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Landscape heterogeneity influences the response of grassland birds to energy development

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Grasslands are inherently dynamic systems having developed with frequent disturbance from fire and grazing that varies in space and time to create heterogeneity. Today, many management practices emphasize the even use of grasslands by grazers and either no fire or uniform fires, resulting in grasslands that lack the variability in plant structure and composition to support the entire suite of grassland biodiversity. Previous research has suggested that the reintroduction of variable disturbance may be among the best conservation strategies for grassland birds, as these practices promote diversity and abundance of many species. However, the reintroduction of heterogeneity is taking place in the context of the continued development of grasslands for energy production, and the utility of heterogeneity based management practices may decline in fragmented landscapes. We investigated how fragmentation from oil and gas may constrain management efforts to promote biodiversity by evaluating changes in bird abundance with distance from roads and conventional oil wells across a gradient of times since fire. We found that time since fire was the primary driver of grassland bird distribution, with dickcissels, eastern meadowlark and grasshopper sparrows occurring in all vegetation patches, while Henslow's sparrows primarily occurred in patches that were greater than 13 months post-fire and upland sandpipers were mostly detected in recent burns. Further, Henslow's sparrows avoided oil wells for considerable distances, while eastern meadowlark was more abundant in areas close to oil wells in vegetation patches that were one-year post-fire. Grasshopper sparrows avoided roads in recent burns and dickcissels, and eastern meadowlarks were attracted to roads in patches that were recently burned and one-year post-fire, respectively. The restoration of heterogeneous fire regimes will benefit bird communities by creating variable vegetation structure that can support multiple grassland bird species; however, energy development has the potential to fragment grasslands for some species.

Keywords: avoidance, eastern meadowlark, Henslow's sparrow, oil development, pyric-herbivory, tallgrass prairie

The interaction of fire and grazing is an essential disturbance process in grasslands (Samson and Knopf 1994, Anderson 2006), and the reintroduction of historic disturbance patterns to create heterogeneity is becoming a high conservation priority in many regions (Fuhlendorf et al. 2006, Twidwell et al. 2013). Specifically, the temporal and spatial scale of fires and selective grazing of herbivores creates a shifting mosaic of seral stages that provide habitat for a variety of organisms (Powell 2008, Ricketts and Sandercock 2016). Further, this vegetation mosaic reduces annual variation in primary production and stabilizes availability of resources for wildlife, such as food sources and nesting cover, during periods of environmental extremes such as drought or high temperatures (Allred et al. 2014, Hovick et al. 2015, Skagen et al. 2017). However, most grasslands are currently managed under significantly altered disturbance regimes where fire is either suppressed or occurs over vast areas resulting in homogeneous landscapes (Fuhlendorf and Engle 2001, Holecheck 2011). In areas where fire is excluded, grasslands can transition to an entirely different vegetative state such as woodlands or shrublands (Briggs et al. 2002), and in areas of homogenous disturbance, such as large-scale prescribed fires, biodiversity is reduced (Coppedge et al. 2008a). In an effort to prevent further loss of biodiversity within grasslands, conservation efforts have placed increasing emphasis on re-establishing historic fire regimes and heterogeneity in grasslands (Fuhlendorf et al. 2006, Twidwell et al. 2013, Limb et al. 2016).

Recently, heterogeneity-based management practices, such as patch burn–grazing, have been proposed as a means

of promoting biodiversity in grasslands through the restoration of the fire–grazing interaction. Generally, these methods restore heterogeneity by burning discrete patches, typically at the pasture or within pasture scale, and allowing grazers, typically domestic cattle *Bos taurus* or bison *Bison bison*, to preferentially graze in recently burned areas while leaving portions of the landscape unburned with minimal grazing pressure for one or more years (Fuhlendorf and Engle 2001). The interactive effects of spatially variable fires and preferential grazing by large herbivores, termed pyric-herbivory, results in a patchwork of vegetation structure where areas that were recently burned and grazed have short sparse vegetation, and unburned and ungrazed patches are characterized by tall, dense, residual vegetation litter. The resulting mosaic of patches mimics historic landscape patterns and have been linked to greater species diversity across multiple taxa (Engle et al. 2008, Powell 2008, Ricketts and Sandercock 2016). Avian communities, in particular, have been shown to benefit from practices that promote grassland heterogeneity, often having greater diversity and densities of species in grasslands managed for heterogeneity as compared to more homogenous grasslands (Hovick et al. 2014, 2015, Duchardt et al. 2016). Many grassland bird species will specialize in the use of specific seral patches in the time since fire mosaic, such as species like the Henslow's sparrow *Ammodramus henslowii* which use only unburned patches with dense litter (Hovick et al. 2015), or migratory shorebirds which use primarily recently burned patches (Hovick et al. 2017). Due to the positive effects of heterogeneity-based management on grassland birds, these practices have been suggested to be among the top strategies for grassland bird conservation.

However, the majority of research on avian response to grassland heterogeneity has focused on relatively continuous grasslands, and the degree of fragmentation in grasslands can have a substantial impact on shaping grassland bird communities (Herkert 1994, Johnson and Igl 2001, Renfrew et al. 2005). Many grassland bird species avoid small or fragmented grasslands or have lower densities and reduced nest success in grasslands adjacent to habitat edge (Winter et al. 2000, Bollinger and Gavin 2004). These edge effects can extend up to several kilometers beyond an edge for some species (Koper et al. 2009, Sliwinski and Koper 2012). The indirect loss of habitat that results from edge avoidance behaviors likely have exacerbated the declines of many grassland species (Koper et al. 2009) as landscape context and grassland structure can influence use and settlement of the landscape by grassland bird species (Winter and Faaborg 1999, Herse et al. 2017, 2018). Among grassland birds, responses to edges is likely associated with avoidance of nest parasites or predators (Winter et al. 2000), changes in vegetation structure (Koper et al. 2014) or an innate avoidance of tall features (Grant et al. 2004). Further, habitat fragmentation can limit the effectiveness of conservation strategies aimed at promoting grassland birds, such as heterogeneity-based management, if species avoid otherwise suitable grasslands due to the presence of an edge. When assessing the effectiveness of heterogeneity-based strategies for bird conservation, interactions between fire and grazing with other landscape characteristics, such as edge, must be taken into account.

