo. Los patrones de variación geográfica en la abundancia de *M. ater* entre regiones y dentro de éstas deben ser tenidos en cuenta al establecer áreas de conservación para aves de pastizal y otros hospederos de esta especie parásita.

BIRDS OFTEN EXHIBIT continent-wide range distributions, yet considerable geographic variation in abundance, as exemplified in continental distribution maps of bird abundance from surveys such as the North American Breeding Bird Survey (BBS) (Price et al. 1995). Such geographic variation in abundance may be attributable to variation in local niche availability (Brown et al. 1995). Biogeographic variation in abundance within species also may be related to magnitudes of interspecific interactions (Wiens 1989), such as competition, predation, and brood parasitism.

The Brown-headed Cowbird (*Molothrus ater*; hereafter "cowbird") is a North American brood parasite that exhibits geographic variation in abundance, which parallels geographic variation in its parasitism frequency on hosts (Hoover and Brittingham 1993, Smith and Myers-Smith 1998, Thompson et al. 2000, Herkert et al. 2003). Geographic variation in cowbird parasitism is especially prominent among grassland-nesting birds. In parts of the Midwest, grassland-nesting songbirds are rarely parasitized (Strausberger and Ashley 1997, Kershner and Bollinger 1998, Robinson et al. 1999, Winter 1999, Peer et al. 2000); whereas those same species are heavily parasitized in the center of the cowbird's distribution in the Great Plains (Elliott 1978, Zimmerman 1983, Koford et al. 2000), where cowbirds are most abundant (Peterjohn et al. 2000). Variation in cowbird parasitism on grassland birds is more

clearly related to variation in regional cowbird abundance than the size of remnant grassland patches (Herkert et al. 2003) or intraspecific behavioral responses of hosts to cowbird parasitism (Peer et al. 2000).

Here, we present a curious geographic pattern in cowbird parasitism on Dickcissel (*Spiza americana*) nests across the tallgrass prairie-dominated landscapes of the Flint Hills of eastern Kansas and Oklahoma. The Dickcissel is the most abundant grassland-nesting bird in the relatively simple avian community of the tallgrass prairie of this region (Zimmerman 1993), and is apparently the most heavily parasitized by cowbirds (Elliott 1978, Jensen 1999). Previous studies of cowbird parasitism on Dickcissel nests from the Flint Hills reported heavy parasitism frequencies (56% to 95% of nests parasitized; Elliott 1978, Hatch 1983, Zimmerman 1983, Jensen 1999), which were attributed to the region lying within the geographic zone of peak cowbird abundance in the Great Plains. However, in concurrently examining Dickcissel nests across several study sites in the Flint Hills (Fig. 1B), we found parasitism frequencies and intensities (number of cowbird eggs per parasitized nest) to vary greatly along a latitudinal gradient, in which nests were rarely parasitized—or unparasitized—on more southerly sites and heavily parasitized farther north (Table 1). That latitudinal gradient in parasitism reflects data from the BBS showing latitudinal variation in cowbird abundance

within the Flint Hills (Fig 1A), which parallel our estimate of female cowbird density (Table 1; derivation of density estimates described below).

What might be causing such great variation in cowbird parasitism frequency across the Flint Hills? Along its latitudinal extent, the region is dominated by the largest remaining expanses of tallgrass prairie in North America (Steinauer and Collins 1996). Although grazing land for domestic cattle (*Bos taurus*) within landscapes can influence local cowbird abundance and parasitism, given that those habitats are used for foraging by cowbirds (Goguen and Mathews 1999), such rangeland is ubiquitous across the entirety of the Flint Hills. We therefore attempted to find other possible correlates with the observed latitudinal gradient in parasitism. If the structure of vegetation used for nesting by Dickcissels differed among the study sites, nest concealment from cowbirds might differ as well. Variation in nest proximity to wooded edges

among sites might also affect parasitism by cowbirds (Johnson and Temple 1990). Because cowbirds have large home ranges (Thompson and Dijk 2000), they might also be more or less selective of grassland- versus woodland-nesting hosts on the basis of the availability of those respective host communities within landscapes (which resembles the “frequency-dependent host” hypothesis of Smith and Myers-Smith 1998). Similarly, perhaps cowbirds are more or less selective of Dickcissels as hosts depending on the local abundance of Dickcissels. We also examined the latitudinal pattern in host abundance within the grassland community. Cowbirds might also be more or less selective of Dickcissel nests if nest-initiation dates were geographically variable. Because cowbird parasitism affects Dickcissel nest productivity (Elliott 1978, Zimmerman 1983), we also examined geographic associations of Dickcissel nest productivity with cowbird parasitism levels.

