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Effects of urbanization on site occupancy and density of grassland birds in tallgrass prairie fragments

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ABSTRACT. Tallgrass prairies are among the most threatened ecosystems in the world. Remaining prairies tend to be small and isolated and many are associated with urban and suburban landscapes. We asked how urbanization might impact the conservation value of tallgrass prairie fragments for grassland birds by comparing the densities and the probability of occurrence of Dickcissels (*Spiza americana*), Grasshopper Sparrows (*Ammodramus savannarum*), and Eastern Meadowlarks (*Sturnella magna*) across 28 grasslands surrounded by low, moderate, and high levels of urbanization. We employed a hierarchical model selection approach to ask how variables that describe the vegetation structure, size and shape of grasslands, and urbanization category might explain variation in density and occurrence over two breeding seasons. Occurrence of all three species was explained by a combination of vegetation and patch characteristics, though each species was influenced by different variables and only Eastern Meadowlark occurrence was explained by urbanization. Abundance of all three species was negatively impacted by urbanization, though vegetation variables were also prevalent in the best-supported models. We found no evidence that vegetation structure or other patch characteristics varied in a systematic way across urbanization categories. Although our results suggest that grassland bird density declines with urbanization, urban tallgrass prairies still retain conservation value for grassland birds because of the limited availability of tallgrass prairie habitat and the limited impact of urbanization on species occurrence.

RESUMEN. **Efectos de la urbanización sobre la ocupación de lugares y densidades de aves de pastizales en fragmentos de praderas con altos pastos**

Las praderas con altos pastos están entre los ecosistemas mas amenazados en el mundo. Los remanentes de estas praderas tienden a ser pequeños y aislados y muchos están asociados con paisajes urbanos y suburbanos. Nos preguntamos como la urbanización puede impactar el valor de conservación de los fragmentos de altos pastos en las praderas para aves de pastizales por medio de la comparación de las densidades y probabilidad de ocurrencia de *Spiza americana, Ammodramus savannarum* y *Sturnella magna* en 28 praderas rodeadas por bajos, moderados y altos niveles de urbanización. Empleamos un modelo jerárquico de selección para preguntar como variables que describen la estructura de vegetación, el tamaño y la forma de la pradera, y la categoría de urbanización pueden explicar la variación en densidad y ocurrencia a lo largo de dos temporadas reproductivas. La ocurrencia de las tres especies se explico por una combinación de vegetación y características del parche, aunque cada especie fue afectada por diferentes variables y solo la ocurrencia de *Sturnella magna* fue explicada por la urbanización. La abundancia de las tres especies fue afectada negativamente por la urbanización, aunque las variables de vegetación fueron también predominantes en los modelos mejor soportados. No encontramos evidencia de que la estructura de la vegetación u otras características del parche variaron de una manera sistemática a lo largo de las categorías de urbanización. Aunque nuestros resultados siguieren que la densidad de las aves de praderas declina con la urbanización, la praderas urbanas de altos pastos todavía retiene un valor de conservación para las aves de praderas debido a la limitada disponibilidad de altos pastos en los hábitats de praderas y el limitado impacto que tiene la urbanización sobre la ocurrencia de especies.

Key words: conservation, Dickcissel, Eastern Meadowlark, Grasshopper Sparrow, Great Plains, vegetation structure

The Tallgrass Prairie ecosystem of the North American Great Plains is of high conservation concern because most of its original extent has been converted to high-intensity agriculture (Samson and Knopf 1994, Mac et al. 1998) and because few remaining prairies are protected and managed for conservation purposes (Hoekstra et al. 2005, Aycrigg et al. 2013). In addition, areas of remaining prairie that are protected tend to be small, isolated fragments (Steinauer and Collins 1996). Many species of plants and animals have experienced population declines in response to this loss of native prairie habitat, but declines in populations of grassland birds have been particularly dramatic (Herkert 1995, Peterjohn and Sauer 1999, Sauer et al. 2011). In response,

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grassland birds have become a conservation priority, and concern over grassland birds has contributed to efforts to protect and restore tallgrass prairies (Vickery et al. 1999).

Many protected prairie remnants were established as part of municipal park systems and are found in and around cities and towns (Schwartz and van Mantgem 1997, Bock and Bock 1998). Other prairie remnants are becoming engulfed by urban and suburban expansion. Increasing urbanization is of concern because it can alter the composition of plant and animal communities, favoring invasive and non-native species (McKinney 2002, Alberti et al. 2003, Marzluff and Ewing 2008). Perhaps most importantly, urbanization may result in prairies becoming fragmented into smaller parcels, increasing the amount of edge and possibly increasing the isolation of prairies from each other (Hamer et al. 2006). Although agriculture has been responsible for much of the loss and fragmentation of native grassland habitat, urbanization may present special challenges for conservation of grassland species. Agricultural areas and their surrounding marginal areas may present fewer barriers to movement and may even act as secondary habitat for some wildlife species. In addition, the potential for restoration to native habitat still exists on many agricultural lands, whereas conversion to urban areas is likely permanent (McKinney 2002, Marzluff and Ewing 2008).

The importance of actively managing tallgrass prairie fragments to maintain habitat quality may make them especially vulnerable to the effects of urbanization. Prairie managers depend on a combination of prescribed fire and grazing to limit encroachment by trees and other woody species, prevent build-up of litter that interferes with the growth of young plants, and increase plant heterogeneity (Knapp et al. 1999). Although mowing prairies may produce many of these benefits (Collins et al. 1998), fire combined with grazing by either cattle (*Bos taurus*) or bison (*Bison bison*) are the preferred tools for management of tallgrass prairies. Urbanization can potentially limit the ability of managers to use these tools because of the risks to humans and property associated with prescribed fire and large grazers, which could result in less suitable vegetation structure (Johnson and Igl 2001, Marzluff 2001, Crooks et al. 2004). Prairie fragments surrounded by urbanized areas may have more woody and invasive plant species (Chapman and Reich 2007), potentially leading to reduced densities of native grassland bird species (Fitzgerald and Pashley 2000, Maestas et al. 2003, Davis 2004).