Energy development has become a dominant issue affecting biodiversity throughout the world (Sawyer et al. 2006, Aldridge and Boyce 2007, Northrup and Wittemyer 2013, Jones et al. 2015), and grassland birds may be particularly vulnerable due to their sensitivity to fragmentation and anthropogenic disturbance (Ribic et al. 2009). Oil and gas production is of particular concern in North American grasslands due to its already extensive footprint (Allred et al. 2015), and the risk of future expansion as new and unconventional methods of production open areas previously unavailable for development (Copeland et al. 2009, EIA 2015). In addition to direct habitat loss and increased risk of mortality from collisions and pollutants, development in grasslands can have a number of indirect effects such as greater light and sound pollution (Longcore and Rich 2004, Francis et al. 2009), increased human activity (Holloran et al. 2015), and the spread of exotic or invasive plant species (Nasen et al. 2011). The presence of infrastructure and the associated changes to grasslands can significantly increase the fragmentation of grasslands through the creation of habitat edge (Thompson et al. 2015). Some grassland birds have reduced abundances or densities in the areas surrounding infrastructure, and for some species, such as Sprague's pipit *Anthus spragueii* and Baird's sparrow *Ammodramus bairdii*, these effects can exist for considerable distances (Thompson et al. 2015, Nenninger and Koper 2018).

To better understand the interaction of edge effects and grassland heterogeneity on species abundance, we investigated grassland bird response to energy development on a landscape in the southern Great Plains that is managed for heterogeneity but has also undergone extensive development for oil production. Our primary objective was to assess if energy development can reduce the effectiveness of heterogeneity-based management by reducing bird abundance near infrastructure. Additionally, we wanted to determine at what distance grassland bird abundance was no longer affected by development and if these avoidance distances are uniform across a structurally heterogeneous grassland. Relatively few studies have attempted to quantify specific avoidance thresholds for grassland bird species around infrastructure, especially in the southern Great Plains, potentially limiting our understanding of the full impacts of energy in grasslands. The multi-use landscape of the southern Great Plains allows for a unique opportunity to investigate if fragmentation from energy development can constrain management and conservation efforts critical to biodiversity in grassland landscapes (Fuhlendorf et al. 2006). To accomplish these objectives, we evaluated grassland bird abundance relative to the distance from roads and oil wells and implemented a relatively new method for testing for the presence of avoidance thresholds. We focused our efforts on five species that make up the core of the grassland bird community and are considered species of conservation concern in the region (Table 1; Vickery et al. 1999, With et al. 2008, Rohweder 2015).

Table 1. Summary of time since fire and vegetation structure associations of five focal species. The selected five species make up the core of the grassland bird community in the southern Great Plains.

Species	Scientific name	Time since fire associations[a]	Habitat associations	References
Dickcissel	*Spiza americana*	1–2 years post fire	tall vegetation, moderate litter cover and depth	Dechant et al. 2002a, b
Eastern meadowlark	*Strunella magna*	1–2 years post fire	intermediate to tall vegetation, high forb cover, high litter cover	Delisle and Savidge et al. 1997, Hull 2000
Grasshopper sparrow	*Ammodramus savannarum*	1–2 years post fire	intermediate grass cover, moderate litter depth	Vickery 1996, Dechant et al. 2002b
Henslow's sparrow	*Ammodramus henslowwii*	2–3 years post fire	tall grass, high litter cover and depth	Cully and Michaels 2000, Herkert et al. 2002
Upland sandpiper	*Batramia longicauda*	0 years post fire	moderate bare ground, moderate to low vegetation height	Sandercock et al. 2015, Hovick et al. 2017

[a] Time since fire associations based on Powell 2008.

Methods

Study site

Our field study took place in Osage County, Oklahoma during 2016–2017. The study site is located in the southernmost extent of the Flint Hills Ecoregion which contains some of the most extensive intact tracts of tallgrass prairie in North America (With et al. 2008). Vegetation in the region is composed primarily of tallgrass prairie dominated by big bluestem *Andropogon gerardi*, little bluestem *Schizachyrium scoparium*, switchgrass *Panicum virgatum*, indiangrass *Sorghastrum nutans*, and a mix of forbs. Cross timber forests dominated by post oak *Quercus stellata* and blackjack oak *Q. marilandica* occur throughout the area but occur mostly in drainages.

Our study took place on private properties in Osage County that are managed to promote heterogeneity using prescribed fire and grazing. Prescribed fires are applied to the landscape on a rotational basis, and grazers are allowed to preferentially graze recently burned areas resulting in a mosaic of patches differing in vegetation structure. The majority of the prescribed fires took place during the early spring (March–May) before the start of the growing season, but a small number of fires also occurred in the fall (September–December) of each year. The fire return interval is approximately 2–4 years. Approximately, 42% (16 868 ha) and 37% (14 908 ha) of the properties included in this study were burned in 2016 and 2017 respectively. The mean (±SE) size of a prescribed burn was 220 ha (21.9), with prescribed burns ranging from 5.75 ha up to 1125 ha. The area is primarily managed for production of domestic cattle. However, one property (The Nature Conservancy's Tallgrass Prairie Preserve) is partially grazed by bison.

