THE EFFECTS OF RANGELAND MANAGEMENT

AND ENERGY DEVELOPMENT ON THE HABITAT

USE OF GRASSLAND BIRDS IN THE SOURTHERN

GREAT PLAINS.

By

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Abstract: Grasslands were historically disturbance dependent systems with the function
and structure of grasslands being shaped by variable disturbance from fire and grazing.
Many grasslands are currently managed under heavily altered disturbance regimes, which
has led to a concomitant decline of diversity and abundance of many grassland wildlife
species. Efforts to prevent further losses of biodiversity in grasslands has emphasized the
restoration of heterogeneity through the reestablishment of the fire grazing interaction.
However, the reintroduction of heterogeneity has taken place in the context of the
continued fragmentation of grasslands for energy development. Fragmentation of
grasslands has the potential to limit the effectiveness of heterogeneity-based management
as many wildlife species avoid or are displaced from otherwise suitable grasslands as a
result of energy development. We examined the habitat and space use of grassland birds
in the Southern Great Plains in a landscape that is managed for heterogeneity with fire
and grazing, but has also experienced substantial development for oil and gas production.
Grassland songbirds showed a highly variable tolerance for energy development.
Henslow's sparrows (*Ammadromous henslowii)* was the most sensitive species, avoiding
oil wells in all unburned patches. Most other species response was highly dependent on
the type of infrastructure and time since fire patch, suggesting heterogeneity may
moderate many species responses to energy development. Female greater prairie-
chickens (*Typmanuchus cupido*) habitat use was primarily driven by use of the vegetation
mosaic that results from fire and grazing, with individuals using unburned patches during
the nesting and lekking seasons then shifting use to recently burned patches in the post-
nesting and nonbreeding season. Greater prairie-chicken response to energy development
was more complex with individuals showing a seasonally dependent avoidance of high
densities of oil wells and power lines. Our results suggest that the use of heterogeneity
based management will continue to be an important conservation strategy for grassland
birds, however efforts should be made to limit further fragmentation of grasslands as the
presence of infrastructure has the potential to significantly degrade significant portions of
the landscape for some grassland bird species.

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CHAPTER I

GRASSLAND BIRDS EXHIBIT VARIABLE RESPONSE TO ENERGY
DEVELOPMENT IN A GRASSLAND MANAGED FOR HETEROGENEITY.

Abstract

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 utilization of grasslands by grazers and either
no fire or uniform fire, 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 patterns may be among the
best conservation strategies for grassland birds, as these practices promote diversity and
abundance of many species through the creation of a mosaic of vegetation patches.
However, the introduction of these management methods is taking place in the context of
the continued rapid development of grasslands for energy production, and 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 heterogeneity 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 only occurred in unburned patches and upland sandpipers were
primarily detected in recent burns. Further, Henslow's sparrows avoided oil wells for
considerable distances, while eastern meadowlark abundance were 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 the all grassland bird species,
however energy development has the potential to fragment grasslands for some species.

Introduction

The interaction of fire and grazing is an essential disturbance process in grasslands (Anderson 2006, Samson and Knopf 1994), and the reintroduction of historic grazing and fire interactions to create heterogeneity in grasslands is becoming a high conservation priority (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 with differing vegetation structure and composition that provide habitat for a variety of species resulting in increased diversity and abundance of many wildlife species (Powell 2008, Ricketts and Sandercock 2016). Further, this vegetation mosaic reduces annual variation in primary production in grasslands, stabilizing availability of resources for wildlife such as food sources and nesting cover during periods of environmental extremes (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 of the landscape resulting in homogeneous landscapes (Fuhlendorf and Engle 2001, Holocheck 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. In an effort to prevent further loss of ecosystem services within grasslands, conservation efforts have placed increasing emphasis on re-establishing historic fire regimes and heterogeneity in grasslands (Fuhlendorf et al. 2006, Limb et al. 2016, Twidwell et al. 2013). As grasslands worldwide are experiencing rapid changes, driven primarily by

human activities, understanding how restored disturbance regimes interact with other processes, such as fragmentation, will be critical for effective conservation of grasslands.

Energy development has become a dominant issue affecting biodiversity throughout the world as ecosystems are becoming increasingly fragmented by energy development (Aldridge and Boyce 2007, Jones et al. 2015, Northrup and Wittemyer 2013, Sawyer et al. 2006), but the effects of development have rarely been considered in the context of local grassland management practices. Oil and gas production is of particular concern in North American grasslands due to its already extensive footprint 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). Construction of oil and gas infrastructure has already led to a significant loss of grasslands, resulting in fragmentation and loss of productivity (Allred et al. 2015). Further, oil and gas development can indirectly degrade remaining grasslands through light and sound pollution (Francis et al. 2009, Longcore and Rich 2004), chemical pollution (Souther et al. 2014), increased human activity (Holloran et al. 2015), and the spread of exotic or invasive plant species (Nasan et al. 2011). Changes in grasslands that result from both direct destruction and indirect alterations have also been linked to population declines, altered demographics (Aldridge and Boyce 2007) and behavioral changes (Jarnevich and Laubhan 2011, Pruett et al. 2009, Sawyer et al. 2006) in many grassland wildlife.

Grassland birds have experienced some of the greatest declines of any other group of North American birds (Askins et al. 2007). Energy development and alterations of historic fire regimes in grasslands are listed as leading conservation threats for grassland

birds (Askins 2007, Northrup and Wittemeyer 2013). However, despite the fact that many species are affected by both altered disturbance regimes and energy development throughout much of their distribution, these two conservation issues have primarily been studied independently. Research has demonstrated that restoration of historical fire regimes may be one of the best conservation strategies for grassland birds as it maintains grassland habitat by preventing woody plant invasions, and ensures adequate variation in vegetation structure to meet the habitat needs of the entire suite of grassland birds likely to occur on these landscapes (Askins 2002). Diversity and density of grassland birds is higher in grasslands managed for heterogeneity as compared to traditionally managed rangelands (Hovick et al. 2014, Hovick et al. 2015, Lindenmayer et al. 2016). Alternatively, the effects of oil and gas development on grassland bird communities is less clear, with tolerance to infrastructure varying considerably among species (Kalyn Bogard and Davis 2014, Ludlow et al. 2015), but for a number of species, such as Sprague's pipit (*Anthus spragueii*) and Baird's Sparrow (*Ammodramus bairdii*), oil and gas has been shown to alter their abundance over considerable distances around development (Linnen 2008, Thompson et al. 2015). Understanding how development and heterogeneity interact to shape species abundance and distribution across the landscape will be critical for guiding grassland bird conservation efforts, as habitat heterogeneity may mitigate some of the negative effects of energy development for some grassland birds by allowing species to alter behaviors to reduce reliance on areas near energy (Toth et al. 2015), or through the use of patches that can act as refugia (Brown 2007).

We investigated grassland bird response to energy development on a landscape in the Southern Great Plains that is managed for heterogeneity with fire and grazing, but has

also undergone extensive development for oil production. This multi-use landscape allows for a unique opportunity to investigate if landscape level fragmentation from energy development can constrain management and conservation efforts critical to biodiversity in grassland landscapes (Fuhlendorf et al. 2006). We hypothesize that landscape-level heterogeneity may allow grassland bird species to be more flexible in their responses to energy development as patches differing in vegetation structure may buffer some species against any potential negative effects of energy development. To address this hypothesis, we evaluated how abundance of grassland birds changed with distance from oil wells and roads across a gradient of times since fire.

Methods

Study site

Our study was conducted from 2016 to 2017 on private property, including the Nature Conservancy's Tallgrass Prairie Preserve in Osage County, Oklahoma. The study site is located in the southern most extent of the Flint Hills Ecoregion which contains some of the largest intact tracts of tallgrass prairie (With et al. 2008). Vegetation in the region is composed primarily of tallgrass prairie dominated by big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), Indian grass (*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 are restricted to drainages. The region is characterized by a temperate climate with hot summers (average high of 31.6ºC for 2002-2016) and cold winters (average low of - 3.89ºC for 2000-2014) (Foraker Mesonet Site; Mesonet 2014). The average growing

season (April-September) rainfall from 2000-2015 was 63.37 centimeters (Foraker

Mesonet Site; Mesonet 2014).