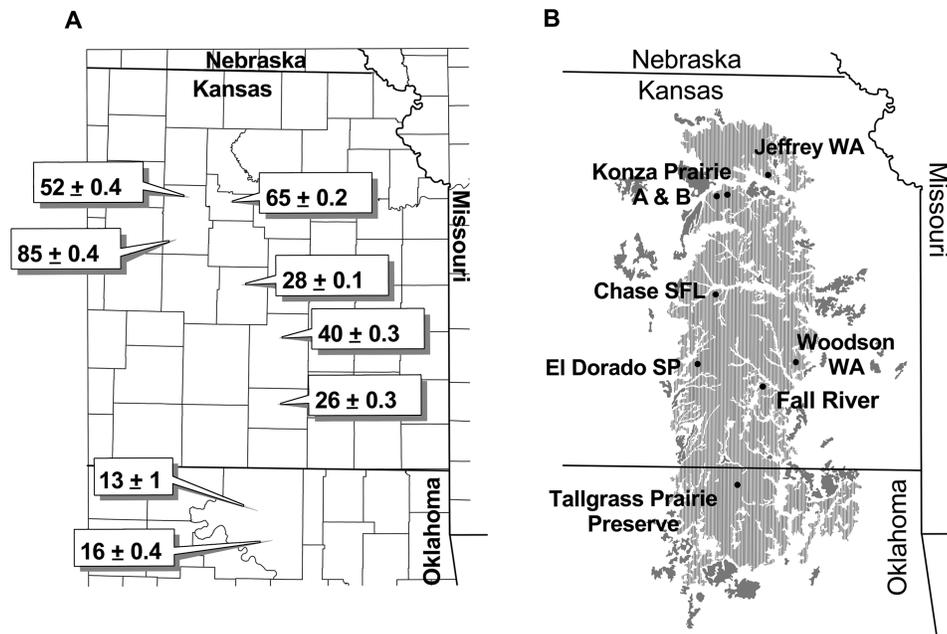


FIG. 1. Map of the Flint Hills region of eastern Kansas and northeastern Oklahoma. (A) Geographic variation in mean count (number of birds per route \pm SE) of Brown-headed Cowbirds across counties of the region from the North American Breeding Bird Survey (BBS) (1966–2002). (B) Distribution of eight study sites (2001–2002) across the tallgrass prairie of the Greater Flint Hills region (gray-shaded area); data from The Nature Conservancy. (Jensen and Cully 2005. Used with permission from Springer ©.)

TABLE 1. Management regimes, forest-to-grassland ratios in surrounding landscapes, nest sample sizes, and cowbird parasitism statistics on Dickcissel nests across eight study sites in the Flint Hills of Kansas and Oklahoma, 2001–2002. Locations of study sites are shown on Fig. 1.

Study site	Year	Prairie management ^a	Forest-to-grassland ratio			Active nests (<i>n</i>) ^b	Percentage of nests parasitized ^c	Cowbird eggs per parasitized nest
			5-km radius	10-km radius				
Jeffrey Wildlife Area	2001	Hayed, unburned	0.12	0.15		32	84.4	2.56
	2002	Hayed, burned	–			22	81.8	2.28
Konza Prairie, A ^d	2001	Not burned or hayed	0.26,	0.35		50	82	3.22
Konza Prairie, B ^d	2002	Not burned or hayed	0.16,	0.35		75	78.7	2.49
Chase County SFL	2001	Hayed and burned	0.18	0.12		28	78.6	2.95
	2002	Hayed and burned	–			24	91.7	2.59
El Dorado State Park	2001	Partially hayed and unburned	0.10	0.08		19	68.4	2.46
	2002	Partially hayed and unburned	–			24	70.8	2.18
Woodson Wildlife Area	2002	Grazed ^e previous summer, unburned	0.24	0.32		65	20	1.15
Fall River Area	2001	Hayed, unburned	0.46	0.29		19	0	0
Tallgrass Prairie Preserve	2001	Unhayed, unburned	0.11	0.18		50	0	0
	2002	Unhayed, burned	–			69	8.2	1.4

^a Refers to management just prior to the Dickcissel breeding season, where burning occurred in early spring the year of the breeding season, and haying occurred in the previous July.