Survey design

We evaluated grassland bird responses to major gravel roadways and conventional oil wells. We choose to focus our efforts on grid-powered pump jacks as this was the most common well type at our study site. Other well types were not considered because of their limited numbers and the substantial variation in noise and well pad sizes. Only oil wells that were actively producing during the survey periods were considered (actively pumping within one month of survey date), however, some wells were inactive during surveys due to normal maintenance. We defined major gravel roadways (hereafter, roads) as county roads that were wide enough for two lanes of traffic (typically greater than 8 m). While secondary access roads may also elicit avoidance from bird species, most secondary roads at our study site are associated with oil wells and bird responses to these roads may be confounded by the presence of wells. Due to the difficulty in separating these sources of disturbance, we considered only major roads in this study.

We used line transect surveys that started at the beginning of the natural vegetation and each transect was 500 m in length. Sites were selected so that transects could extend 500 m from the edge without crossing landscape features that may influence bird abundance (e.g. crosstimber forest, burn unit boundaries) while remaining greater than 500 m from other roads or oil wells except for those located at the start of the transect. We only placed one transect per oil well and spaced road transects at least 500 m apart. Additionally, transects were selected to represent three categories of time since fire: current year burns (0–12 months), one-year post-fire (13–24 months), and areas greater than two years post-fire (greater than 24 months) as these were the most commonly available time since fires across the study site (Table 2). These time since fire intervals were selected as they were the most common patches on the landscape and allowed us to capture the entire suite of grassland birds that may occur in this region. Additionally, control surveys,

Table 2. Number of transects surveyed to determine grassland bird response to energy development in 2016 and 2017 in Osage County, Oklahoma. In each year, oil wells, road sites, and control transects were surveyed within patches that were 0–12 months post-fire, 13–24 months post-fire, and greater than 24 months post-fire.

	0–12 months	13–24 months	>24 months
2016			
Control	3	5	2
Road	16	10	14
Oil wells	16	10	8
2017			
Control	4	4	5
Road	8	6	10
Oil wells	12	8	9
Total			
Control	5	9	7
Road	24	16	24
Oil wells	26	18	17

located at least 500 m from energy infrastructure, woodlands and burn unit boundaries, were used to evaluate if our survey design influenced bird behavior. Specifically, we used the control transects to verify that our methodology of using 500 m transects did not result in biased results from birds moving in response to the observer. To assess differences in vegetation structure between the different time since fire patches, vegetation surveys were conducted along bird survey transects. On each transect at 100-m intervals we placed a 1-m^2 quadrat and assessed percent cover of live grasses, forbs, grass litter, bare ground, and shrubs. Additionally, we measured litter depth (cm) and vegetation height (cm) in the center of the plot, and visual obstruction using a Nudd's profile board (Nudds 1977).

Surveys started in mid-May when breeding activity began, and ended in early to mid-June with every transect being visited twice in a season. Different observers were used for each visit, to minimize biases introduced by observer effects. Surveys began one-half hour before sunrise and ended around 10:00 when singing activity declines, and we visited transects in a random order on the day of the survey to reduce time of day effects. We only conducted surveys on mornings with winds less than 24 km h^{-1} precipitation that was no more than light to intermittent, and clear visibility. On the morning of the survey, the observer began either at the structure or the far end of the transect and walked the survey route at a slow pace (about 1 m s^{-1}) using a handheld GPS unit to guide. Distances to birds was estimated using a laser range finder and only individuals detected within 50 m of either side of the transect were recorded to minimize detection and identification errors by observers (Pillsbury et al. 2011, Hovick et al. 2015). Every bird heard or observed within 50-m of the transect was recorded, along with the perpendicular distance of the bird to the transect and the distance from disturbance. The order in which transects were surveyed was randomized during the season with the constraint that there was a minimum of seven days between visits to a single transect.

We used unadjusted averages in subsequent analyses. Use of statistical methods to adjust detection probability in datasets that violate assumptions of these methods have been shown to result in increased error (Marques 2004, Efford and Dawson 2009). Our dataset violated common assumptions of distance-based detection methods (few individuals recorded close to the observer; Buckland 2001), and no other method was believed to provide reliable estimates of detection probabilities (Efford and Dawson 2009) or were suitable for our methods (Farnsworth et al. 2002). Further, the use of unadjusted raw counts has been suggested to be an acceptable index of species abundance by Johnson (2008), and Henderson and Davis (2014). However, we did attempt to limit common types of detection biases through our field methodology. We tried to restrict detection bias by limiting surveys to 50 m of either side of the transect as detection of grassland birds have been shown to be relatively high within this threshold (Leston et al. 2015). Additionally, we used different observers for each survey and differed the order surveys were conducted to reduce the potential effects of observer and time of day bias.

Data analysis

Differences in vegetation structure among the three times since fire categories was assessed using an analysis of variance (ANOVA). Vegetation structure measurements were averaged for each transect and the transect level means were used as response variables to compare vegetation structure among the three time since fire categories. When the ANOVA reported significant differences in vegetation structure, differences were determined using Tukey multiple comparison tests. All differences were considered significant at the $p < 0.05$ level.