Our study site is managed for heterogeneity using prescribed fire and grazing.

While individual properties differ in management specifics, generally, fire is applied on a

rotational basis and bison (*Bison bison*) or domestic cattle (*Bos taurus)* are allowed to

preferentially graze recently burned patches resulting in the creation of a mosaic of

patches differing in vegetation structure and composition. The fire return interval is

approximately 2-4 years, with the majority of prescribed fires taking place in the spring

(March-May) before the start of the growing season. Most properties were managed

primarily for livestock and grazed seasonally with cattle, and The Tallgrass Prairie

Preserve is grazed by a combination of bison and cattle.

Survey Design

We evaluated grassland bird responses to major gravel roadways and

conventional oil wells. Major gravel roadways (hereafter, roads) were defined as county

roads that were a minimum of 8 m wide. While secondary access roads may also illicit

avoidance from bird species, most secondary roads at our study site were 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.

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 25 months). Areas greater than two years post fire were

combined due to the limited availability of patches older time since fire patches and the fact that biomass accumulation begins to slow substantially between 24 and 36 months post fire (Fuhlendorf et al. 2009). Surveys consisted of a single transect starting at the beginning of the natural vegetation and extending 500 meters away from the source of disturbance. Sites were selected so that transects could extend 500 meters beyond the source of disturbance without encountering other landscape features that may influence bird abundance (e.g., crosstimber forest, oil pads, roads, burn unit boundaries). Additionally, control surveys, located at least 500 meters from energy infrastructure, woodlands and burn unit boundaries, were used to evaluate if our survey methodology influenced bird behavior.

We began surveys in mid-May when breeding activity began and ended surveys in early to mid-June. Surveys began one-half hour before sunrise and ended around 10:00 when singing activity declines. We only conducted surveys on mornings with winds less than 24 km per hour, 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 meter per second) using a hand held GPS unit to guide. Every bird heard or observed was recorded, along with the perpendicular distance of the bird to the transect and the distance from disturbance. Distance was estimated using a laser range finder and only individuals detected within 50 meters of either side of the transect were recorded to minimize detection and identification errors by observers (Hovick et al. 2015, Pillsbury et al. 2011).

Data analysis

Species' response to roads or oil wells was analyzed separately for each time since fire where the species had greater than 25 detections associated with either roads or oil wells. 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 m, 51-100 m, etc.). In each time since fire, species observations were pooled across all sites for each structure, and average abundance calculated for each distance bin. For control sites, the end that would correspond to 0 meters was randomly assigned before surveys started. All transects were surveyed an equal number of times, and year effects were not of interest, which allowed us to pool our data by year and site (Murtaugh 2007, Thompson et al. 2015). In addition to individual species, total species abundance and total grassland obligate abundance was calculated for each survey type. Habitat associations for grassland birds were based on Coppedge et al. (2008).

We tested for three possible scenarios describing bird abundance relative to energy development 1) no response (null model), 2) linear response (slope models), and 3) a plateau response (plateau models) (Tanner et al. 2017, Thompson et al. 2015). The plateau model describes a situation where a species may increase or decrease to a point less than 500 meters, then abundance having a null relationship to distance after that point. Abundance estimates were used as the response variable to test for the three response scenarios. The null model was tested with an intercept only model, where the slope was limited to zero. The slope model was tested using simple linear regression fitted to abundance. The first two models were generated using the base program R (R Core Team, 2014). The plateau model was modeled with segmented linear regression models using package "segmented" in program R (Muggeo 2008). For segmented linear

models, abundance is allowed to increase or decrease up to a breakpoint estimated by the package, and then the slope is constrained to zero after the breakpoint. The models were compared using Akaike's Information Criteria adjusted for small sample sizes (AIC_C) (Burnham and Anderson 2002). Models with the lowest AICc score were considered the best models describing species abundance in relation to distance from development. The three models tested were nested within each other, so the slope model was not considered competitive when less than 2 AICc of the null model, and the plateau model was not competitive when less than 2 AICc units of the slope model (Arnold 2010, Thompson et al. 2015).

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 1). We recorded 36 bird species during the study, but most of the observations (94%) were attributed to five grassland obligate species (Table 2). Individual species response to energy development was evaluated for dickcissels, eastern meadowlarks, grasshopper sparrows, Henslow's sparrows, and upland sandpipers. These five species were the only species used for the combined grasslands obligate tests. Dickcissels, eastern meadowlarks and grasshopper sparrows were common in all times since fire, while Henslow's sparrows were detected almost entirely in one and two years post fire patches. Upland sandpipers occurred primarily in recently burned patches (Figure 1).

Dickcissels, grasshopper sparrows, and eastern meadowlarks showed variable responses to roads across different post disturbance stages (Table 3). Grasshopper sparrow abundance was best described by the slope model in current year burns with abundance increasing linearly away from the roads (Figure 2b, β= 0.14, CI= 0.004 − 0.03). Grasshopper sparrows showed no response to roads in any other time since disturbance (Table 3). The slope model was the top ranked model for dickcissels in current year burns (Figure 2a, β= -0.0358, CI=-0.059 − -0.013) and for eastern meadowlarks in one year post fire (Figure 2c, β= -0.012, CI=-0.066 − -0.01), with abundances for both species declining with distance from roads. Neither species responded to roads in any other time since disturbance. 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 wre not responding to roads (Table 3). Total species abundance and total grassland obligate abundance was best described by the null model suggesting that pooled species abundances does not change with distance from roads (Table 4).

Response to oil wells varied among species. The slope model best described Henslow's sparrow abundance around oil wells (Table 3). Fitted models indicate that Henslow's sparrow abundance increased linearly up to 500 meters away from oil wells in patches that were 12-23 months post fire (Figure 2e, β= 0.026, CI= 0.0057 – 0.0472) and greater than 24 months post fire (Figure 2f, β= 0.039, CI= 0.008 – 0.069). Model selection supported the slope model as the top model for eastern meadowlark abundance increasing around oil wells in one year post fire patches but not responding to any other times since fire (Figure 2d, β= -0.026, CI= -0.046 – -0.06). Abundances of dickcissels,

grasshopper sparrows, and upland sandpipers did not show evidence of responding to distance from oil pads under any time since disturbance (Table 3). Abundance for all species and grassland obligates in relation to oil wells was best described by the null model (Table 4).

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 3), however the null model was within 2 AICc units of the slope model and was considered a competitive model.

Discussion

The response of grassland birds of the Southern Great Plains to energy development was highly variable. Henslow's sparrow, a species of conservation concern (Cooper 2012), showed the most consistent response, avoiding oil wells in all unburned patches, while all other species tolerance for energy was mixed. Similar to previous research, we found that the effects of energy development can extend well beyond the physical structure itself (Thompson et al. 2015), but these effects were not uniform across a heterogeneous landscape for most species. While, the development of grasslands for energy can fragment the landscape for some species, the use of management practices that emphasize heterogeneity may serve to buffer some species against the negative effects of development.

Similar to previous studies, we found that species varied in their tolerance for conventional oil wells (Kalyn Bogard and Davis 2014, Ludlow et al. 2015, Thompson et al. 2015). Most species were unaffected by the presence of oil wells, with the exception

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of Henslow's sparrows which had reduced abundance out to 500 meters from well pads. Variable tolerance of anthropogenic noise has been suggested as a possible explanation for differing tolerances to energy development by birds (Francis et al. 2011). For example, forest bird species that vocalize in similar acoustic ranges to road traffic have been shown to have reduced occupancy near roads likely due to greater levels of acoustic masking, which may make an individual's vocalizations difficult to detect by conspecifics (Goodwin et al. 2011). Henslow's sparrows may choose to avoid placing territories near oil wells because their low decibel songs and secretive nature may make them more susceptible to acoustic masking than other grassland bird species. In contrast, eastern meadowlarks showed increased abundances around oil wells in patches that were one-year post fire. Eastern meadowlarks may be less susceptible to acoustic masking from oil wells due to their relatively loud song and preference for singing from conspicuous perch sites (Hull 2000). Additionally, increased eastern meadowlark abundances may be explained by their preferences for singing perches such as fences around oil wells or increased bare ground associated with energy infrastructure (Nasen et al. 2011, Koper et al. 2014, Rodgers et al. 2017).