^b Includes only nests that survived until incubation had begun.

^c Nests containing one or more cowbird egg or nestling.

^d Site at Konza Prairie moved 4 km in 2002 because of a late-burning-season fire.

^e Grazed by domestic cattle (*Bos taurus*).

METHODS

Study area.—The study area was the Flint Hills region, which stretches from northeastern Kansas to northeastern Oklahoma within the central Great Plains of North America. The region is dominated by treeless expanses of remnant tallgrass prairie, the soils of which are typically too thin for cultivation (Fig. 1). The prairie is dominated by the grasses *Andropogon gerrardii*, *Panicum virgatum*, *Sorghastrum nutans*, *Schizachyrium scoparium*, and numerous forb species. Gallery forests, oak-prairie savannahs, and other woodlands form woodland edges of tallgrass prairie, though they are a relatively small component of the region's landscapes. Six study sites were monitored in each of two years (mid-May to mid-July, 2001 and 2002) and were located across the latitudinal extent of the Flint Hills, from Konza Prairie Biological Station, Kansas (The Nature Conservancy, Kansas State University) in the north to The Tallgrass Prairie Preserve, Oklahoma (The Nature Conservancy) in the south. Other study sites were managed by the Kansas Department of Wildlife and Parks or the U.S. Army Corps of Engineers. The 2001 Konza Prairie study site was relocated to the other side of that preserve (~4 km away) in the second year of the study because of a fire late in the burning season (May 5). The Fall River Lake area was discontinued in 2001 because of a lack of cowbirds (a companion study [Jensen and Cully 2005] required cowbirds to be present) and its small area, which resulted in low nest-sample sizes, and was replaced with a study site at the nearby Woodson Wildlife Area in 2002. Prairies were burned every one to six years, and some were hayed in mid-July. Table 1 shows the variation in burning across the eight study-site replicates. Areas chosen for study plots within each site were ungrazed to prevent cattle damage to experimental perches in a related study (Jensen 2003, Jensen and Cully 2005). Because all study sites were contiguous with larger expanses of tallgrass prairie, they were not prairie fragments. However, study sites ranged from approximately 40–100 ha.

Data collection.—Habitat characteristics believed to be potentially important to local cowbird parasitism frequencies on Dickcissel nests were measured at local and landscape scales. At the scale of local nesting habitat, vertical structure (density) of the prairie vegetation

on each site was measured using the visual obstruction readings (VOR) of Robel et al. (1970). Vegetative concealment of individual nests after nest completion was not measured, because of changes in vegetation structure that occur during nesting attempts, especially early in the growing season. However, a yearly “snapshot” of overall vegetation structure per study site was assumed to be a reasonable index of nest vegetation structure. Five VOR measurements were taken every 20 m along three 100-m transects extending from the centers of three point-count circles (used to estimate avian abundance for related studies; Jensen 2003, Jensen and Cully 2005) located throughout the prairie of each study site. Those measurements were made during the first week in July on all sites in each year, prior to any mowing. The readings (in centimeters) were then averaged within each site to yield one overall estimate of VOR per site. Distances (in meters) of nests to the nearest wooded edge were measured using a laser range finder and averaged per study site. At much larger habitat scales, the proportion of forest to grassland habitats within 5- and 10-km radius circles around study-site centers was measured. Landcover databases from Kansas and Oklahoma GAP projects were used, in which landscape proportions of pooled grassland and forest vegetation types within each radius were measured using ARCVIEW, version 3.2 (Environmental Systems Research, Redlands, California). Coverage of grazed land around study sites was not measured because grazing is the predominant range management practice throughout the Flint Hills, and all study sites were immediately adjacent to prairie grazed by domestic cattle. Thus, foraging habitat was readily accessible to cowbirds on all study sites.