Species response and potential edge effects were evaluated using methods outlined in Thompson et al. (2015). The following methods assume that species abundance relative to an edge can follow one of three patterns 1) no response, 2) plateau response, and 3) linear response (Thompson et al. 2015, Tanner et al. 2017). If a species abundance is unaffected by development, abundance should vary randomly over the length of a transect and could be described by a model with no slope. Alternatively, if a species does respond to development, that species abundance will increase or decrease up to a certain distance beyond which abundance no longer changes with increasing distance. This threshold can be estimated using the following formula originally presented in Thompson et al. (2015): $y[x < t] = a + b \times x$; $y[x > t] = a + b \times t$ where y is species abundance, x is distance from edge, t is the distance at where species abundance is no longer affected by the feature and the slope of abundance becomes zero, and a and b are the model slope and intercept respectively. However, because a species response to edges can extend up to several kilometers beyond a feature (Koper et al. 2009, Sliwinski and Koper 2012) and our surveys were limited to 500 m, it is possible that a structure can influence a species abundance beyond the length of our transects. In this case, abundance would appear to change over the entire length of the transect and could be described by a linear model with a slope that is greater or less than zero.

Our analysis focused on five species that make up the core of the grassland bird community in the region (Coppedge et al. 2008b Hovick et al. 2015). These species included dickcissel, eastern meadowlark, grasshopper sparrow, Henslow's sparrow, and upland sandpiper. Abundance of these species within 50-m distance intervals was used as the response variable in the subsequent analysis. Species' response to roads or oil wells was analyzed separately for each time since fire patch. We only examined species response to a structure if that species had greater than 25 detections associated with all transects for that structure for the time since fire considered (Thompson et al. 2015, Tanner et al. 2017). Observations were categorized into 50 m distance bins (10 total bins) beginning at the end of the transect closest to the disturbance (e.g. 0–50, 51–100 m, etc.) and we used the average of the two surveys to calculate bird abundance in each distance bin for a transect. This allowed us to avoid temporal pseudoreplication within season, and to minimize observer effects (Koper et al. 2009). For control sites, the end that would correspond to 0 meters was randomly assigned before surveys started. Species response to oils wells and roads were evaluated for each time since fire/edge type separately.

Models were developed in program R to describe the three possible response scenarios previously described (Thompson et al. 2015, Tanner et al. 2017). To model the case where species abundance does not change with increasing distance from a feature (hereafter null model) we fitted an intercept-only model where the slope was constrained to zero. To model the case where avoidance extends beyond the length of the transect (hereafter slope model) we used simple linear regression to find a fixed slope describing species abundance over the entire length of the transect. Finally, to test for avoidance less than 500 m (hereafter plateau model) we performed segmented linear regression using package 'segmented' in program R (Muggeo 2008), where abundance was allowed to increase or decrease up to a breakpoint estimated by the package, and then the slope is constrained to zero after the breakpoint. We compared models in an AICc framework, and the models with the lowest AICc score were considered the best for describing species abundance in relation to distance from development (Burnham and Anderson 2002). We considered models competitive in if they were within 2 AICc units of the top model, however, model parameters and confidence intervals were inspected for all competitive models and models were excluded from further consideration if they differed from a more parsimonious model by the addition of a single parameter and had 85% confidence intervals that included zero (Arnold 2010).

We chose to analyze species response to development for each time since fire and structure separately and to pool by transect as the statistical software used to estimate avoidance thresholds in the subsequent analysis typically would not converge under more complex model structures. Separating the data by time since fire allowed us to obtain these threshold estimates for more species. We felt that this approach was justified over more traditional analysis methods (generalized linear mixed models), as one of our specific objectives was to estimate these avoidance thresholds, and our survey methods allowed us to use models without random effects previously described. Our use of the average count of a species for each distance bin on a transect allowed us to avoid within season pseudoreplication by ensuring that each transect was only represented once per year. Averaging among visits was appropriate in this case as our survey efforts were balanced (each transect surveyed an equal number of times, and all distance bins had the same number of observations within a year; Murtaugh 2007, Thompson et al. 2015). Further, as no transect was the same time since fire in both years of the study we treated surveys in different years independently minimizing the need for random effects for years and sites.

In addition to individual species response, we also performed the above analysis for all grassland birds and all bird species pooled together. Similar to individual species, we calculated the abundance of grassland obligate species and all species combined for each distance bin for roads or oil wells in each time since fire patch, and the same set of models describing abundance were compared using AICc.

Sources of variation in bird detections

Though we attempted to account for common sources of variation in bird detection during the data collection process by alternating observers, randomizing the order of surveys, and restricting surveys to only days with moderate weather conditions, we attempted to identify potential sources of variation in detections for each species using generalized linear mixed models (GLMM) and used site as a random effect as we used the unpooled abundance data for this analysis. We modeled total number of birds detected in each distance bin by time of day (measured as minutes past sunrise), Julian date, air temperature (°C), wind speed (km h^{-1}), and cloud cover. We derived weather variables from a nearby weather station (<10 km from all transects; Brock et al. 1995). We conducted GLMs using package 'lme4' and 'AICcmodavg' in program R. We used AICc models to select the best model describing factors influencing detections for each of the five focal species separately. We considered the best models the model with the lowest AICc score, and any models within 2 AICc units of the top model were considered competitive (Burnham and Anderson 2002).

Results

During 2016 and 2017, we surveyed transects associated with 61 oil wells, 64 road sites, and 20 control sites, representing three different times since disturbance for each survey type (Table 2). Dickcissels, eastern meadowlarks and grasshopper sparrows were common in all times since fire, while Henslow's sparrows were detected primarily in patches that were 13–24 months post fire and >24 months post fire. Upland sandpipers occurred mainly in recently burned patches (Table 3; Supplementary material Appendix 1 Table A1).