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 illicit 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 (Dechant et al. 2002, Kahl 1985), and the presence of fences or dense vegetation in ungrazed ditches associated with roads may make these areas more attractive for these species (Rodgers et al. 2017).

Overall, energy development appears to affect grassland bird communities in the Southern Great Plains to a lesser degree than other North American bird communities where the effects of conventional oil wells have been examined (Linnen 2008, Francis et al. 2011, Thompson et al. 2015). However, the grassland bird communities of the Southern Great Plains are composed of a small numbers of species, with the most common species, dickcissel and eastern meadowlarks, having relatively generalized habitat requirements within grasslands (Powell 2008). These more generalist species may have a greater degree of behavioral plasticity that allows them to better accommodate anthropogenic changes in their environment. In contrast, habitat specialists, such as the Henslow's sparrow, may be more susceptible to energy development due to their strict habitat requirements (Aitken et al. 2008). Several grassland bird species have been shown to be able to alter resource use or behavior patterns in heterogeneous landscapes to cope with environmental stressors (Carroll et al. 2017, Skagen et al. 2017, Winder et al. 2017). Heterogeneous grasslands may allow some species a wider variety of behavioral responses to mitigate the effects of energy development (Toth et al. 2015), or to seek patches with vegetation that can serve as refuge from energy (Brown 2007).

Our study focused on bird abundances which may not actually 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 and gas 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 (Linnen 2008, Ludlow et al. 2015, Yoo and Koper 2017). However, our use of abundance as an indicator of habitat use and quality is justified, as evidence of the decoupling of density and reproductive rates is rare (Bock and Jones 2004). Further, grasslands managed for heterogeneity have been linked to improved reproductive output among grassland birds compared to traditionally managed grasslands, which may potentially mitigate the negative effects of development (Churchwell et al. 2007, Davis et al. 2016).

While our analysis focused on distance to structures, the spatial arrangement and density of structures can have an important impact on species response to development. A number of shrubland and grassland birds have been shown to respond more strongly to density of structures rather than distance to structures (Doherty et al. 2008, Hagen et al. 2011, Mutter et al. 2015, Gilbert and Chalfoun 2010), suggesting that species may be responding to the cumulative effects of multiple wells or increased activity in highly developed areas (Holloran et al. 2015, Lyon and Anderson 2003). The relatively small footprint of development at our study site and the interspersion of generally high quality prairie between developed areas may mitigate some species responses for development. Despite this, our results demonstrated that areas as much as 500 meters from the edges of oil fields may be degraded for more sensitive species, such as Henslow's sparrows.

Restoration of heterogeneity in grasslands is a critical component of grassland bird conservation efforts, but the continued development of grasslands for energy may limit the effectiveness of management strategies that aim to promote heterogeneity for some species (Askins et al. 2007, Fuhlendorf et al. 2017). While our results suggest grassland birds in the Southern Great Plains exhibit considerable variation in their tolerance for energy development, the presence of energy-related infrastructure can still impact some species by degrading otherwise high quality grasslands for considerable distances. 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. Further, grassland bird response to energy development differed across different times since fire, suggesting that the reintroduction of heterogeneity to grasslands may also buffer some species against the effects of energy development.

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Table 1. 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 25 months post fire.

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

Table 2. Common names and scientific name of all bird species detected during transect surveys in Osage County, Oklahoma between 2016 and 2017. Each species is summarized by the number of individuals encountered in each time since fire treatment.

Common Names	Scientific Name	0-12 months post fire	13-24 months post fire	>25 months post fire
American Goldfinch	*Spinus tristis*	2	3	0
Barn Swallow	*Hirundo rustica*	1	0	2
Bell's Vireo	*Vireo bellii*	2	4	7
Brown-headed Cowbird	*Molothrus ater*	5	13	7
Brown Thrasher	*Toxostoma rufum*	3	2	2
Canda Goose	*Branta canadensis*	6	0	0
Cliff Swallow	*Petrochelidon pyrrhonota*	1	0	0
Common Grackle	*Quiscalus quiscula*	7	1	1
Common Nighthawk	*Chordeiles minor*	8	3	3
Common Yellowthroat	*Geothlypis trichas*	4	14	10
Chuck-will's-widow	*Antrostomus carolinensis*	0	1	0
Dickcissel	*Spiza americana*	1051	1170	1101
Eastern Kingbird	*Tyrannus tyrannus*	6	1	0
Eastern Meadowlark	*Sturnella magna*	449	396	369
European Starling	*Sturnus vulgaris*	1	0	0
Field Sparrow	*Spizella pusilla*	9	3	1
Great Blue Heron	*Ardea herodias*	1	0	0
Greater Prairie-chicken	*Tympanuchus cupido*	22	3	0
Grasshopper Sparrow	*Ammodramus savannarum*	306	289	124
Henslow's Sparrow	*Ammodramus henslowii*	8	302	348
Horned Lark	*Eremophila alpestris*	1	0	0
Killdeer	*Charadrius vociferus*	7	1	3
Lark Sparrow	*Chondestes grammacus*	1	0	0
Loggerhead Shrike	*Lanius ludovicianus*	1	0	0
Mallard	*Anus platyrhynchos*	1	0	0
Mourning Dove	*Zenaida macroura*	12	8	5
Northern Bobwhite	*Colinus virginianus*	8	14	25
Northern Mockingbird	*Mimus polyglottos*	2	0	0
Orchard Oriole	*Icterus spurius*	5	2	1
Red-bellied Woodpecker	*Melanerpes carolinus*	0	1	0
Red-tailed Hawk	*Buteo jamaicensis*	1	0	0
Ruby-throated Hummingbird	*Archilochus colubris*	1	1	0
Red-winged Blackbird	*Agelaius phoeniceus*	13	24	18
Scissor-tailed Flycatcher	*Tyrannus forficatus*	12	6	0
Upland Sandpiper	*Bartramia longicauda*	99	11	6

Table 2. 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.

Time since disturbance	Survey Type	Species	n	Δ AICc		
				Null	**Slope**	**Plateau**
0-12 Months Post Fire	Control	Dickcissel	102	0	4.122	17.144
		Eastern Meadowlark	29	0	5.386	16.771
		Grasshopper Sparrow	25	0	3.845	20.457
	Roads	Dickcissel	494	5.173	0	6.772
		Eastern Meadowlark	214	0	4.188	NA
		Grasshopper Sparrow	154	3.566	0	10.815
		Upland Sandpiper	40	0	4.188	NA
	Oil Wells	Dickcissel	455	0	3.683	16.535
		Eastern Meadowlark	206	0	2.818	15.029
		Grasshopper Sparrow	127	0	3.144	14.625
		Upland Sandpiper	34	0	3.714	NA
13-24 Months Post Fire	Control	Dickcissel	267	0	2.41	15.86
		Eastern Meadowlark	74	0	4.161	13.527
		Grasshopper Sparrow	66	0	3.669	NA
		Henslow's Sparrow	67	0	3.312	10.25
	Roads	Dickcissel	385	0	0.215	15.266
		Eastern Meadowlark	146	3.575	0	11.184
		Grasshopper Sparrow	88	0	4.144	17.123
		Henslow's Sparrow	140	0	1.053	14.068
	Oil Wells	Dickcissel	518	0	4.274	NA
		Eastern Meadowlark	176	3.195	0	0.622
		Grasshopper Sparrow	135	0	1.468	15.441
		Henslow's Sparrow	95	3.02	0	NA
>24 Months Post Fire	Control	Dickcissel	179	0.054	0	14.273
		Eastern Meadowlark	56	0	4.278	13.114
		Henslow's Sparrow	48	0	4.284	12.997
	Roads	Dickcissel	503	0	4.269	14.792
		Eastern Meadowlark	181	0	3.924	15.205
		Grasshopper Sparrow	88	0	3.661	17.055
		Henslow's Sparrow	121	0	4.171	16.122
	Oil Wells	Dickcissel	419	0	2.226	NA
		Eastern Meadowlark	132	0	3.224	20.085
		Grasshopper Sparrow	35	0	0.844	4.805
		Henslow's Sparrow	179	2.988	0	12.906

Table 3. Model comparisons for total bird abundances and grassland obligate bird abundances comparing three scenarios describing the response to oil wells and roads across a gradient of times since fire in Osage County, Oklahoma 2016 and 2017.