Host community attributes that might influence cowbird parasitism were measured to obtain estimates of overall host availability per site. Those attributes were (1) relative abundance of all potential hosts (“accepter” and “rejecter” species [Rothstein 1975] that cowbirds may attempt to parasitize, excluding excessively large or aggressive hosts and cavity nesters; Robinson et al. 1999), and (2) absolute densities of Dickcissels. Relative abundances and densities were measured using variable-width line transect surveys (Burnham et al. 1980). Those transects extended from a randomly selected

point along a wooded edge within each site to a random location in the center of the prairie of each site. All transects ran at acute angles to wooded edges so that woodland-nesting hosts could be sampled, but those transects were disproportionately situated in prairie because of the relative availability of habitats. The length of each transect per study site varied from 427 to 1,530 m in length, but that variable "effort" was accounted for with the abundance and density metrics used. Each transect was sampled five times each year from 27 May to 30 June, between 0600 to 1000 hours (CST) each day. All males heard or seen per species were recorded as an index of nest territory abundance. Estimates of absolute densities (individuals per hectare) of Dickcissels were calculated using DISTANCE, version 4.1 (Thomas et al. 1998), in which a global detection probability across all sites was used to estimate Dickcissel density per transect sample. Absolute densities of female cowbirds were similarly calculated (cowbirds are sexually dimorphic in their plumage and vocalizations). Estimation of absolute densities of pooled host species is problematic because of the variety of different host species with different detection probabilities. Instead, the relative abundance of those hosts was simply measured as detections per kilometer of transect sampled. Host relative abundance, Dickcissel density, and female cowbird density were estimated for each transect sampling date and were then averaged across sampling dates and years (see below) per study site.

Nest searching began prior to nest initiation by Dickcissels in each study year. Dickcissel nests were found from mid-May to mid-July by observing female activity or opportunistically by observers flushing birds while walking through study plots. Blue surveyor flags were placed 5 m from each nest. Nests were monitored to record nest contents every three to four days until completion. Most nests were monitored through to nest completion (fledging, desertion, or predation), except for some nests on study sites mowed for hay. Average nest-initiation date was measured as the average date of detection of first Dickcissel nests across years per site (discussion of year pooling below). Daily nest mortality rates (Mayfield 1975) of Dickcissel nests per site were measured as number of nest losses divided by total nest exposure days. Nests that failed prior to incubation were

not included in analyses, because the window of parasitism opportunity during host egg-laying and early incubation stages (Lowther 1993, Johnsgard 1997) is incomplete for such nests. Nest mortality was mostly attributable to predation (58.5% of all nests), and less so to nest desertion (5% of all nests).

Response variables of interest.—Response variables were (1) cowbird parasitism frequency, (2) parasitism intensity on Dickcissel nests, and (3) measures of Dickcissel nest success. Female cowbird density was explored as both an explanatory variable in relation to parasitism levels and a response variable in relation to local and landscape habitat variables, host community variables, and Dickcissel nest attributes. Parasitism frequencies were measured as the proportion of nests containing ≥ 1 cowbird egg or nestling when found, whereas parasitism intensity was measured as the number of cowbird eggs or nestlings per parasitized nest.

The main cost of cowbird parasitism expected to affect Dickcissel reproductive success was removal of host eggs by female cowbirds (Zimmerman 1983), which obviously results in fewer Dickcissels fledged per nest. However, there is also evidence that parasitism intensity influences predation rates during the nestling stage (Jensen and Cully 2005). Therefore, daily nest mortality rates were measured separately for incubation and nestling stages (Mayfield 1975). Final clutch size of Dickcissel nests (after all apparent egg removal by cowbirds) was recorded, in addition to the number of Dickcissel young present in nests on visits prior to fledging (assumed fledged), for all nests and for successful (undepredated) nests only. These Dickcissel nest-success parameters were analyzed at two scales. First, they were compared with levels of parasitism intensity (0 to ≥ 6 cowbird eggs per nest) across all nests to examine the effect of parasitism intensity at the level of individual nests. Then those parameters were calculated for all nests per study site and compared to geographic variation in cowbird parasitism frequency and intensity.

Statistical analyses.—The many explanatory variables of interest in the current study were too numerous for inclusion in a single, global categorical regression (e.g. logistic regression) for selection of "best-fit" models including several explanatory variables, or to examine interactions among the explanatory variables.

Therefore, we separately compared the measures of parasitism with each explanatory variable using a nonparametric correlation analysis. Spearman rank correlation was used to examine categorical cowbird parasitism frequencies and parasitism intensities on Dickcissel nests in relation to the many habitat and host community attributes, Dickcissel nest attributes, and female cowbird density per site. Female cowbird density was compared with the same habitat and host community attributes using Pearson correlation, because cowbird density estimates were continuous and not proportional data. As noted below, the results should be interpreted with caution, because multiple comparisons increase the probability of Type I error.