Our current understanding of urbanization and grassland birds is based primarily on short- or mixed-grass prairie in Colorado (Bock et al. 1999, Haire et al. 2000, Lenth et al. 2006), and a study of grasslands in the eastern United States (Forman et al. 2002). In those studies, density, abundance, and presence of most native grassland bird species were negatively correlated with urbanization. However, the difficulty of extrapolating across communities highlights the need for additional research, specifically involving tallgrass prairie.

Urbanization can have direct impacts on the use of prairie fragments if birds avoid sites surrounded by more urban features. For grassland ecosystems, urbanization might also have indirect effects if increased urbanization results in smaller patches with more edge relative to their size, or if urbanization interferes with habitat management, such as prescribed fire, resulting in less suitable vegetation structure (Johnson and Igl 2001, Marzluff 2001, Crooks et al. 2004). Previous studies indicate that the abundance and reproductive success of grassland birds may be influenced by vegetation structure (Hilden 1965, Herkert 1994, Herkert et al. 1996, Winter et al. 2005, Chapman and Reich 2007). Native grassland birds respond to factors such as the amount of grass and forb cover (Rotenberry and Wiens 1980, Temple 2002), shrub density (Vickery 1996), and litter depth (Swengel and Swengel 2001). Thus, studies of the effects of urbanization on grassland birds also need to account for these factors.

We measured species occurrence and the density of grassland birds in tallgrass prairies located along an urban to rural gradient. Our objective was to determine how urbanization might impact the value of prairie fragments for grassland bird conservation. If urbanization prevents active management, we expect the tallgrass prairie community to become degraded and less attractive to grassland birds. We first addressed this potential indirect impact of urbanization by examining the hypothesis that grassland bird occurrence and density are indirectly affected by urbanization through a relationship with vegetation structure within prairie fragments.

Next, we asked whether the occurrence and density of birds was affected by the size and shape of prairie fragments and by the degree of urbanization surrounding them. There are a significant number of prairie remnants in and around urban areas and, although there are compelling reasons to maintain them for social and educational purposes (Miller and Hobbs 2002), the question remains whether small fragments of tallgrass prairie still retain their conservation value as surrounding landscapes become more urbanized (Shafer 1997).

METHODS

Study area. We studied tallgrass prairie fragments in and around Omaha and Lincoln, Nebraska, and Council Bluffs, Iowa (Mount 2013). Prior to European settlement, the region was dominated by tallgrass prairie, but is now dominated by suburban and urban areas surrounded by row-crop agricultural fields. Sites included remnant tallgrass prairies that have been protected, as well as sites that have been restored from agriculture to tallgrass prairie. We included all accessible urban and suburban prairie remnants, whereas rural sites were selected from among available grasslands nearest to the urban areas. All sites are managed in a similar fashion by prescribed burning, grazing, or mowing. Prairies burned in the spring were not surveyed that season. In 2011, we surveyed 20 sites. Extreme flooding the summer of 2011 resulted in the loss of five rural grasslands located at DeSoto and Boyer Chute National Wildlife Refuges along the Missouri River. In addition, two sites used in 2011 were burned in the spring of 2012. In 2012, we retained 13 original sites and added eight new sites.

We quantified urbanization surrounding each study site based on 1-m-resolution digital orthoimagery acquired by the U.S. Farm Service Agency in 2010 and obtained from the Nebraska Department of Natural Resources (http://www.dnr.ne.gov/digital-imagery-1993-through-2012-1-2-meter). Images were imported into ArcGIS 10.1 (ESRI 2010) and the boundaries of each study site were digitized. We created a 1600-m buffer around the borders of each grassland and used ArcGIS to create 500 random points within each buffer. Land use under each of the points was visually classified as buildings, roads, and other impermeable surfaces (i.e., parking lots and driveways), lawn, agricultural, trees, wetlands, grassland, or open water. In addition, we used ArcGIS to determine the area (m^2) and perimeter (m) of the digitized grassland boundaries and then calculated the ratio of the perimeter to the area (hereafter, edge-to-interior ratio) of each grassland site.

Bird surveys. We sampled grassland bird species richness and density during the 2011 and 2012 breeding seasons using distance sampling at point transects (Thomas et al. 2009). Surveys were done within 4 h after sunrise from 10 May to 10 June 2011, and from 14 May to 10 June 2012. We surveyed each site three times during each breeding season, visiting each site early in the survey period, in the middle, and then late in the survey period. We included each visit in analyses. Points were located near the center of the grassland and, when possible, at least 100 m from all prairie edges. For small sites, points were located as far from edges as possible. During each count, we recorded all birds seen or heard during a 10-min period and their distances from the point location (Thomas et al. 2009). Surveys were not conducted when wind speeds were > 20 km/h or when it was raining.

Vegetation sampling. We measured vegetation structure at each grassland between 27 May and 13 June 2011, and between 29 May and 21 June 2012. We used ArcGIS 10.1 (ESRI 2010) to select nine random points for vegetation sampling in each grassland patch and located these points in the field using GPS. We measured vertical vegetation structure following Rotenberry and Wiens (1980) and Martin et al. (1997). This method is based on recording the number of "hits" of grass, forbs, and shrubs within 10-cm height intervals on a 110-cm pole. We calculated the mean height of vegetation density using the total hits weighted by the midpoint of each height interval. We used the point-centered quarter method at each point to measure forb and shrub density around each random point (Cottam and Curtis 1956).

Statistical analysis. We used the Ward method for hierarchical clustering to categorize levels of urbanization of our study sites (high, moderate, or low) based on the percentage of surrounding areas classified as urban (i.e., lawn, roads, impervious surfaces, and buildings: JMP v. 10.0.2, SAS Institute, Cary, NC; Mount 2013). Based on these clusters, we incorporated urbanization as a categorical variable in our analyses. We used ANOVA to test whether there were significant differences among the categories of urbanization in vegetation characteristics (forb density, shrub density, mean vegetation height, and total grass hits) and site characteristics (area and edge-to-interior ratio). We chose these vegetation characteristics because each describes a different aspect of vegetation in grassland habitats. Forb density and shrub density provide an indication of the structural diversity of the grassland, mean vegetation height provides an indication of vegetation height, weighted by vegetation density, and total grass hits indicate the overall density of grass (Fisher and Davis 2010). Summary descriptions of habitat variables are presented as means $\pm$ SE.