Time since disturbance	Survey Type	Species	n	Δ AICc		
				Null	Slope	Plateau
0-12 Months	Control	All Species	243	0	1.715	10.605
		Grassland Obligates	150	0	3.683	NA
	Roads	All Species	843	0	3.349	NA
		Grassland Obligates	788	0	3.369	NA
	Oil Wells	All Species	755	0	4.254	16.295
		Grassland Obligates	700	0	4.183	15.563
13-24 Months	Control	All Species	458	0	3.969	7.354
		Grassland Obligates	436	0	3.38	8.75
	Roads	All Species	701	0	4.124	16.506
		Grassland Obligates	666	0	4.203	NA
	Oil Wells	All Species	880	0	3.239	NA
		Grassland Obligates	845	0	3.639	NA
>24 Months	Control	All Species	312	0	2.132	NA
		Grassland Obligates	788	0	2.042	NA
	Roads	All Species	950	0	4.22	11.727
		Grassland Obligates	882	0	4.119	13.736
	Oil Wells	All Species	751	0	3.027	NA
		Grassland Obligates	742	0	2	12.075
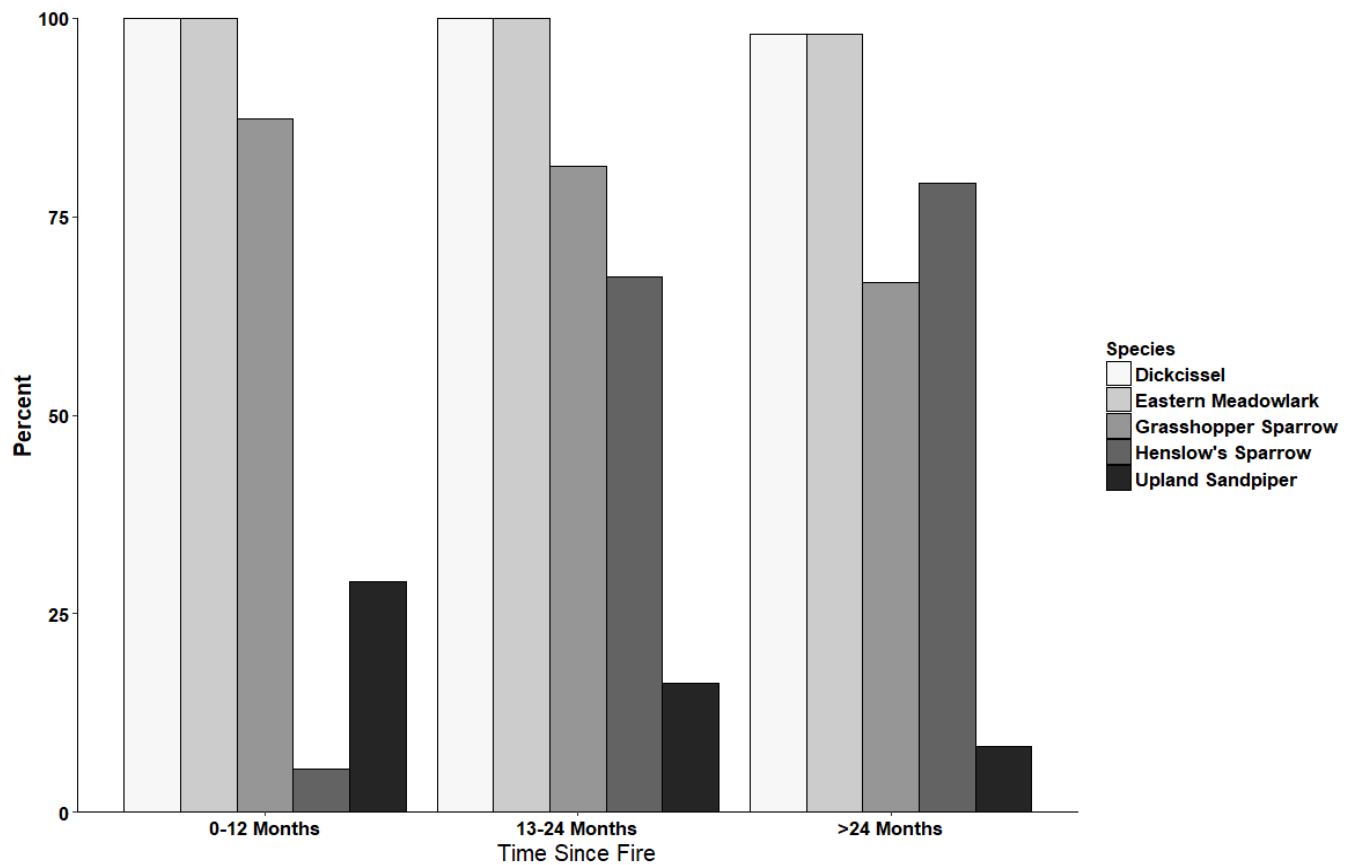
Figure 1. Proportion of transects grassland bird species were detected by time since fire in Osage County, Oklahoma during breeding season in 2016 and 2017. A total of 55 transects were surveyed in the 0-12 month category, 43 transects in 13-24 months post fire, and 48 transects in > 24 months post fire.
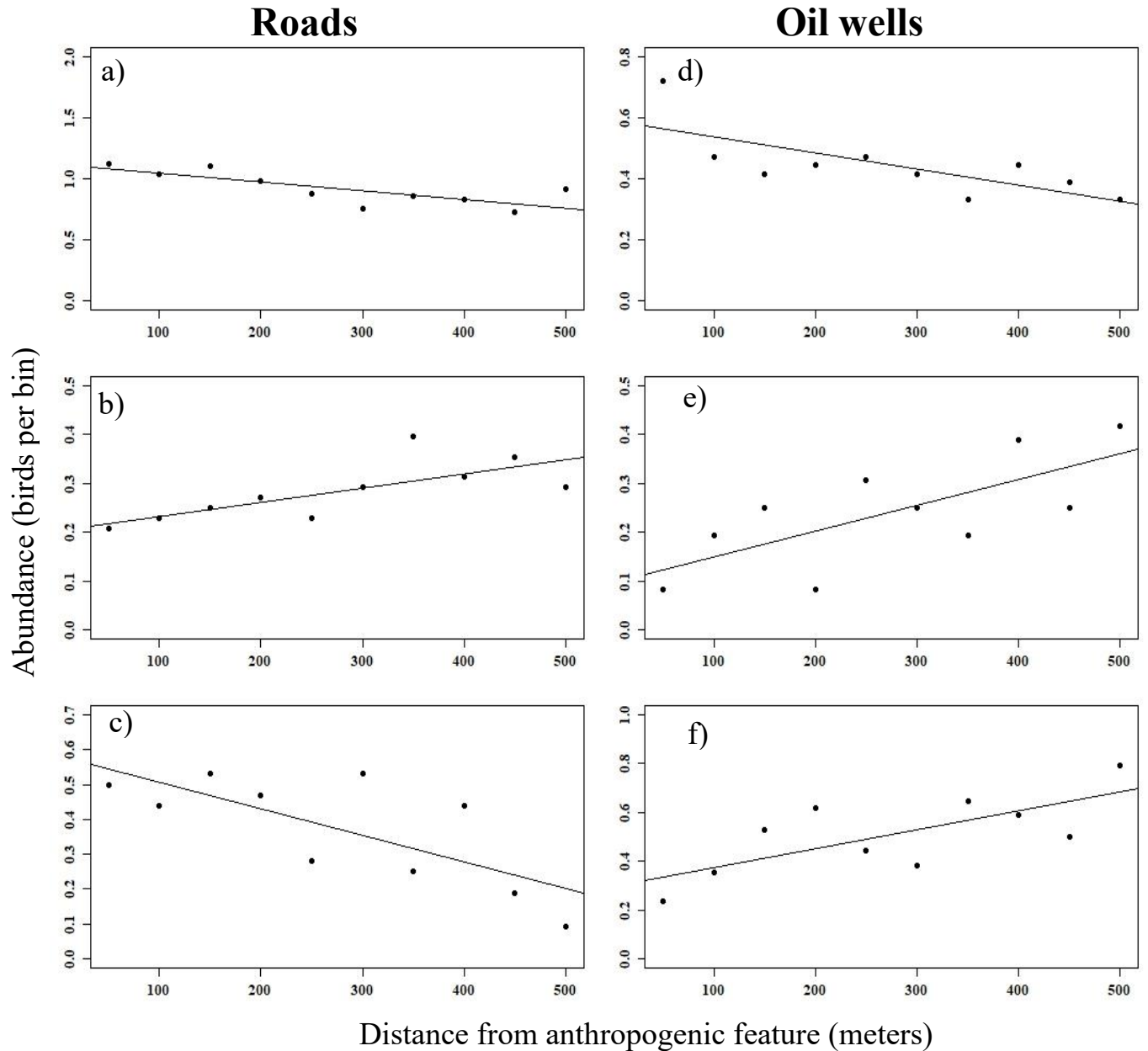
Figure 2. Trends in grassland bird abundances relative to roads (left) and oil wells (right) for a) dickcissels in patches 0-12 months post fire, b) grasshopper sparrows in patches 0-12 months post fire, c) eastern meadowlark in patches 13-24 months post fire d) eastern meadowlarks in patches 13-24 months post fire, e) Henslow's sparrows in patches 13-24 months post burn, and f) Henlsow's sparrows in patches greater than 24 months post burn.