The effect of cowbird parasitism on the various nest productivity parameters of Dickcissels across all nests was assessed using categorical regression analyses (logistic and Poisson rate regression), where the independent variable was parasitism intensity (i.e. maximum number of cowbird eggs found per nest: 0 to ≥ 6). Logistic regression was used to compare Dickcissel egg hatchability (number of eggs hatched divided by eggs incubated in nests surviving until the nestling stage) and daily nest mortality during incubation and nestling stages (number of nest losses per total exposure days; Mayfield 1975, Hazler 2004) in relation to parasitism intensity. Poisson rate regression was used to compare Dickcissel final clutch size (number of host eggs incubated after egg removal by cowbirds) and number of Dickcissels fledged per nest ("apparent fledge rate") and per successful nest (i.e. undepredated nests) in relation to parasitism intensity. Lastly, associations of Dickcissel nest productivity parameters with local cowbird parasitism rate and intensity were assessed using Spearman rank correlation.

Justification for pooling data across years, for all analyses, is as follows. Only a single year of data was available for four of the eight study-site replicates because of study-site relocations. Moreover, in 2001, nests were either heavily parasitized (frequencies from 68% to 85%), or not parasitized at all (of 48 nests at Tallgrass Prairie Preserve and 19 nests at the Fall River site). However, 8% of the 61 Dickcissel nests found on the Tallgrass Prairie Preserve in 2002 were parasitized. On sites where parasitism was observed, parasitism frequencies did not differ significantly among years (with sites as blocks;

Cochran-Mantel-Haenszel $\chi^2 = 2.07$, $df = 1$, $P = 0.15$).

RESULTS

Female cowbird density, parasitism rate, and multiple parasitism intensity were not significantly ($P > 0.05$) related to local or landscape habitat variables, host-community variables, or Dickcissel nest initiation dates (Table 2). Burning of prairies was not related to parasitism levels among the study sites (Table 1; e.g. 79–92% of nests were parasitized on burned sites in the northern Flint Hills, whereas only 8% of nests were parasitized on burned sites in the Tallgrass Prairie Preserve in 2002). Thus, variation in cowbird parasitism levels seemed independent of habitat and host-community attributes. Both parasitism measures were only significantly related to geographic variation in the density of female cowbirds (Table 2). We acknowledge that the alpha level of significance (traditionally 0.05) may be divided by the number of correlations performed (i.e. 8) to account for amplified Type I error probability as the number of tests performed increases. After that adjustment, only parasitism intensity appears to be significantly related to female cowbird density.

Dickcissel final clutch size, hatchability of eggs, apparent fledge rate, and number fledged per successful nest were all significantly and negatively related to parasitism intensity across Dickcissel nests (Table 3). Daily nest mortality rate during the nestling period increased significantly with increasing parasitism intensity, but was independent of parasitism intensity during incubation. All statistically significant relationships with nest-level parasitism intensity remained so when adjusting for the number of regression models run ($\alpha = 0.05 / 6$ tests = $\alpha = 0.008$).

When those measures of Dickcissel nest productivity were pooled per study site, only Dickcissel final clutch size and number of Dickcissels surviving to fledging in successful nests were significantly and negatively associated with parasitism rate per study site (Table 4). Those same nest-success parameters, in addition to apparent fledge rate, were also significantly and negatively related to parasitism intensity per site (Table 4). Only the relationship of clutch size with parasitism levels is

TABLE 2. Correlation results of female cowbird density, parasitism frequency (percentage of nests parasitized), and parasitism intensity (number of cowbird eggs per parasitized nest) on Dickcissel nests by Brown-headed Cowbirds in relation to local prairie vegetation structure, nest proximity to forest edge, forest-to-grassland ratios within landscapes, abundance of potential hosts, Dickcissel attributes, and female cowbird density across eight study sites within the Flint Hills tallgrass prairie of Kansas and Oklahoma.