Although we recorded all species seen or heard during bird surveys, our analyses are limited to three obligate grassland bird species (Dickcissels [*Spiza americana*], Grasshopper Sparrow [*Ammodramus savannarum*], and Eastern Meadowlarks [*Sturnella magna*]) for which we recorded sufficient observations to analyze their densities and occurrence. Other obligate grassland bird species, including Henslow's Sparrows (*Ammodramus henslowii*), Bobolinks (*Dolichonyx oryzivorus*), Western Meadowlarks (*Sturnella neglecta*), and Sedge Wrens (*Cistothorus platensis*), were not abundant enough for us to analyze the effects of urbanization on occurrence or density.

We used a model selection approach to determine the effect of urbanization on the occurrence and density of Dickcissels, Grasshopper Sparrows, and Eastern Meadowlarks (Burnham and Anderson 2002). Because other variables may also influence the occurrence and density of grassland obligate species, we employed a hierarchical approach that compared models from three candidate model sets that included (1) year, (2) measures of vegetation structure, and (3) urbanization and patch characteristics (Hamer et al. 2006, Winter et al. 2006, Klug et al. 2009). Within each candidate set, we assessed whether the inclusion of possible covariates (year and vegetation characteristics) increased the explanatory power of the models. If they did, these variables were carried forward into subsequent model sets in the hierarchy. We carried forward variables when they occurred in the top-ranking model and when there was strong support for the top-ranking model compared to the null. We evaluated the AIC weight of the top ranking model compared to the null model's AIC weight, which is a measure of the strength of evidence for one model over another (Burnham et al. 2011). We considered models equivalent when the ratio between the weights was < 2, which would indicate that the top-ranking model was less than twice as likely as the null. For the occurrence analysis, the hierarchy was as follows: (1) year, (2) vegetation (mean grass hits, mean vegetation height, forb density, and shrub density; Table 1) and (3) urbanization and patch characteristic (area and edge-to-interior ratio; Table 1). For the density analysis, we first modeled a detection function and then followed the same hierarchy as for the occurrence analysis (Table 2). We analyzed the multicollinearity of mean forb density, mean shrub density, mean vegetation height, total grass hits, and edge to interior ratio using VIF (variance inflation factor); all had VIF <1.5, indicating no evidence of multicollinearity of the variables used in our models. Because of the significant correlation between area and edge-to-interior ratio (Pearson correlation test, 2011: $r = -0.65$, $N = 20$, $P < 0.001$; 2012: $r = -0.69$, $N = 21$, $P < 0.001$) and variance inflation ratio >2.0, we did not include both of these variables in the same models (Table 1).

To analyze the effect of year, vegetation characteristics, and patch characteristics on occurrence of Dickcissels, Grasshopper Sparrows, and Eastern Meadowlarks, we used mixed effects, nominal logistic regressions using the glmer function from the lme4 package in R 2.15.2 (Bates et al. 2012, R Core Team 2013). The null model was the model with only "site" included as a random effect.

To model detection and density of Dickcissels, Grasshopper Sparrows, and Eastern Meadowlarks, we used the package "unmarked" in R 3.0.2 (R Core Team 2013). We used the generalized distance sampling "gdistsamp" within the package to model the detection function and to analyze the effect of site covariates on density (Table 2; Chandler et al. 2011, Fiske and Chandler 2011). When modeling the detection function, we tested whether observer effects, wind speed, or both of these covariates affected detection. We standardized continuous covariates (wind speed, vegetation characteristics, site area, and edge-to-interior ratio) to a mean of zero

Table 1. Model selection results for testing hypotheses about the effects of vegetation and patch characteristics on grassland bird occurrence.

	K[a]	AICc[b]	ΔAIC[c]	w_i[d]
Dickcissels				
Vegetation Characteristics + Year				
Vegetation Height + Year	4	82.07	0.00	0.22
Year	3	82.58	0.51	0.17
Forb Density + Veg H + Year	5	83.80	1.73	0.09
Grass Hits + Year	4	84.12	2.05	0.08
Shrub Density + Veg H + Year	5	84.23	2.16	0.08
Grass Hits + Veg H + Year	5	84.23	2.16	0.08
Shrub Density + Year	4	84.53	2.47	0.06
Forb Density + Year	4	84.63	2.57	0.06
Forb Density + Shrub Density + Veg H + Year	6	85.99	3.92	0.03
Grass Hits + Forb Density + Veg H + Year	6	86.01	3.95	0.03
Forb Density + Grass Hits + Year	5	86.25	4.18	0.03
Grass Hits + Shrub Density + Veg H + Year	6	86.43	4.36	0.03
Forb Density + Shrub Density + Year	5	86.66	4.59	0.02
Shrub Density + Forb Density + Grass Hits + Veg H + Year	7	88.24	6.18	0.01
Shrub Density + Forb Density + Grass Hits + Year	6	88.39	6.32	0.01
Patch + Year				
Edge + Year	4	79.87	0.00	0.55
Area + Year	4	82.23	2.36	0.17
Year	3	82.58	2.71	0.14
Urban + Edge + Year	5	83.21	3.34	0.10
Urban + Year	4	85.03	5.17	0.04
Grasshopper Sparrows				
Vegetation Characteristics + Year				
Shrub Density + Year	4	100.29	0.00	0.27
Shrub Density + Grass Hits + Vegetation Height + Year	6	100.65	0.37	0.23
Shrub Density + Grass Hits + Forb Density + Year	6	101.96	1.68	0.12
Shrub Density + Forb Density + Year	5	102.24	2.05	0.10
Shrub Density + Grass Hits + Forb Density + Veg Height + Year	7	102.34	2.05	0.10
Shrub Density + Veg H + Year	5	102.46	2.18	0.09
Forb Density + Shrub Density + Veg H + Year	6	104.3	4.02	0.04
Grass Hits + Veg H + Year	5	106.44	6.15	0.01
Grass Hits + Year	4	106.68	6.4	0.01
Year	3	106.93	6.65	0.01
Forb Density + Grass Hits + Year	5	108.2	7.92	0.01
Patch Characteristics + Vegetation Characteristics + Year				
Edge + Shrub Density + Year	5	100.17	0.00	0.28
Shrub Density + Year	4	100.29	0.12	0.26
Urban + Shrub Density + Year	5	100.86	0.69	0.20
Edge + Urban + Shrub Density + Year	6	101.49	1.32	0.14
Area + Shrub Density + Year	5	101.78	1.61	0.12
Eastern Meadowlarks				
Vegetation Characteristics				
Grass Hits + Vegetation Height	4	135.90	0.00	0.41
Grass Hits + Forb Density + Vegetation Height	5	138.03	2.13	0.14
Grass Hits + Shrub Density + Vegetation Height	5	138.12	2.22	0.13
Forb Density + Grass Hits	4	140.27	4.36	0.05
Shrub Density + Forb Density + Grass Hits + Veg H	6	140.29	4.39	0.05
Veg H	3	140.44	4.54	0.04
Forb Density	3	140.72	4.82	0.04