CHAPTER II

EFFECTS OF RANGELAND MANAGEMENT AND ENERGY DEVELOPMENT ON

GREATER PRAIRIE-CHICKEN HABITAT USE.

Abstract

Grasslands are among the most threatened ecosystems in the world due to widespread conversion to other land uses. Many remaining grasslands also face additional conservation threats such as altered fire regimes and continued fragmentation from energy development. Understanding how wildlife species respond to human activities in grasslands will be critical for the conservation of grassland fauna. We examined habitat use of female greater prairie-chickens (*Tympanuchus cupido*), a species of conservation concern though out much of its distribution. We developed models for four behaviorally distinct live history stages to evaluate how habitat use may change through the year in relation to rangeland management and energy development. We found that time since fire, avoidance of woodlands, and use of areas near leks were the most consistent predictors of habitat use during most periods. Use of time since fire varied through the year with hens primarily using unburned patches in the lekking and nesting season and recently disturbed patches in the post-nesting and nonbreeding season. Additionally, greater prairie-chickens demonstrated a seasonally dependent response to energy development, avoiding power lines and high densities of oil wells in the post-nesting and nonbreeding season. Management actions that promote heterogeneity will benefit greater prairie-chickens by creating a variety of seral stages used during different life stages, but efforts should be made to limit future fragmentation of grasslands by energy development. Further, energy development may limit the utility of heterogeneity based management through displacement of individuals and loss of usable space for greater prairie-chickens.

Introduction

Grasslands are among the most threatened ecosystems in the world with losses primarily resulting from extensive conversion of grasslands to row crops (Hoekstra et al. 2005). In North America, as much as 80-90% of the tallgrass prairie ecosystem has been altered or lost since European settlement in the 1800's (Samson and Knopf 1994). While the conversion of grasslands to row crops has slowed substantially in the last half century (Waisanen and Bliss 2002), many North American grasslands are still threated by various anthropogenic activities including altered fire and grazing regimes (Fuhlendorf and Engle 2001), and fragmentation from energy development (Copeland et al. 2009). Combinations of these factors has resulted in a concomitant decline in grassland wildlife, in particular grassland birds, many of which have experienced significant distribution and population declines over the last 60 years (Askins et al. 2007, Brennan and Kuvlesky 2005). As grasslands worldwide are experiencing rapid changes driven by human activity, conservation of grasslands and grassland fauna will require an understanding of the relative importance of different factors and an understanding of how they interact to shape species declines.

Grasslands are naturally heterogeneous systems that were historically shaped by the interaction of fire and grazing animals (Anderson 2006, Fuhlendorf and Engle 2001). However, most North American grasslands are presently managed for domestic cattle (*Bos taurus*) production, and traditional management methods emphasize uniform and moderate grazing resulting in relatively homogenous grasslands characterized by short statured vegetation (Fuhlendorf and Engle 2001, Holecheck et al. 2011). While these types of management paradigms have benefited cattle production, the loss of natural

variability has resulted in a decline in overall function and biodiversity (Derner et al. 2009, Fuhlendorf et al. 2009). In an effort to prevent further loss biodiversity, conservation efforts in the Southern Great Plains emphasize the application of fire and grazing to restore heterogeneity on the landscape (Fuhlendorf et al. 2006, Limb et al. 2016, Twidwell et al. 2013). By burning portions of the landscape annually and allowing grazers to preferentially graze in recently burned areas, heterogeneity-based management results in a mosaic of seral stages differing in vegetation structure that can serve as habitat for a variety of grassland fauna (Powell 2008, Ricketts and Sandercock 2016). Heterogeneity-based management has been suggested as one of the best strategies for grassland conservation because it increases biodiversity and stabilizes resources in grasslands (Allred et al. 2014, Askins et al. 2007, Fuhlendorf et al. 2006). In addition to altered fire regimes, grasslands are threatened by a variety of anthropogenic activities that have the potential to fragment remaining grasslands. As grasslands are becoming increasingly fragmented it is unclear how effective heterogeneity-based management practices will be in the future.

In addition to cattle grazing, grasslands are widely developed for energy production, an increasingly serious threat to biodiversity (Aldridge and Boyce 2007, Jones et al. 2015, Northrup and Wittemyer 2012, Sawyer et al. 2006). Many North American grasslands have already been widely developed for oil and gas production and are at high risk of further development as new and unconventional forms of energy production, such as hydraulic fracturing, become more common (Copeland et al. 2009, EIA 2015). In addition to the direct loss of habitat that results from the construction of infrastructure, energy development has been linked to a number of negative consequences

for grassland wildlife. Although direct mortality due to collisions or pollution has been documented for some types of infrastructure (Erickson et al. 2001, Wolfe et al. 2007, Ramirez 2010), the greatest threat to most species appears to be avoidance or displacement of individuals from areas around infrastructure (Hovick et al. 2014a, Winder et al. 2014b, LeBeau et al. 2017, Thompson et al. 2015, Sawyer et al. 2006). Many wildlife species will avoid otherwise suitable areas for considerable distances around energy infrastructure resulting in a considerable loss of usable space. Energy development may potentially reduce the utility of management actions that aim to promote diversity and abundance of grassland birds if use or settlement of areas is reduced by the effects of fragmentation (Duchardt et al. 2016, Herkert 1994). Understanding how fragmentation may alter use of the landscape by wildlife will be critical for adapting and applying alternative management strategies to increasingly altered landscapes.