	Female cowbird density		Parasitism frequency		Parasitism intensity	
	<i>r</i>	<i>P</i>	<i>r_s</i>	<i>P</i>	<i>r_s</i>	<i>P</i>
Mean visual obstruction of prairie vegetation	0.21	0.61	-0.24	0.57	0.14	0.74
Mean distance to forest edge	0.04	0.92	-0.38	0.35	0.07	0.87
Forest-to-grassland ratio, 5-km radius	-0.11	0.80	-0.12	0.78	-0.05	0.91
Forest-to-grassland ratio, 10-km radius	0.43	0.29	-0.19	0.65	0.10	0.82
Mean host relative abundance	-0.04	0.92	-0.21	0.61	-0.19	0.65
Male Dickcissel density	-0.13	0.76	-0.26	0.53	-0.10	0.82
Mean Dickcissel nest initiation	0.11	0.79	0.66	0.08	0.44	0.27
Female cowbird density	-	-	0.79	0.02	0.90	<0.01

TABLE 3. Logistic and Poisson rate-regression results of Dickcissel final clutch size (after egg removal by cowbirds) and egg hatchability (proportion of incubated eggs that hatched), daily nest mortality rates during incubation and nestling stages of Dickcissel nests, and Dickcissel fledge rate per each nest and per successful (undepredated) nests in relation to cowbird parasitism intensity across Dickcissel nests (0 to >6 cowbird eggs per nest). Wald chi-square statistics and *P*-values for categorical regression slope parameters (β) are given, where positive and negative slopes indicate trends in the response variable as parasitism intensity increases across nests.

	<i>n</i>	β	χ^2	<i>P</i>
Final clutch size ^a	392	-0.18	77.71	<0.01
Egg hatchability ^b	597	-0.35	29.84	<0.01
Daily nest mortality rates				
During incubation ^b	2,463.5	-0.06	1.41	0.23
During nestling stage ^b	839	0.25	12.11	<0.01
Number fledged per nest ^a	392	-0.48	60.15	<0.01
Number fledged per successful nest ^a	82	-0.33	32.11	<0.01

^a Analyzed using Poisson rate regression (*n* = total number of nests).

^b Analyzed using logistic regression (*n* = number of host eggs in clutches that survived to nestling stage for hatchability analysis, and number of nest exposure days for analyses of daily mortality rates).

statistically significant when adjusting for Type I error.

Because the Dickcissel was the focal host species, few nests of other species were found. Of those, 52 were Eastern Meadowlark (*Sturnella magna*) nests. The Eastern Meadowlark is another grassland “core species” in the Flint Hills tallgrass prairie (Zimmerman 1993) and a regionally common cowbird host (Elliott 1978, Jensen 1999). Parasitism frequencies on Dickcissels and Eastern Meadowlarks were positively correlated among the six study sites where five or more Eastern Meadowlark nests were found (*r* = 0.83, *P* = 0.04). None of the 14

Eastern Meadowlark or 19 Dickcissel nests found on the Fall River site were parasitized. Therefore, we suspect that the geographic pattern in parasitism on Dickcissel nests is common to other grassland-nesting songbirds in the Flint Hills region.

DISCUSSION

In contrast to the findings of previous research (e.g. Elliott 1978), cowbird parasitism frequency on Dickcissel nests—and likely other grassland bird nests (e.g. Eastern Meadowlark)—is highly variable across the Flint Hills tallgrass prairie of

TABLE 4. Spearman rank-correlation results of Dickcissel nest productivity parameters in relation to parasitism frequency (percentage of nests parasitized) and parasitism intensity (number of cowbird eggs per parasitized nest) by Brown-headed Cowbirds, across eight study sites within the Flint Hills tallgrass prairie of Kansas and Oklahoma.

	Parasitism frequency		Parasitism intensity	
	r_s	P	r_s	P
Final clutch size	-0.81	0.01	-0.83	0.01
Egg hatchability	-0.31	0.46	-0.33	0.42
Daily nest mortality, incubation	-0.62	0.10	-0.24	0.57
Daily nest mortality, nestling stage	0.55	0.16	0.67	0.07
Number fledged per nest	-0.67	0.07	-0.79	0.02
Number fledged per successful nest	-0.75	0.03	-0.72	0.04

the Great Plains. The latitudinal pattern of parasitism was independent of habitat structure at local and landscape scales, host abundance, and Dickcissel density or nesting attributes. Local levels of parasitism rate and intensity were only related to the local density of female cowbirds. The latitudinal gradient in cowbird abundance and parasitism roughly corresponds with the larger latitudinal pattern of cowbird abundance seen within the Great Plains from BBS data (Price et al. 1995). Cowbird abundance increases with latitude in the Great Plains.