The three time since fire categories showed significant differences across several vegetation structure metrics. Patches 13–24 months post fire and >24 months post fire had significantly taller vegetation and had higher visual obstruction readings compared to patches that were burned 0–12 months prior (Table 4). Both litter depth and percent cover of litter increased with greater times since fire which resulted in a corresponding decrease in percent cover of bare ground (Table 4). Percent cover of grass was highest in intermediate times since fire (13–14 months post fire) but only differed significantly from patches 0–12 months post fire (Table 4).

Species response to energy development

Dickcissels, grasshopper sparrows and eastern meadowlarks showed variable responses to roads across different post-disturbance stages (Table 5; all model coefficients and standard errors are located in Supplementary material Appendix 2 Table A1). The slope model was the best model for grass-

Table 3. Average counts per transect and the percent of transects (in parenthesis) each of the five focal species was detected on in three time since fire categories in Osage County, Oklahoma.

	0–12 months	13–24 months	>24 months
Dickcissel	8.1 (100)	12.3 (100)	11.7 (100)
Eastern meadowlark	3.6 (100)	4 (100)	3.7 (100)
Grasshopper sparrow	2.5 (94)	3.1 (81)	1.2 (66)
Henslow's sparrow	0 (1)	3.2 (67)	3.4 (81)
Upland sandpiper	0.2 (32)	0.1 (16)	0.03 (8)

Table 4. Mean vegetation structure (±SE) on breeding bird transects in three time since fire categories in Osage County, Oklahoma. Means with different letters are significantly different (Tukey's HSD, $p < 0.05$) among different time since fire treatments.

	0–12 months post fire	13–24 months post fire	>24 months post fire
% grass*	44.9 (±4.5)[a]	57.1 (±4.7)[b]	48.3 (±4.6)[ab]
% forb	11.2 (±2.9)	16.1 (±3.6)	13.9 (±3.1)
% litter**	0.5 (±0.4)[a]	14 (±3)[b]	34.1 (±5)[c]
% shrub	0.4 (±0.5)	2.3 (±1.6)	3.1 (±2.3)
% bare ground**	34.1 (±4.3)[a]	9.3 (±2.9)[b]	4.9 (±1.9)[b]
Litter depth (cm)**	0.1 (±0.1)[a]	6.7 (±1.3)[b]	10.9 (±1.5)[c]
Vegetation height (cm)**	43.8 (±2.8)[a]	70.5 (±4)[b]	71.6 (±3.7)[b]
Visual obstruction (cm)**	26 (±2)[a]	44 (±3)[b]	42 (±2)[b]

* $p < 0.05$.
** $p < 0.001$.

hopper sparrow abundance in current year burns showing abundance increasing linearly away from the roads (Fig. 1A, $\beta = 0.14$, CI = 0.004–0.03). Grasshopper sparrows showed no response to roads in any other time since fire (Table 5). The slope model was the top-ranked model for dickcissels in current year burns (Fig. 1B, $\beta = -0.0358$, CI = −0.059 to −0.013) and for eastern meadowlarks in one-year post-fire (Fig. 1C, $\beta = -0.012$, CI = −0.066 to −0.01), with abundances for both species declining with distance from roads. The null model was the top ranked model for dickcissel abundance relative to roads in patches 13–24 months post fire, and the slope model was within 2 AICc units of the null model. However, the slope estimate for this model was considered uninformative as the 85% confidence intervals overlapped zero. Henslow's sparrow and upland sandpiper abundances around roads were best described by the null model in all times since fire where these species were detected, suggested these species were not responding to

Table 5. Model comparisons for individual grassland bird species with more than 25 detections ($n > 25$) for models describing their responses to oil wells, roads or control surveys across a gradient of times since fire in Osage County, Oklahoma 2016 and 2017. Bolded text indicates models were either the slope or plateau model are considered the top ranked model. NAs indicates cases where model solutions could not be estimated.

				ΔAICc		
Time since fire	Survey type	Species	n	Null	Slope	Plateau
0–12 months post fire	Control	dickcissel	102	0.0	4.1	17.1
		eastern meadowlark	29	0.0	5.4	16.8
		grasshopper sparrow	25	0.0	3.8	20.5
	Roads	**dickcissel**	**494**	**5.2**	**0.0**	**6.8**
		eastern meadowlark	214	0.0	4.2	NA
		grasshopper sparrow	**154**	**3.6**	**0.0**	**10.8**
		upland sandpiper	40	0.0	4.2	NA
	Oil wells	dickcissel	455	0.0	3.7	16.5
		eastern meadowlark	206	0.0	2.8	15.0
		grasshopper sparrow	127	0.0	3.1	14.6
		upland sandpiper	34	0.0	3.7	NA
13–24 months post fire	Control	dickcissel	267	0.0	2.4	15.9
		eastern meadowlark	74	0.0	4.2	13.5
		grasshopper sparrow	66	0.0	3.7	NA
		Henslow's sparrow	67	0.0	3.3	10.3
	Roads	dickcissel	385	0.0	0.2	15.3
		eastern meadowlark	**146**	**3.6**	**0.0**	**11.2**
		grasshopper sparrow	88	0.0	4.1	17.1
		Henslow's sparrow	140	0.0	1.1	14.1
	Oil wells	dickcissel	518	0.0	4.3	NA
		eastern meadowlark	**176**	**3.2**	**0.0**	**0.6**
		grasshopper sparrow	135	0.0	1.5	15.4
		Henslow's sparrow	**95**	**3.0**	**0.0**	**NA**
>24 months post fire	Control	dickcissel	179	0.1	0.0	14.3
		eastern meadowlark	56	0.0	4.3	13.1
		Henslow's sparrow	48	0.0	4.3	13.0
	Roads	dickcissel	503	0.0	4.3	14.8
		eastern meadowlark	181	0.0	3.9	15.2
		grasshopper sparrow	88	0.0	3.7	17.1
		Henslow's sparrow	121	0.0	4.2	16.1
	Oil wells	dickcissel	419	0.0	2.2	NA
		eastern meadowlark	132	0.0	3.2	20.1
		grasshopper sparrow	35	0.0	0.8	4.8
		Henslow's sparrow	**179**	**3.0**	**0.0**	**12.9**