(Continued)

Table 1. Continued

	K[a]	AICc[b]	ΔAIC[c]	w_i[d]
Grass Hits	3	140.77	4.87	0.04
Forb Density + Veg H	4	141.42	5.52	0.03
Null	2	141.49	5.59	0.02
Shrub Density + Forb Density + Grass Hits	5	142.27	6.37	0.02
Shrub Density + Veg H	4	142.61	6.71	0.01
Forb Density + Shrub Density	4	142.81	6.91	0.01
Shrub Density	3	143.42	7.52	0.01
Forb Density + Shrub Density + Veg H	5	143.64	7.74	0.01
Patch Characteristics + Vegetation Characteristics				
Urban + Grass Hits + Vegetation Height	5	134.79	0.00	0.43
Grass Hits + Vegetation Height	4	135.90	1.11	0.25
Edge + Urban + Grass Hits + Vegetation Height	6	137.08	2.29	0.14
Area + Grass Hits + Veg H	5	137.93	3.84	0.07
Edge + Grass Hits + Veg H	5	137.96	3.87	0.07

[a]Number of parameters.
[b]Akaike's information criterion corrected for small sample sizes.
[c]The difference in AICc values between the current and top-ranked model's AICc value.
[d]Weight of evidence supporting the model.

and a standard deviation of one. We transformed year into a dummy variable so we could determine the effect of urbanization while controlling for year effects. We binned the observations into equal distance categories. We determined the breaking points so that the first bin had the highest number of observations per unit area (26 m for Dickcissels, 19 m for Grasshopper Sparrows, and 86 m for Eastern Meadowlarks) and each subsequent bin decreased monotonically (Buckland et al. 2001). Right truncation is recommended for outlying observations at the farthest distances (Buckland et al. 2001). We truncated four Dickcissel observations where distance was >190m. No truncation was necessary for Grasshopper Sparrow or Eastern Meadowlark observations because observations were well-distributed among the bins. We tested the fit of models for detection and for density using a Freeman-Tukey test with bootstrap resampling where $P > 0.05$ indicates adequate fit. We used model-averaging to determine the magnitude and direction of covariates of selected models and presented these as $\beta \pm$ SE (Burnham and Anderson 2002).

RESULTS

Cluster analysis of study sites based on percentages of the surrounding land use classified as urban (i.e., lawn, roads, impervious surfaces, and buildings) resulted in three distinct groupings of sites, designated as high, moderate, or low urbanization. In 2011, we classified six prairies as high, five as moderate, and nine as low urbanization. In 2012, seven sites were classified as high, five sites as moderate, and nine as low urbanization. Total land cover classified as urban differed significantly among sites ($F_{2,25} = 251.4$, $P < 0.001$) in the high (50.2 ± 1.7% urban), moderate (17.5 ± 2.0% urban), and low urbanization categories (3.7 ± 1.2% urban).

Changes in vegetation structure and site characteristics along the urban gradient. We analyzed the effects of urbanization (low, moderate, or high) and year (2011 and 2012) on vegetation variables and found no significant effects on forb density (low = 17.5 ± 7.3 forbs/m^2, moderate = 23.8 ± 9.8 forbs/m^2, high = 41.2 ± 8.6 forbs/m^2; $F_{3,37} = 1.5$, $P = 0.22$), shrub density (low = 0.46 ± 0.19 shrubs/m^2, moderate = 0.15 ± 0.25 shrubs/m^2, high = 0.32 ± 0.22 shrubs/m^2; $F_{3,37} = 0.7$, $P = 0.54$), mean vegetation height (low = 20.7 ± 1.1 cm, moderate = 21.7 ± 1.5 cm, high = 23.4 ± 1.3 cm; $F_{3,37} = 0.9$, $P = 0.45$), or total number of grass hits (low = 12.6 ± 1.1, moderate = 16.8 ± 1.4, high = 13.6 ± 1.3; $F_{3,37} = 1.9$, $P = 0.15$). Among 13 sites studied in both years, we also found no significant change in vegetation between years (matched pairs *t*-tests, df = 12, all $P > 0.10$).

Table 2. Model selection results of the effects of vegetation and patch covariates on densities of Dickcissels, Grasshopper Sparrows, and Eastern Meadowlarks. Models with w_i < 0.01 are not presented.