Smith and Myers-Smith (1998) found geographic variation in cowbird parasitism on Song Sparrow (*Melospiza melodia*) nests among islands to be most related to spatial variation in cowbird density, where cowbird density appeared to be a function of isolation from mainland cowbird foraging opportunities. Others also have found cowbird abundance and parasitism to be related to the landscape availability of cowbird feeding habitats, namely agricultural areas or grazed pastures (Goguen and Mathews 2000, Thompson et al. 2000). In the current study, nests were located in ungrazed areas only; however, all study sites were in rangeland-dominated landscapes and immediately adjacent to grazed prairie, requiring only short commuting distances by cowbirds to and from foraging habitat.

We put forth the caveat that our study sites were not representative of the vast majority of tallgrass prairie in the Flint Hills, because they were ungrazed by cattle. Parasitism frequencies appear to be higher in the grazed areas surrounding study sites in the southern Flint Hills (W. E. Jensen pers. obs.), where we found parasitism frequencies to be low. However, we feel that the latitudinal pattern in parasitism would

still be evident among grazed prairie throughout the Flint Hills (and is supported by recent observations; W. E. Jensen pers. obs.). Nests are infrequently parasitized in grazed areas of the Tallgrass Prairie Preserve (D. Reinking pers. comm.). Moreover, we found Dickcissel nests to be heavily parasitized on the northern Flint Hills study sites, despite those prairies not being grazed.

Variation in local habitat structure failed to explain variation in parasitism levels among study sites. The structure of local prairie vegetation was not related to local parasitism levels on Dickcissel nests. Only 5% of Dickcissel nests were parasitized on the Tallgrass Prairie Preserve, where vegetation was tallest and densest among sites (VOR: $\bar{x} = 40.2 \pm 2.1$ cm (SE), $n = 30$), but Dickcissel nests on the nearby Fall River site experienced 0% parasitism, where vegetation density was lowest among all sites (VOR: $\bar{x} = 22.7 \pm 1.5$ cm, $n = 15$). Moreover, 82% of Dickcissel nests were parasitized at the site with the second highest average VOR (Konza Prairie 2001; VOR: $\bar{x} = 36.3 \pm 2.0$ cm, $n = 15$). Winter (1999) similarly found vegetation structure at Dickcissel nest sites to be unrelated to parasitism by cowbirds. Variation in parasitism levels across study sites was also not related to differences in nest proximity to wooded edges among study sites. However, cowbirds exhibit density-dependent selection of wooded edge versus prairie interior habitats in the region (Jensen and Cully 2005). As mentioned above, local burning management of prairie vegetation seemed to have no effect on local parasitism levels (Table 1).

The "frequency-dependent host" hypothesis (Smith and Myers-Smith 1998) states that

variation in local parasitism levels within a host species is a function of that species' abundance rank in local host communities. In accordance with that hypothesis, there was previous suggestion that the high level of cowbird parasitism on grassland birds found in the Great Plains (e.g. Elliott 1978, Zimmerman 1983) might be an artifact of the region's grassland host community being spatially and numerically greater than woodland host communities (Peer et al. 2000, Jensen and Finck 2004). That is a logical hypothesis, especially to explain why grassland birds are parasitized by cowbirds where forests are absent, but it was evidently not the case in the present study, because there was no correlation between parasitism on Dickcissel nests and relative proportions of forest and grassland habitats in landscapes surrounding study sites (Table 1). All sites were located in tallgrass prairie-dominated landscapes (Fig. 1). However, there was forest habitat available in some study landscapes; forest habitat was 26% as common as grassland in landscapes around Konza Prairie (Table 1) where parasitism frequencies on Dickcissel nests were ~80%. It is worth mentioning here that the forest-to-grassland landscape ratio of the current study should not be interpreted as the forest-cover landscape metrics related to parasitism of forest birds and cowbird abundance in the midwestern U.S. (e.g. Robinson et al. 1995, Donovan et al. 1997, Thompson et al. 2000). The latter studies highlighted the inverse relationship between forest cover and cowbird feeding habitat as a major limitation of cowbird occurrence and parasitism in forest-bird communities. The forest-to-grassland ratio we used was not intended or expected to be an index of cowbird feeding habitat. Our landscape metric was intended as an index of the availability of forest-to-grassland host communities for cowbirds, assuming that the cover of those habitat types across landscapes was correlated with the relative abundance of the hosts that use those habitats.