The greater prairie-chicken (*Tympanuchus cupido*; hereafter prairie-chicken), is a grassland obligate species that was once widely distributed throughout the tallgrass prairies of North America (Johnson et al. 2011). As a result of substantial distribution and population declines the prairie chicken is now considered a species of conservation concern throughout much of its distribution (Svedarsky et al. 2000). The reintroduction of heterogeneous disturbance regimes has been suggested as a conservation strategy for prairie-chickens as these practices maintains grasslands by limiting encroachment of trees, and creates a variety of seral stages that prairie-chickens use during different parts of their lifecycle (Hovick et al. 2015c, McNew et al. 2013, McNew et al. 2015). However, prairie-chickens are highly sensitive to fragmentation, making the continued

development of grasslands for energy production a serious conservation threat for prairie-chickens (Pruett et al. 2009, Winder et al. 2014b). Development of grasslands could potentially reduce the effectiveness of heterogeneity based management if significant portions of the landscape receive reduced use as a result of avoidance behaviors or displacement of individuals. While previous studies have shown that both rangeland management and energy development can alter how prairie-chickens use the landscape (Winder et al. 2014b, Winder et al. 2017), these factors have rarely been studied together. Understanding how management and fragmentation interact to shape prairie-chickens use of the landscape throughout the year will be critical for the conservation of this species.

We examined the habitat use of prairie-chickens in a multi-use landscape that is managed for heterogeneity with fire and grazing and has also been developed for oil and gas production. In order to assess how use of a complex landscape may change throughout the year, we separated the year into four behaviorally distinct life history stages: the lekking, nesting, post-nesting, and nonbreeding seasons. Our objective is to identify how prairie-chicken use of a heterogeneous landscape created by a fire and grazing interaction may shift throughout the year, and if and how development related to oil and gas infrastructure alters this use. Additionally, we intended to evaluate how the relative importance of different landscape features change through the year. Our study identifies how prairie-chickens use a multiuse landscape, and improves our understanding of the spatial ecology of a species of conservation concern.

Study site

Our study took place on a combination a private ranch and The Nature
Conservency's Tallgrass Prairie Preserve in Osage County, Oklahoma from 2014 to
2016. The study site is located in the southern most extent of the Flint Hills Ecoregion
which contains some of the largest remaining intact tracts of tallgrass prairie (With et al.
2008). Topography is rolling hills underlined with a bedrock of shale, sandstone, and
limestone (Web Soil Survey 2011). Vegetation in the region is composed primarily of
tallgrass prairie vegetation dominated by big bluestem (*Andropogon gerardi*), little
bluestem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), Indian grass
(*Sorghastrum nutans*), and a mixture of forbs. Crosstimber forests, dominated by post
oak (*Quercus stellata)* and blackjack oak (*Q. marilandica*), occur throughout the study
site but are primarily restricted to areas along drainages. The growing season in the
region is approximately April to September. The climate is temperate with hot summers
(average high of 31.6°C for 2002-2016) and cold winters (average low of -3.89°C for
2000-2014) (Foraker Mesonet Site; Mesonet 2014). The average growing season (April-
September) rainfall from 2000-2015 was 63.37 centimeters (Foraker Mesonet Site;
Mesonet 2014).

Our study site is managed for heterogeneity using prescribed fire and grazing. In
general, fire is applied on a rotational basis where approximately a quarter of the
landscape is burned annually leaving the rest unburned. The fire return interval is
approximately 2-4 years, with the majority of prescribed fires taking place in the spring
(March-May), before the start of the growing season. Prairie-chickens were primarily
monitored on privately owned land that is managed for livestock and grazed seasonally
with cattle. The Tallgrass Prairie Preserve is grazed year round by Bison (*Bison bison*)

and seasonally by cattle. Stacking rates are light to moderate throughout the area (2-2.5

AUM per ha; Hamilton 2007)

Methods

Capture and Monitoring Prairie-chickens

Prairie-chickens were captured on leks between mid-March and late-April using

standard walk-in funnel traps (Shroeder and Braun 1991). Individuals were aged and

sexed based on plumage and secondary sex characteristics (Henderson et al. 1967,

Johnson et al. 2011). All captured prairie-chickens were marked with uniquely numbered

metal legs bands, and females were equipped with a rump-mounted 22-g solar powered

ARGOS/GPS transmitters (PTT-100, Microwave Telemetry, Columbia, Maryland, USA).

GPS transmitters collected locations throughout the year with an estimated error of ±18

meters. From March 1st to August 31st transmitters recorded approximately one location

per hour from 6:00 to 19:00 and two nocturnal locations at 0:00 and 1:00. To conserve

battery life in the winter months, transmitters collected one location approximately every

two hours from 6:00 to 19:00 and two nocturnal locations at 0:00 and 1:00 from

September 1st to February 28th. Hens were monitored remotely by downloading GPS

locations from the ARGOS server as data became available.

Female locations were monitored daily during the spring for nesting activity using

GPS satellite locations. Once female activity became localized to a small area for greater

than 3 days, nests were located by ground searching the area corresponding to the

transmitter error around GPS points where the hen had localized. Females were flushed

only once during the incubation period to record clutch size and the UTM (Universal

Transverse Mercator) coordinates of the nest. The nest was revisited only after the hen was determined to have departed the nest based on GPS locations to determine nest fate.

To account for changes in resource use throughout the year, prairie-chicken locations were separated into four distinct time periods: the lekking season, nesting season, post-nesting season, and the nonbreeding season. Individuals could transition between seasons independently resulting in considerable temporal overlap for some periods among individuals. The lekking period began on March 15th of each year, corresponding to the earliest date hens begin attending leks, and ended when an individual began incubating a nest. The nesting period was defined as the period from start of nest incubation for each hen to when each nest hatched or failed. Only nest locations were used for analysis during the nesting period. The post-nesting breeding season encompasses all locations after a hen's nest hatched or failed until September 14th which corresponds to the approximate timeframe the last broods are breaking up for the fall/winter season. Data on broods was not available for this dataset, so hens were initially separated based on if females were known to not have broods due to nest failure and females where brood status was unknown. Initial analysis revealed little difference in selection between these two groups so all hens were pooled during the period for the final analysis. The nonbreeding season encompassed the remainder of the year (September 15-March 14) and included all nonbreeding activities.

Data Analysis

Acquisition of GIS Data

The location of all oil facilities (pump jacks and tank batteries), power lines, and county roads were manually digitized using aerial imagery from the National Agricultural

Imagery Program (NAIP) acquired in 2015 and were further ground-truthed using hand held GPS units in the field. Similarly, continuous woodland patches of greater than 0.5 hectares were digitized using NAIP imagery. The timing and distribution of prescribed fires and wildfires was derived from GIS (Geographic Information Systems) layers acquired from land managers where birds were monitored. All digitization and data management was done in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands CA, USA).

We developed a suite of covariates related to energy development, rangeland management, and known greater prairie-chicken ecology for use in model development. We included the minimum distance to primary roads, oil facilities (wells and tank batteries), power lines, woodlands and distance to the lek where an individual was captured. All distance variables were log transformed to model the decreasing effect of a feature with increasing distance (Dzialak et al. 2012). Additionally, we included density of oil wells measured across multiple scales. To measure density, we buffered each point on the landscape by a given distance and divided the number of wells within the buffer by the area of the buffer. The smallest buffer had an area of 100 hectares and each successive buffer increased by fifty hectares up to 500 hectares (Plumb 2015). Multiple spatial scales were used as the scale of selection may differ throughout the year, and we did not have *a priori* assumptions on the most relevant scale to measure oil well density. We choose to focus on density of oil wells as other open country grouse have been shown to respond strongly to oil well density (Doherty et al. 2008, Hagen et al. 2011, LeBeua et al. 2017, Walker et al. 2007), and density of roads and power lines was highly correlated with density of oil wells.

Time since fire was defined as the difference in months between the most recent

prescribed fire and the date associated with a used or available location. Time since fire

was later converted to four discrete categories, 0-12 months since fire, 13-24 months

since fire, 25-36 months since fire and patches greater than 36 months since fire. Patches

that were greater than 36 months post fire were combined because biomass accumulation

slows substantially around 36 months post fire in this plant community (Fuhlendorf et al.