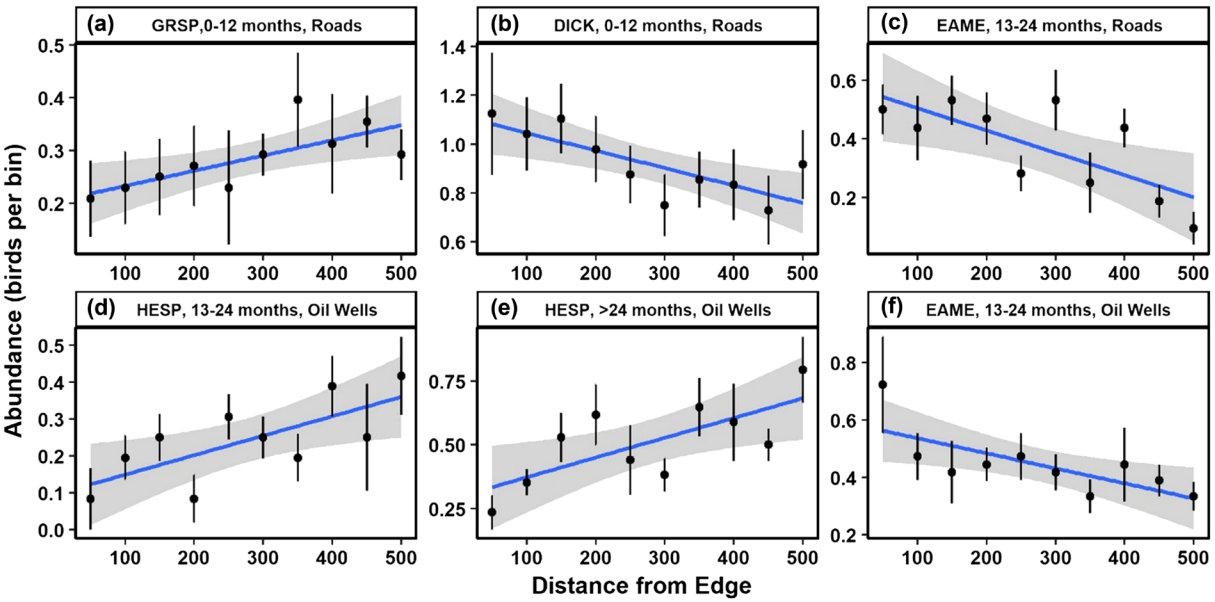

Figure 1. Trends in grassland bird abundances relative to roads (top) and oil wells (bottom). Each panel is labeled with the species, time since fire interval and type of infrastructure. The blue line and grey area represent the trend line and 95% confidence interval. Dots with error bars are the average abundance per distance bin and standard errors. Species code dickcissels (DICK), eastern meadowlark (EAME), grasshopper sparrow (GRSP), Henslow's sparrow (HESP).

roads (Table 5). The slope model was within 2 AICc for Henslow's sparrow in one-year post-fire, but the slope estimate was considered uninformative.

Response to oil wells varied among species. The slope model best described Henslow's sparrow abundance around oil wells (Table 5). Fitted models indicate that Henslow's sparrow abundance increased linearly up to 500 m away from oil wells in patches that were 13–24 months post-fire (Fig. 1D, $\beta = 0.026$, CI = 0.0057–0.0472) and greater than 24 months post-fire (Fig. 1E, $\beta = 0.039$, CI = 0.008–0.069). Model selection supported the slope model as the top model for eastern meadowlark abundance around oil wells in one-year post-fire patches, showing a decline in abundance with increasing distance from the well (Fig. 1F, $\beta = -0.026$, CI = −0.046 to −0.06). However, the plateau model was competitive for eastern meadowlarks, indicating a potential threshold at 102 m (CI = 72.2–132.4). The null model best described eastern meadowlark abundance in all other times since fire (Table 5). Abundances of dickcissels and upland sandpipers did not show evidence of responding to distance from oil pads under any time since fire (Table 5). The null model had the lowest AICc value for grasshopper sparrow around oil wells in all times since fire (Table 5). The slope model was within 2 AICc units of the null model for grasshopper sparrows in both one and two-year post-fire patches, but the confidence intervals for the slope estimates included zero in both cases.

Due to concern that observed trends for some species were the result of chronic noise near oil wells that reduced observer's ability to detect individuals, all analyses were rerun with oil wells separated into active or inactive during surveys. There was no consistent pattern of avoidance for only active wells, indicating that observed trends were not likely the result of chronic noise reducing our ability to detect individuals (Supplementary material Appendix 1 Table A2). However, species response did differ between active and inactive wells in several cases, suggesting species response may be conditional on well activity (coefficients and standard errors in Supplementary material Appendix 2 Table A2). Notably, the null model was the top-ranked model for Henslow's sparrow for inactive wells in two-years post-fire and was competitive with the slope model for Henslow's sparrow for active and inactive wells and in patches one-year post-fire. In all cases where the slope model was competitive for Henslow's sparrow, the model estimates still indicate an avoidance of wells. Eastern meadowlarks showed similarly variable patterns, with the null model being considered top-ranked for inactive wells in one-year post-fire patches. However, the slope model outperformed the null model for active wells in one-year post-fire patches indicating an attraction to wells. While the slope model was considered competitive for active wells in patches 0–12 months post fire, the parameter estimates were considered uninformative based on their confidence intervals. Similarly, dickcissels showed a possible avoidance of inactive wells in patches 0–12 months post fire, but the confidence interval for the slope estimate overlapped zero ($\beta = 0.01$, CI = 0–0.01). Grasshopper sparrow abundance was best described by the slope models relative to inactive wells in two-year post-fire patches, while abundance was best described by the null model for active wells. The slope model indicated a possible attraction to inactive wells in two-year post-fire patches.