	K[a]	AICc[b]	ΔAICc[c]	w_i[d]
Dickcissel (N = 752, 26 m, 182 m)[e]				
Density Models: Vegetation Characteristics + Year				
Vegetation Height + Year (P = 0.59)[f]	6	1255.85	0.00	0.40
Vegetation Height + Shrub Density + Year	7	1257.24	1.39	0.20
Vegetation Height + Forb Density + Year	7	1258.09	2.24	0.13
Vegetation Height _ Shrub Density + Grass Hits + Year	8	1259.22	3.37	0.07
Vegetation Height + Shrub Density + Forb Density + Year	8	1259.52	3.67	0.06
Vegetation Height + Grass Hits + Year	6	1259.73	3.88	0.06
Vegetation Height + Forb Density + Grass Hits + Year	8	1260.14	4.29	0.05
Veg. Height + Shrub Density +Forb Density + Grass Hits + Year	9	1261.49	5.63	0.02
Density Models: Patch + Vegetation Characteristics + Year				
Urban + Edge + Vegetation Height + Year (P = 0.66)	9	1234.45	0.00	0.97
Edge + Vegetation Height + Year	7	1241.46	7.01	0.03
Grasshopper Sparrow (N = 200; 19 m, 95 m)				
Density Models: Vegetation Characteristics				
Vegetation Height + Shrub Density (P = 0.44)	6	681.63	0.00	0.32
Vegetation Height	5	682.58	0.95	0.20
Vegetation Height + Shrub Density + Forb Density	7	683.85	2.22	0.10
Vegetation Height + Shrub Density + Grass Hits	7	683.86	2.23	0.10
Vegetation Height + Grass Hits	6	684.70	3.07	0.07
Vegetation Height + Forb Density	6	684.76	3.13	0.07
Shrub Density	5	685.88	4.25	0.04
Veg. Height +Shrub Density + Forb Density + Grass Hits	8	686.09	4.46	0.03
Vegetation Height + Forb Density + Grass Hits	7	686.87	5.23	0.02
Shrub Density + Forb Density	6	686.91	5.28	0.02
Shrub Density + Forb Density + Grass Hits	7	688.75	7.12	0.01
No covariates (null)	4	689.50	7.87	0.01
Forb Density	5	689.87	8.23	0.01
Density Models: Patch + Vegetation Characteristics				
Urban + Vegetation Height + Shrub Density (P = 0.40)	8	677.79	0.00	0.68
Edge + Vegetation Height + Shrub Density	7	680.09	2.30	0.22
Vegetation Height + Shrub Density	6	681.63	3.84	0.10
Eastern Meadowlark (N = 82; 86 m, 258 m)				
Density Models: Vegetation Characteristics				
Vegetation Height + Grass Hits (P = 0.52)	6	409.78	0.00	0.34
Vegetation Height + Grass Hits + Shrub Density	7	410.40	0.62	0.25
Vegetation Height + Grass Hits + Forb Density	7	410.60	0.82	0.23
Vegetation Height + Grass Hits + Shrub Density + Forb Density	8	411.40	1.62	0.15
Density Models: Patch + Vegetation Characteristics				
Urban + Grass Hits + Vegetation Height (P = 0.55)	8	394.02	0.00	0.73
Urban + Edge + Grass Hits + Vegetation Height	9	396.03	2.01	0.27

[a]Number of parameters.
[b]Akaike's information criterion corrected for small sample sizes.
[c]The difference in AICc values between the current and top-ranked model's AICc value.
[d]Weight of evidence supporting the model.
[e]Number of birds detected, distance bin size, and the maximum distance included in each analysis.
[f]P-values from Freeman-Tukey goodness of fit test, with values >0.05 indicating adequate fit.

Study sites ranged in area from 0.9 ha to 55.6 ha, and had edge-to-interior ratios ranging from 0.044 to 0.006. We studied 28 sites across the 2 yr, and found no systematic differences among sites with low, moderate, and high levels of surrounding urbanization in either total area (low = 15.5 ± 3.5 ha, moderate = 21.1 ± 5.5 ha, high = 15.6 ± 5.1 ha; $F_{2,25}$ = 0.4, P = 0.67) or edge-to-interior ratio (low = 0.013 ± 0.002 m/m^2, moderate = 0.014 ± 0.003

m/m^2, high = 0.018 ± 0.003 m/m^2; $F_{2,25}$ = 0.9, P = 0.41). There was a significant negative correlation between the edge-to-interior ratio and area among sites (r = −0.68, N = 28, P < 0.001).

Occurrence of grassland birds and vegetation and patch characteristics. In 2011, we recorded 293 Dickcissels, 121 Grasshopper Sparrows, and 44 Eastern Meadowlarks. Numbers of these same species recorded in 2012 were 463, 79, and 49, respectively. We used all sampling periods for analysis of occurrence.

Including year as a factor explained the occurrence of Dickcissels better than the null model ($\Delta AICc_{Null\text{-}Year}$ = 3.4). The model with mean vegetation height and year was the best model among those including vegetation characteristics (Table 1). However, the model including only year as a covariate had a ΔAICc = 0.51 and the AICc weights of the two models were similar ($w_{Veg\ Ht + Year}$ = 0.22, w_{Year} = 0.17). Therefore, we concluded that the addition of vegetation variables did not improve the explanatory power of the models.

When comparing models of patch characteristics, those including edge-to-interior ratio had the lowest ΔAICc values and a cumulative AICc weight of 0.82 (Table 1). Model averaging indicated that Dickcissel occurrence was negatively related to edge-to-interior ratio (β = −160.9 ± 66.3; Fig. 1A). Models containing urban category had a cumulative weight of 0.14, indicating that urbanization did not explain occurrence as well as edge-to-interior ratio.

The model including "year" predicted the occurrence of Grasshopper Sparrows better than the null model ($\Delta AICc_{Null\text{-}Year}$ = 12.1). Models with year and shrub density best explained the occurrence of Grasshopper Sparrows (Table 1). Shrub density was present consistently in all top-ranking models, and these models had a cumulative AICc weight of 0.95. Based on model averaging, the occurrence of Grasshopper Sparrows had a positive relationship with shrub density (β = 7.4 ± 3.4; Fig. 1B).

The best model for the occurrence of Grasshopper Sparrows included edge-to-interior ratio, shrub density, and year (Table 1). However, several other models had ΔAICc values < 2 and similar AICc weights (Table 1). In particular, because the model with shrub density and year had a similar weight to the best model, we concluded that variables describing patch characteristics did not improve the likelihood of explaining Grasshopper Sparrow density.

The model best describing the occurrence of Eastern Meadowlarks included urbanization (Table 1), and sites with more surrounding urbanization had lower occurrence of Eastern Meadowlarks than sites with less urbanization surrounding them (β_{Low} = 2.40 ± 1.03; $\beta_{Moderate}$ = 2.45 ± 1.19; Fig. 1A). In contrast, models with edge-to-interior ratio and with area had higher ΔAIC values than the model with no patch characteristics. Occurrence of Eastern Meadowlarks was positively related to the average number of grass hits (β = 0.25 ± 0.11) and negatively related to mean vegetation height (β = −0.26 ± 0.12; Fig. 1C).