Geographic variation in cowbird parasitism was not the result of differences in local host availability or Dickcissel density. Dickcissel nest initiation was likewise not correlated with cowbird activity in tallgrass prairie. The laying period of cowbirds across the Flint Hills begins well before Dickcissels initiate nesting in mid-to late May (W. E. Jensen pers. obs.). However, the timing of nest initiation of other cowbird

hosts across other habitats (e.g. forest and shrubland birds) was not recorded and could be explored further in relation to geographic variation in cowbird activity within tallgrass prairie. We also note that Dickcissels and Eastern Meadowlarks may exhibit some low level of cowbird egg rejection behavior (Peer et al. 2000), but we found no clear evidence of that behavior in our study. Moreover, we do not expect that rejection behavior would vary in those species across the latitudinal extent of the Flint Hills and therefore discount the possibility as an explanation for the geographic parasitism gradient observed.

Variation in cowbird abundance and parasitism across the Flint Hills seems most related to geographic variation in cowbird density. Many studies of different host species and host communities (in grassland, forest, shrubland) have shown local parasitism frequencies across the continental United States to correlate more strongly with geographic variation in cowbird abundance than with variables of landscape configuration or habitat availability (Hoover and Brittingham 1993, Smith and Myers-Smith 1998, Thompson et al. 2000, Herkert et al. 2003). Parasitism on Dickcissel nests by cowbirds is highly variable across this host species' geographic range, ranging from 7% to 95% of nests parasitized (summaries in Ortega 1998 and Koford et al. 2000). The lowest levels documented by Ortega (1998) and Koford et al. (2000) were from Louisiana and Oklahoma and are comparable with the low parasitism frequencies on Dickcissels in Missouri (10% of 242 nests; Winter 1999), Illinois (13% of 222 nests; Peer et al. 2000), and the southeastern Flint Hills (Table 1). The highest levels of parasitism on Dickcissels are from the northern Flint Hills (Table 1; Elliott 1978, Hatch 1983, Zimmerman 1983). Our results most closely support Smith and Myers-Smith's (1998) "parasite density" hypothesis that geographic variation in brood parasitism is mostly dependent on geographic variation in brood parasite density. Studies demonstrating geographic variation in cowbird parasitism (Hoover and Brittingham 1993, Smith and Myers-Smith 1998, Thompson et al. 2000, Herkert et al. 2003) often highlight distance from the center of the cowbird's geographic range and zone of peak abundance in the Great Plains. However, much variation in cowbird abundance and parasitism within the

Great Plains is evident and can occur across relatively small geographic areas and uniform landscapes (e.g. within states).

The geographic variation in cowbird parasitism is paralleled by geographic variation in nesting success of Dickcissels. Final clutch sizes (after parasitism by cowbirds) and fledging rates of Dickcissels were negatively correlated with cowbird parasitism frequency and intensity across sites (Tables 3 and 4). Because local cowbird parasitism rate and intensity were not related to nest depredation rates (Table 4), it seems that latitudinal variation in Dickcissel nesting success was mostly driven by cowbird parasitism and not by predation. The most severe effect of cowbird parasitism on Dickcissel reproductive success appears to be host egg removal by cowbirds (Tables 3 and 4; Zimmerman 1983). Average final clutch sizes on sites of low parasitism (0–20% of nests parasitized; Table 1) ranged from 3.9 to 4.0 Dickcissel eggs incubated per nest, whereas Dickcissel final clutch sizes ranged from 2.3 to 3.1 eggs on the remaining sites where parasitism frequencies were 70% or greater.

Because the tremendous sizes of remnant prairies in the Flint Hills may provide for areas of low predation on grassland bird nests (Herkert et al. 2003), low levels of cowbird parasitism in the southern Flint Hills may facilitate valuable source populations for many Midwestern grassland songbirds. Further demographic data and modeling are needed to test that idea. Continental and regional variation in cowbird abundance should be considered when establishing reserves or restoring habitat for certain hosts. Areas of low cowbird parasitism may be globally valuable if hosts from such areas provide immigrants to more heavily parasitized, otherwise unviable populations.

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