For the control transects, abundance for most of the species did not vary with distance. The only exception was dickcissels in two years post-fire, where the slope model was the best-ranked model (Table 5); however, the null model was within 2 AICc units of the slope model and was considered a competitive model. The null model best described abundance of grassland obligate species and all bird species

pooled together in all cases (Supplementary material Appendix 1 Table A3).

Potential sources in variation in detection

Eastern meadowlarks was the only species whose detections were influenced by weather variables with detections for this species increasing on days with increased cloud cover ($\beta = 0.10$, CI = 0.046–0.15). While the univariate model for wind speed was the top ranked model for upland sandpipers the null model was within 2 AICc units, and the 95% confidence intervals for the effects of wind speed overlapped 0 suggesting this model may not be informative ($\beta = -0.131$, CI = −0.277 to 0.05). Detection of both sparrow species was negatively related to time of day indicating that fewer of both species were detected on transects conducted later in the morning (grasshopper sparrow $\beta = -0.21$, CI = −0.34 to −0.10; Henslow's sparrow $\beta = -0.28$, CI = −0.42 to −0.13). AICc tables are presented in (Supplementary material Appendix 1 Table A4).

Discussion

We found that the response of grassland birds to energy development in a grassland managed for heterogeneity was highly variable, but in instances where species did respond the effects appeared to extend significant distances beyond the physical structure. Increased fragmentation and edge that results from oil and gas development did not result in consistent responses among grassland bird species, suggesting that the impacts of grassland fragmentation on the effectiveness of conservation efforts such as heterogeneity-based management is species specific. The Henslow's sparrow, a species of conservation concern and strict habitat requirements (Cooper 2012), showed the most consistent response to development, avoiding oil wells for considerable distances in patches greater than one-year post-fire (this species rarely occurred in recently burned patches). All other species, which are more generalists, showed variable tolerance for development that varied across patches that differed in time since fire. Our results illustrate that species responses are not uniform and vary depending on habitat requirements and the unique ecology of each species. Therefore, broad generalizations about groups of species (e.g. grassland birds) responding either positively or negatively to disturbance ignores the uniqueness of each species.

Many grassland birds exhibit reduced abundances near habitat edge; however, relatively few studies have attempted to quantify the distances at which a species no longer responds to the presence of habitat edge associated with energy development (Thompson et al. 2015). We attempted to identify these response distances for five grassland bird species common to the southern Great Plains relative to oil and gas infrastructure, but notably, species response to oil wells and roads frequently extended beyond the length of our transects limiting our ability to quantify this distance. These results are similar to previous studies that have found that habitat edge can influence species abundance for considerable distances and in some cases, these effects can extend up to several kilometers (Koper et al. 2009, Sliwinski and Koper 2012). Due to this edge avoidance, estimates of the impacts of development on grassland birds that rely only on direct habitat loss may significantly underestimate the effects of development on grassland birds.

Various mechanisms have been proposed explaining changes in grassland bird abundance surrounding infrastructure. These include: 1) variability of vegetation around infrastructure including invasive species (Kalyn Bogard and Davis 2014, Ludlow et al. 2015), 2) avoidance of predators and nest parasites that may be more abundant near development (Hethcoat and Chalfoun 2015, Bernath-Plaisted et al. 2017), 3) avoidance of increased human activity (Holloran et al. 2015), 4) chronic noise (Francis et al. 2011), and 5) innate avoidance or attraction to tall structures in an otherwise open landscape (Grant et al. 2004). While our analysis was not designed to test these alternatives, heterogeneity-based management can influence a number of these mechanisms, particularly vegetation structure, potentially explaining the variation in response to infrastructure by species such as eastern meadowlarks, dickcissels and grasshopper sparrow across patches with different times since fire. For example, disturbance during construction and altered herbivore behaviors around infrastructure have been linked to different vegetation structure surrounding roads and wells, such as lower amounts of litter, increased bare ground, shorter vegetation, and increased abundances of invasive plants (Nasen et al 2011, Koper et al. 2014, Rodgers and Koper 2017). These differences in vegetation may influence the abundance or densities of grassland birds in these areas (Kalyn Bogard and Davis 2014, Ludlow et al. 2015). However, the effects of pyric-herbivory may play a greater role in determining vegetation structure within a patch, overriding the impact of energy development on bird abundance within a patch. Further, the presence of fences or inactive wells may serve as an attractor for some species that require tall singing perches, such as the eastern meadowlark, in time since fire patches with short or moderate vegetation structure. Identifying the mechanisms that shape species tolerance for development will be critical for effective mitigation, and the potential role of grassland management practices in managing the impacts of development.