Effects of vegetation and patch characteristics on grassland bird densities. The detection function for estimating density of Dickcissels best fit a half normal, negative binomial model (Freeman-Tukey goodness-of-fit test, P = 0.41). The minimum AICc model included observer effects and was 2.5 times more likely than the second-ranked model including wind speed and observer as covariates, and 13 times more likely than the null model. Including year as a factor improved the fit of the best detection model (ΔAICc = 2.3, w_i = 0.75, β = 0.46 ± 0.25) and we included year as a factor in all subsequent model selection.

When we compared models with site-level vegetation characteristics, the best model included mean vegetation height and year (Table 2). The probability of the top model with vegetation height was 0.4 compared to 0.2 for the next best model. Mean vegetation height was also found in the subsequent models with lower AIC values and overall the group of models including mean vegetation height contributed 0.99 of the cumulative AICc weights (Table 2). Dickcissel density was higher at sites with taller mean vegetation height (β = 0.32 ± 0.07; Fig. 1D). No other vegetation characteristic consistently occurred in selected models.

Among the models including the patch characteristics of urbanization, patch area, and patch edge-to-interior ratio, we found strong support for an effect of urbanization on the density of Dickcissels (Table 2). The model with urbanization, edge-to-interior ratio, mean vegetation height, and year was the best model

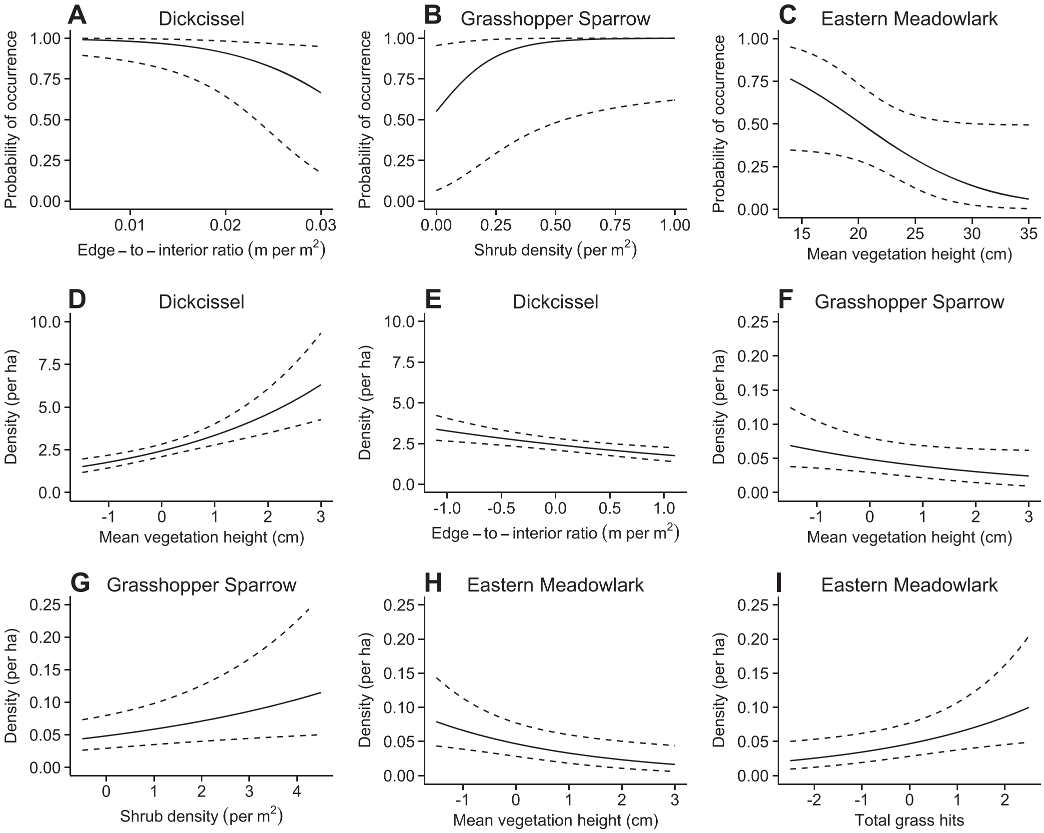

Fig. 1. The relationship between patch characteristics and vegetation structure on the occurrence and density of birds in grasslands in Nebraska and Iowa. Solid lines represent the predicted probability of occurrence and density from the most informative models. Dashed lines represent the upper and lower 95% confidence intervals for the predictions. Probability of occurrence in a patch was associated with patch-level edge-to-interior ratio (m per m^2) for Dickcissels (A), shrub density (per m^2) for Grasshopper Sparrows (B), and mean vegetation height (cm) for Eastern Meadowlarks (C). Density of Dickcissels was associated with (D) mean vegetation height and (E) edge-to-interior ratio. Density of Grasshopper Sparrows was explained by (F) mean vegetation height and (G) shrub density, whereas density of Eastern Meadowlarks was related to (H) mean vegetation height and (I) total grass hits.

with an AICc weight of 0.97 (Table 2). Sites embedded in an urban landscape had the lowest densities of Dickcissels compared to sites with less or no urbanization ($\beta_{\text{Low}} = 0.50 \pm 0.16$, $\beta_{\text{Moderate}} = 0.52 \pm 0.17$; Fig. 2B), and sites with higher edge-to-interior ratios had lower densities ($\beta = -0.29 \pm 0.13$; Fig. 1E).

For Grasshopper Sparrow density, both null detection models had lower AICc values than any detection model with covariates (Freeman-Tukey goodness of fit test, $P = 0.38$). The hazard rate, negative binomial function was the top-ranked detection model and was used in subsequent tests of hypotheses. The null detection model was more likely to fit the data than the model with year added as a density covariate ($w_{null} = 1.0$).