2009). The 0-12 month category was used as the reference category in subsequent

analysis (Thurneau 2015), as we wanted to compare use of different times since fire to

what would be the most common seral stage under traditional management practices

(Robbins et al. 2002).

Discrete Choice Models

We used discrete choice models to evaluate prairie-chicken resource use during the

lekking, nesting, post-nest and nonbreeding seasons. Discrete choice assumes selection is

the result of a decision between a finite set of habitat units that are available to an

individual at a given time, known as a choice set. We chose to use discrete choice as this

method allows the resource units available to an individual to change with time, which

was necessary to account for changing availability of seral stages associated with the time

since fire. This method can also accommodate continuous and categorical variables

(Cooper and Millspaugh 1999, McDonald et al. 2006). We conducted analysis using Cox

Proportional Hazard Mixed Models where individuals were included as a random

intercept using the COXME package in program R (Brooks et al. 2015, Thurneau 2015).

Choice sets were composed of a single used point and three available points

randomly drawn from the landscape. As resource selection is likely the result of a

hierarchal process with selection for different landscape features occurring at different spatial scales, we choose to carry out our analysis at two spatial scales that would correspond to second order and third order selection as defined by Johnson (1980). For second order selection (e.g., selection of home ranges within the wider landscape) we defined availability using movement based buffers. Choice sets were drawn from a circular buffer around each used point with radii of the buffer corresponding to the average distance moved in a 24-hour period by all individuals during a season (Boyce et al. 2003). Distances were calculated as cumulative distance between successive locations per single day averaged across individuals within a season (lekking= 1755 meters, post-nesting= 905 meters, nonbreeding= 1755 meters). Availability for third order selection (e.g., selection within a home range), choice sets were drawn from within an individual's home range for the lekking, post-nesting or nonbreeding period. Home ranges were calculated using Brownian Bridge Movement Models (BBMM; Horne et al. 2007) using the BBMM package (Nielsen et al. 2013) in program R. BBMMs are movement based models that estimate the probability of being in a location based on a starting location, an ending location, the time between the two relocations, and measurement error associated with the transmitter. BBMMs are advantageous compared to more traditional home range estimators because they explicitly make use of highly auto-correlated telemetry datasets that result from GPS transmitters (Horne et al. 2007, Walter et al. 2011), and they offer a mechanistic prediction of space use based on an animal's behavior and movement.

As we were only considering landscape level variables and nest sites represent discrete points on the landscape, we only analyzed nest site selection at one scale of selection corresponding to second order selection (Hovick et al. 2015c). Available

locations were drawn from a 2 kilometer buffer around nest sites. This buffer size was selected as previous literature has found that the majority of nests occur within 2 kilometers of lek sites so this distance buffer would capture a realistic area of availability for individuals to select nest sites (Hovick et al. 2015c, McNew et al. 2013).

Model Development

As we were considering a large number of covariates across several scales and seasons, we used a multi-step information theoretic approach to develop models describing prairie-chicken habitat use for each season and definition of availability (Burnham and Anderson 2002, LeBeau et al. 2017). We compared all subsequent models using small sample corrected Akaike's Information Criterion (AICc) (Burnham and Anderson 2002). To avoid multicollinearity, we used Pearson's Correlation to test for correlations among all pairwise combinations of variables and no correlated variables ($r > |0.70|$) were included in the same model. Additionally, as many of our habitat models were nested, we did not consider models competitive if they were within 2 AICc units of a more parsimonious model and they differed by the addition of a single covariate (Arnold 2010). Further, to ensure uninformative parameters were not unintentionally introduced into subsequent models, we assessed individual models at each step and variables with 95% confidence intervals that included zero were not passed on to subsequent models (Arnold 2010).

We separated habitat variables into three groups representing oil well density variables, proximity to energy variables, and environmental variables that are known to shape prairie-chicken habitat use based on the literature (Table 1, Hovick et al. 2015a,

Hovick et al. 2015c, Winder et al. 2014b, Winder et al. 2017). To control for known prairie-chicken habitat associations we developed a base model for each season and availability from the environmental variable group (Webb et al. 2012, LeBeau et al. 2017). We compared combinations of univariate and multivariate models using AICc and the model with the lowest AICc for each season and scale was used in subsequent steps. To determine if proximity to energy development and density of oil wells influenced prairie-chicken habitat use once other factors were controlled for, we added each development variable to the best supported habitat model for each period. We considered energy development variables as influencing selection if they substantially improved model fit (models performed better than 2 AICc units than the base habitat model). If more than one density variable was supported, we retained only the scale with the lowest AICc score. We added combinations of supported energy development variables to the base model to develop the "best" model describing prairie-chicken resource use based on AICc scores. We only considered covariates significant within the top model if beta estimates had 95% confidence intervals that did not overlap zero.

Compositional Analysis

To further investigate second order selection, we used compositional analysis to evaluate home range placement during the lekking, post-nesting, and nonbreeding periods relative to energy development and time since fire (Aebisher et al. 1993). Compositional analysis was conducted for distance to oil wells, power lines, roads and time since fire at the home range level for all three periods. For energy development we categorized the landscape into four categorical distance classes based on distance from infrastructure. Each distance class represented a 400-meter interval from an anthrophonic feature with

all distances beyond 1600 meters being classified together. To evaluate the effects of rangeland management, we used the same four time since fire classes that were used in the discrete choice analysis. We considered the proportion of each patch class within a 5 kilometer buffer around the lek where an individual was captured on as available for that individual as these buffers capture almost all of an individual's locations. We defined use of a patch by an individual during a period as the proportion of each patch class within an individual's seasonal home range. Preference for a distance class or time since fire was calculated as the log ratio of the proportion of a home range in a patch type to the proportion of that patch type available. A multivariate analysis of variance (MANOVA) was used to test whether log ratios differed significantly from zero based on the Wilks' lamda (λ) test statistic at a significance level of $P \leq 0.05$. If use was determined to differ significantly from zero, a preference matrix was constructed where the rows and columns are indexed by the different patch types (time since fire or distance bin) and the values in the matrix are the difference of log ratios of the patch types in the column and the patch type in the row. A preference ranking among patch types was determined by counting the number of times a patch type was preferred over another patch type (positive difference between log ratio of two patch types) (Aebischer et al. 1993). We used t-tests to determine significance among ranks for patch types (Aebisher et al. 1993).

Results

We monitored a total of 30 female prairie-chickens between 2014 and 2016, with all individuals contributing locations to the lekking period, 27 to the post-nest period and 23 individuals were included in the nonbreeding season analysis (Table 2). Thirty-eight nests (33 first attempts and 5 re-nests) were included in the nest site selection analysis.

Nest success was 48% and 40% for first attempts and renests, respectively, during the study period.

Habitat Selection

*Lekking period-*The movement buffer model for the lekking period included time since fire, distance to woodlands and distance to leks (Table 3). Female prairie-chickens maximized their distance from woodlands and remained relatively close to leks during this period. Further, prairie-chickens used all unburned patches more than recently disturbed areas at the landscape level (Table 4).

Within home range selection for the lekking period was best described by a model that only contained times since fire and distance to oil wells (Table 3). Patches 13-24 months post fire were used more than recently burned areas and the 95% confidence intervals for patches 13-24 months post fire and greater than 36 months post fire suggesting similar use to recently burned patches (Table 4). Additionally, probability of use increased in areas of prairie-chicken home ranges that were relatively closer to oil wells (Table 4).

Nesting period- Time since fire was the only supported variable for nest site selection when using a 2 kilometer buffer to define availability (Table 3). Female prairie-chickens showed a trend toward using unburned patches for nesting compared to recently disturbed patches, however, the confidence intervals for patches 13-24 months post fire included zero suggesting similar use to recently burned patches. Nests were most likely to be placed in patches 25-36 months post fire and patches greater than 36 months post fire (Table 5).