Henslow's sparrows showed the most constant response to oil wells, having reduced abundances to 500 m or more from well pads. Henslow's sparrows have previously been shown to be highly sensitive to edges, having reduced densities and nest success near wooded edges (Winter et al. 2000, Bajema and Lima 2001). As a habitat specialist within grasslands, Henslow's sparrows are especially sensitive to changes in grassland continuity, vegetation structure, and the addition of tall structures to otherwise open areas, making them particularly sensitive to the presence of oil and gas infrastructure. Additionally, variable tolerance of chronic noise associated with energy infrastructure has been suggested as a possible explanation for differing responses to energy development by birds (Francis et al. 2011, Goodwin and Shriver 2011). Henslow's sparrows may choose to avoid placing territories near oil wells because their low decibel songs and secretive nature may make individual's vocalizations difficult to detect by conspecifics. However, other grassland birds with similar

songs have been show to alter their singing behavior in the presence of anthropogenic noise (Curry et al. 2018), and it is unclear if the broad frequency range of the Henslow's sparrow song would allow for similar adjustments (Leftwich and Ritchison 2000). For species of conservation concern, such as the Henslow's sparrow, understanding the exact mechanisms that cause their response to anthropogenic features will be especially important in managing for this species in increasingly fragmented landscapes.

Our findings of little or positive effects of roads on grassland bird abundance contrast with other studies that have shown that roads can reduce bird densities and occupancy in grassland and sagebrush communities (Ingelfinger and Anderson 2004, Mutter et al. 2015). Avoidance of roads is likely linked to traffic volume with more heavily used roads causing greater avoidance due to increased noise or dust from passing vehicles (Sutter et al. 2000, Ingelfinger and Anderson 2004). While we attempted to control for traffic volume by surveying only primary county roads, roads at our study site have relatively light traffic levels. Therefore, the low traffic volume in otherwise continuous grasslands may not be enough to elicit a response from most bird species. Additionally, species preferences for specific structural features may have driven increased abundances of dickcissel and eastern meadowlark responses to roads in some times since fire. Both species use tall vegetation for singing perches (Kahl 1985, Dechant et al. 2002a, b), and the presence of fences or dense vegetation in ungrazed ditches associated with roads may make these areas more attractive for these species (Rodgers and Koper 2017).

Our study focused on bird abundances which may not reflect habitat quality as certain landscapes may have high densities of individuals but relatively low reproductive potential (Van Horne 1983). While energy development may not have a significant effect on abundance, areas around roads and oil facilities may act as sink habitat as these areas have been linked to reduced nest densities, nest success rates, and reproductive output in some grassland bird species (Ludlow et al. 2015, Yoo and Koper 2017). Therefore, the use of abundance as an index of species response to development may offer a conservative estimate of the impact of development on grassland birds in the region.

In a post hoc analysis where we evaluated species response for wells that were actively pumping during surveys and wells that were temporarily off, we found that several species responses to oil wells appeared to differ between active and inactive wells. The difference in response may be due to differences in levels of noise, lack of moving parts at inactive wells, or reduced human activity (Francis et al. 2011, Holloran et al. 2015). Some species, such as eastern meadowlarks, may be attracted to inactive wells because of their resemblance to perch sites (Rodgers and Koper 2017). However, previous research has suggested that presence of infrastructure appears to be more important for grassland bird response than activity levels and well type (Bernath-Plaisted and Koper 2016, Nenninger and Koper 2018). Further, the differences in species response patterns should be interpreted with caution as this analysis was done opportunistically, resulting in relatively small samples sizes in some cases, potentially limiting our ability to infer patterns related to well activity. However, these results in addition to our main analysis suggest that the mechanisms that shape species responses to oil wells may be variable and future research and conservation efforts should endeavor to identify the mechanisms that drive species responses to oil wells.

Previous literature has shown that a number of factors can influence detectability of grassland bird species and failure to account for these can result in incorrect or biased estimates of abundance (Diefenbach et al. 2003, Johnson 2008). One of the most common means of accounting for detection is to adjust counts or averages using statistical methods that estimate detection probabilities (Efford and Dawson 2009). However, recognizing that our choice of survey methods (500-m transects) would likely violate the assumptions of common methods of estimating detection probability (Buckland 2001), we attempted to account for common sources of bias in our field methods (Diefenbach et al. 2003, Koper et al. 2009). While, our use of unadjusted averages likely still incorporate variation in detection for many species, we avoid introducing additional error associated with using biased estimates of detection probability (Efford and Dawson 2009). Further, by accounting for common sources of detection bias in our field methods by alternating observers and the order of surveys through the season, bias is likely minimal for any given time since fire/structure combination.

Restoration of heterogeneity in grasslands is a critical component of grassland bird conservation efforts, however, the continued fragmentation of grasslands that results from development for energy may limit the effectiveness of management strategies that aim to promote grassland bird abundance at least for some species (Askins et al. 2007, Fuhlendorf et al. 2017). Avoidance of edges associated with oil and gas can degrade the quality of grasslands for considerable distances around a structure for some species, potentially reducing the effectiveness of conservation strategies if species are avoiding otherwise suitable grasslands. However, grassland bird response to energy development was not consistent among species, and in some cases differed within species across different times-since-fire patches, suggesting that the mechanisms determining tolerance for development differed among species and may be independent of the structure itself for some species. Restoration of ecological processes that generate heterogeneity in grasslands will benefit grassland birds by creating sufficient habitat diversity for the entire suite of grassland bird species. However, management efforts should also aim to limit anthropogenic processes that fragment the landscape. Consideration of edge effects and how they may differ in heterogeneous grasslands will be critical for managing the impacts of development and ensuring the successful implementation of management aimed at promoting grassland birds.

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Supplementary material (available online as Appendix wlb-00523 at <www.wildlifebiology.org/appendix/wlb-00523>). Appendix 1–2.