The minimum AICc model of vegetation characteristics influencing Grasshopper Sparrow density included mean vegetation height and shrub density (Table 2). Overall, mean vegetation height and shrub density were included in models with cumulative weights of 0.91 and 0.62, respectively. Mean vegetation height negatively influenced density ($\beta = -0.18 \pm 0.12$; Fig. 1F), whereas shrub density positively

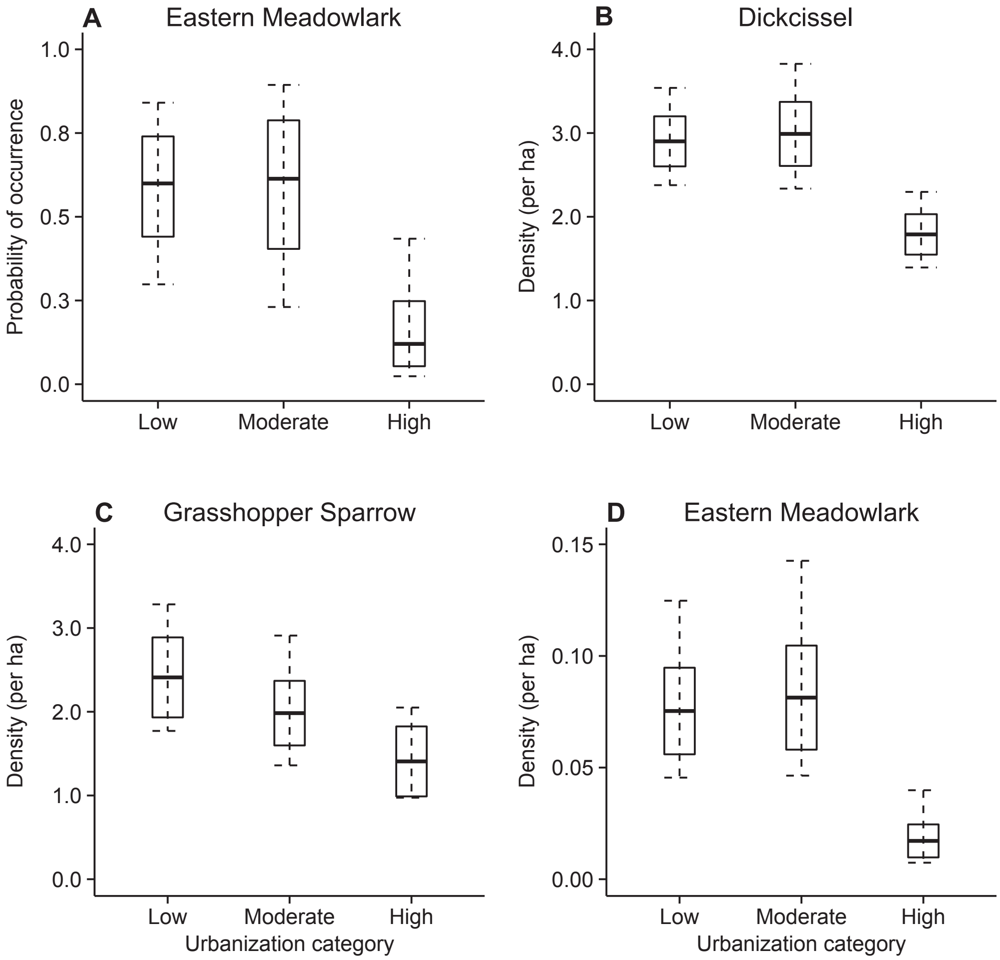

Fig. 2. The influence of urbanization on the probability of occurrence of (A) Eastern Meadowlarks and the density of (B) Dickcissels, (C) Grasshopper Sparrows, and (D) Eastern Meadowlarks. Bold crossbars indicate the predicted probability of occurrence and density produced from the most informative models, boxes encompass ± SE of the predicted value, and dashed lines represent upper and lower 95% confidence bounds for the predictions.

affected Grasshopper Sparrow density ($\beta = 0.19 \pm 0.09$; Fig. 1G).

Among models addressing hypotheses about patch characteristics, the most likely model included urbanization, and was three times more likely than the model including edge-to-interior ratio, and nearly seven times more likely than the null vegetation model with vegetation height and shrub density (Table 2). Sites with the highest levels of surrounding urbanization had the lowest densities of Grasshopper Sparrows ($\beta_{moderate} = 0.51 \pm 0.30$, $\beta_{low} = 0.77 \pm 0.26$; Fig. 2C).

For Eastern Meadowlarks, the minimum AICc model for the relationship between detection and distance from the observer was a half normal, negative binomial function with no covariates of detection (Freeman-Tukey goodness-of-fit test, $P = 0.46$). When year was included, the detection model with no covariates remained the model most likely to explain the data (ΔAICc $= 2.12$, $w_{null/year} = 2.84$).

For models with vegetation covariates, the top model included mean vegetation height and total number of grass hits (Table 2). Models including mean vegetation height and the number of grass hits had cumulative weights of 0.97 and 0.96, compared to 0.02 for the null model. Eastern Meadowlark density decreased as mean vegetation height increased ($\beta = -0.35 \pm 0.14$; Fig. 1H) and increased with a greater number of grass hits ($\beta = 0.31 \pm 0.12$; Fig. 1I).

Among models including patch variables, the top two models included urbanization category as well as the vegetation variables (Table 2). Models containing urbanization had a cumulative weight of 1.0, supporting a strong effect of urbanization on density of Eastern Meadowlarks in grassland habitats. Urbanization negatively affected the density of Eastern Meadowlarks ($\beta_{\text{Moderate}} = 1.49 \pm 0.41$; $\beta_{\text{Low}} = 1.56 \pm 0.43$; Fig. 2D).

DISCUSSION

Our direct measure of urbanization in the surrounding landscape emerged as important in explaining variation in density of all three focal species (Fig. 2). Densities of all three species were negatively related to urbanization, and Eastern Meadowlarks showed the strongest response. Eastern Meadowlarks were the only one of the three species where urbanization was important in models of occurrence. Both Grasshopper Sparrows and Dickcissels occurred at grasslands regardless of the level of urbanization in the surrounding landscape. Such species-specific responses are common in studies of urban bird communities, and densities of Grasshopper Sparrows and other grassland birds are known to decline in short- and mixed-grass prairies in urban areas (Bock et al. 1999, Lenth et al. 2006).

We found that several measures of vegetation structure explained variation in both occurrence and density of grassland birds. All three focal species responded differently to vegetation structure (Tables 1 and 2). As expected based on previous work, Dickcissels were positively associated with taller vegetation structure (Wiens 1973, Davis 2004, Winter et al. 2005). We found that both Dickcissel density and occurrence increased with taller mean vegetation height, though the occurrence model based on year alone was equivalent to the one including mean vegetation height. Mean vegetation height was also an important parameter in models for Grasshopper Sparrow density and both the density and occurrence of Eastern Meadowlarks, but both species were negatively associated with taller vegetation. This finding is consistent with earlier work on Grasshopper Sparrows indicating a preference for shorter vegetation (Wiens 1973, Davis 2004). Prior studies of Eastern Meadowlarks have suggested a preference for "moderately tall" vegetation < 50 cm tall (e.g., Hull 2003). Our sites were dominated by tallgrass prairie plant species such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), so many sites had maximum vegetation heights well above 50 cm. This overall tall vegetation structure likely explains the negative association between Eastern Meadowlarks and vegetation height that we observed. The positive association between grass density, measured by total grass hits, and the occurrence and density of meadowlarks was also consistent with previous studies (Granfors et al. 1996, Hull 2003).

We found that shrub density was positively associated with the occurrence and density of Grasshopper Sparrows. Invasion of grasslands by shrubs and other woody vegetation is considered a significant threat to tallgrass prairie communities (Briggs et al. 2005, Ratajczak et al. 2012). Evidence from previous work suggests that higher densities of shrubs have a negative effect on Grasshopper Sparrows (Wiens 1973, Vickery 1996, Grant et al. 2004) and several other grassland bird species (Herkert et al. 1996, Grant et al. 2004, Jacobs et al. 2012). We also found that the density of forbs was not an important variable in the models of occurrence or density of grassland birds. Again, this finding contrasts with the focus on including a large component of forbs in restorations and previous studies indicating the importance of forb density and diversity for grassland bird communities (Wiens 1973, Herkert et al. 1996, Dechant et al. 2003a, 2003b, Hull 2003, Fisher and Davis 2010). These relationships may reflect the nature of the grasslands we studied. Our sites consisted of unplowed prairie remnants and well-established, moderate-to-high diversity restored sites. All of the sites we studied, including the urban and suburban prairies, are intensively managed, most with regular prescribed burns. Analyses of forb density, shrub density, mean vegetation height, and total number of grass hits all indicated that mean values were not different among sites in different urbanization categories suggesting that management has not suffered as a result of urbanization. The absence of low quality or poorly managed sites in our study limited the range of variation in habitat characteristics. A study including sites with more trees and shrubs or low plant-species diversity, such as conservation reserve program fields, might reveal a stronger relationship between bird occurrence and measures of density and vegetation.

The size of prairie fragments did not emerge as an important determinant of either occurrence or density of the three focal species, even though several grasslands were very small (< 10 ha). However, the ratio of length of the grassland edge to the area of the grassland was informative for Dickcissel occurrence and density, and was correlated with fragment size. The correlation between fragment area and edge-to-interior ratio makes it difficult to distinguish area sensitivity (Herkert 1994, Ribic et al. 2009) from edge effects. Both Grasshopper Sparrows and Dickcissels have been shown to be sensitive to edge habitat (Helzer and Jelinski 1999, Jensen and Finck 2004, Hamer et al. 2006, Patten et al. 2006). In addition, reproductive success may be lower in smaller patches with more edge (Winter and Faaborg 1999, Winter et al. 2000, Fletcher and Koford 2003), though how these patterns translate to urban prairies would depend on how the predator community responds to urbanization. For example, Marzluff (2001) found some evidence that populations of nest parasites and avian predators increased in urban areas, whereas, in some cases, nest predators such as snakes might decrease in abundance with urbanization (Patten and Bolger 2003). In either case, more abundant nest predators in urban areas may not always translate into higher rates of nest predation (Stracey and Robinson 2012) and birds in urban areas may even have lower risks of predation (Ryder et al. 2010, Ausprey and Rodewald 2011, Friesen et al. 2013).

As with vegetation, urbanization might indirectly impact grassland birds if grassland patches become smaller and more fragmented (Marzluff 2001, Marzluff and Ewing 2001). Although this is likely to occur in most community types, tallgrass prairie is almost unique in that virtually all remaining patches are already small and fragmented, regardless of the surrounding landscape (Steinauer and Collins 1996, Robertson et al. 1997). This result is reflected in our study sites where neither area nor edge-to-interior ratio of grasslands varied among urbanization categories. Many other tallgrass prairie species appear to be resilient in the face of fragmentation, with even relatively small prairie remnants retaining a higher than expected number of native species (Robertson et al. 1997, Cully et al. 2003, Wilsey et al. 2005, Koper et al. 2010), and suggesting that non-avian species may respond more strongly to vegetation composition and structure than fragmentation and isolation (Stoner and Joern 2004).

Our results suggest that increasing urbanization surrounding grassland fragments may decrease their quality as habitat for grassland birds. Densities of all three focal species were lowest at sites with the highest levels of urbanization. Increasing urbanization is associated with a number of changes that could potentially have negative impacts on breeding grassland birds, including visual obstructions, disturbance from human activities, traffic and noise pollution (Forman et al. 2002, Slabbekoorn and den Boer-Visser 2006, Wood and Yezerinac 2006), and changes in incidence of predators or nest parasites (Chace et al. 2003, Burhans and Thompson 2006). Any of these factors could influence birds at the sites we studied. All of the highly urbanized sites were surrounded by single-family housing and several were located in parks or other areas used by the public.

Although densities of grassland birds may be lower at urbanized sites, these sites are still used by grassland birds of conservation interest, as indicated by our observation that the probability of occurrence of grassland birds was not lower at urbanized sites for two of three focal species. Although we have not measured reproductive success in relation to urbanization, our results do suggest that, given the severe limits on the amount of tallgrass prairie habitat available for breeding, grasslands in suburban and urban areas may retain conservation value (Adams et al. 2013). We found no indirect effects of urbanization in the form of degraded vegetation structure, but this remains a concern for prairies in urban landscapes. Most urban fragments are too small to be efficiently managed with grazing, and use of prescribed fire in suburban and urban areas can pose significant challenges, both from perceived risks associated with fire and from smoke production (Bock and Bock 1998). Given the scarcity of opportunities to conserve prairies, maintaining the quality of management at these sites to also maximize their contribution to conservation of native grassland species is important.

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