Post-nesting period- The top model for availability based on the movement buffers during the post-nesting period contained time since fire, distance to roads, distance to leks, distance to power lines and oil well density (Table 3). Probability of use increased with increasing distance from woodlands and with decreasing distance to leks and females avoided areas close to power lines and areas of high oil well density (Table 6). Oil well density was best described by the smallest spatial scale measured (number of wells within 1 km^2) (Table 6). Female prairie-chickens used recently burned patches over any other time since fire at the landscape scale (Table 6).

During the post-nesting period within home range selection was driven by time since fire, distance to woodlands, distance to leks, and distance to power lines (Table 3). Similar to the movement buffer based models female prairie-chickens avoided woodlands and power lines and showed an attraction to areas relatively close to leks (Table 6). Female prairie-chickens used areas 13-24 months post fire less than recently burned areas but the confidence intervals for patches 24-36 months post fire and >36 months post fire included zero suggesting there was no difference in use between these patches and recently burned areas with in home ranges (Table 6).

Nonbreeding season- Landscape level selection during the nonbreeding season indicated an avoidance of power lines, woodlands, primary roads, and high oil wells densities, and an attraction to recently burned areas and locations close to leks (Table 3,7). Prairie-chickens responded to oil well density at fairly course scales using areas with lower numbers of wells with 4 km^2. Recently burned patches were used preferentially over patches that were 13-24 months post fire and greater than 36 months post fire, but the 95% confidence interval for patches 24 -36 months post fire included zero (Table 7).

The model describing within home range selection during the nonbreeding season was similar to the movement based model, containing density of oil wells, time since fire and distance to power lines, woodlands, and leks (Table 3). Female prairie-chickens avoided areas close to woodlands, power lines and in areas with high numbers of oil wells within 3.5 km^2. Additionally females were attracted to areas close to leks within their home ranges (Table 7). Prairie-chickens showed a trend toward using recently burned areas more than any other times since fire but the 95% confidence intervals for patches 25-26 months post fire included zero (Table 7).

Compositional Analysis

During the lekking period, prairie-chickens home range placement was nonrandom relative to oil wells (Wilks' lambda = 0.58, p= 0.008), power lines (Wilks' lambda = 0.57, p=0.004) and roads (Wilks' lambda = 0.70, p= 0.05), however use was random relative to time since fire (Wilks' lambda = 0.88, p= 0.34). Based on differences in log ratios of used and available, prairie-chickens preferentially used areas between 400 meters and 1200 meters from oil wells with use of areas 400-800 meters significantly greater than areas between 0 and 400 meters from oil wells (Table 8). Prairie-chickens used areas between 400 meters and 1600 meters from power lines with use of areas between 400 and 800 meters significantly greater use of areas less than 400 meters (Table 9). Similarly, areas between 400 meters and 1600 meters from roads were preferred with use of areas 400 and 1200 meters significantly greater than use of areas less than 400 meters (Table 10). For all structures, intermediate distances were preferred to areas greater than 1600 meters from infrastructure, however this is likely the result of minimal availability of areas greater than 1600 meters (Table 8,9,10). Home range placement was

not different from random in relation to time since fire in the lekking period (Wilks'
lambda = 0.88, p= 0.34).

During the post nesting period, home range placement was nonrandom for oil
wells (Wilks' lambda = 0.48, p= 0.002) power lines (Wilks' lambda = 0.47, p= 0.004),
and time since fire (Wilks' lambda = 0.52, p= 0.002), but not for roads (Wilks' lambda =
0.75, p= 0.152). Home ranges were preferentially placed in areas greater than 400 meters
from oil wells, with use of the 400-800 meters and 800-1200 meters distance significantly
greater than use of areas less than 400 meters (Table 8). Home range placement relative
to power lines was similar, with home ranges placed in areas greater than 400 meters
being used significantly more than areas less than 400 meters (Table 9). Intermediate
distances from power lines and oil wells were used significantly more than use of areas
greater than 1600 meters, however, similar to other periods limited availability of areas
over 1600 meters may have resulted in reduced use of these areas (Table 8, 9, 10). During
this season prairie-chicken home ranges contained greater proportions of patches 0-12
months post fire (Table 11).

During the nonbreeding season, home range placement was nonrandom relative to
power lines (Wilks' lambda= 0.55, p= 0.008) and roads (Wilks' lambda= 0.59, p= 0.014).
Home range placement relative to oil wells was not significantly different from random
(Wilks' lambda= 0.67, p= 0.062), but home ranges still showed a trend toward containing
greater proportions of areas between 400 and 1600 meters (Table 8). Home ranges
contained greater proportions of areas between 400 meters and 1600 meters from power
lines, with use of all distance classes greater than areas less than 400 meters (Table 9).
Additionally, home ranges were preferentially placed in areas between 400 meters and

1200 meters from roads (Table 10). Similar to other periods, limited access to areas greater than 1600 meters may have resulted in reduced use compared to other distance categories (Table 8, 9, 10). Home ranges placement was not different from random with relation to time since fire in the nonbreeding season (Wilks' lambda = 0.73, p= 0.09)

Discussion

Resource selection is a dynamic feature of a species' ecology, varying across spatial scales and time of year (Johnson 1980, Fuhlendorf et al. 2002, Boyce et al. 2003). Our study provides new insights into the habitat use of a species of conservation concern in a multiuse landscape that is managed to restore heterogeneous disturbance patterns, and has also been developed for oil and gas production. In a relatively continuous grassland, prairie-chicken habitat use was primarily driven by selection for different vegetation patches that result from the interaction of fire and grazing, and the avoidance of woodland areas. Prairie-chicken's response to energy development was more complex with individuals making decisions about energy development at course spatial scales, and the relative importance of energy infrastructure varying through different life stages. Notably, avoidance of energy development was detected in the post-nesting and nonbreeding seasons, two life stages that have been relatively neglected in the literature. These results add to the growing body of literature that emphasizes the importance of landscape heterogeneity for wildlife conservation, however the continued development of grasslands for energy production may reduce the utility of heterogeneity based management through displacement or loss of usable space by wildlife species from areas around energy development.

Our results support previous work that suggests restoration of historic fire and grazing regimes may be one of the best strategies for prairie-chicken conservation (Fuhlendorf et al. 2017, Hovick et al. 2015c, McNew et al. 2012). Reintroduction of heterogeneous disturbance regimes will offer two primary benefits for prairie-chickens, the limitation of tree invasion in grasslands and the creation of variable vegetation structures needed to meet specific habitat needs during different life stages. Similar to previous research that found prairie-chickens avoid nesting and establishing leks in areas with high tree cover, we found that avoidance of woodlands was a consistent driver of prairie-chicken space during most of the year (Merrill et al. 1999, Hovick et al. 2015a, Hovick et al. 2015c). Due to a history of fire suppression in much of the Great Plains the region is threatened with invasion by eastern redcedar (*Juniperus virginiana*) (Briggs et al. 2002, Engle et al. 2008), potentially affecting remaining prairie-chicken populations (Merrill et al. 1999, Fuhlendorf et al. 2002, McNew et al. 2012). Application of frequent fires is a critical component of grassland maintenance, because fire limits tree invasion into grasslands (Bond and Keeley 2005). Additionally, the use of different seral stages in the fire grazing mosaic to meet specific habitat needs during different life stages, emphasizes the need for maintaining heterogeneity in grasslands. For example, prairie-chickens primarily used unburned patches during the lekking and nesting season, then shifted use to recently disturbed patches during the post-nesting and nonbreeding season. Further, despite shifting preferences for patches of different seral stages, prairie-chickens selected areas close to leks through all periods, suggesting the optimal landscape for prairie-chickens should have a variety of seral stages juxtaposed in relatively close proximity.

Prairie-chickens have a complex life history and require a variety of resources and vegetative conditions during different stages of their life cycle (Johnsgard 1983, Hovick et al. 2015c, McNew et al. 2015). Selection for specific fine scale conditions likely shapes use of the vegetation mosaic on broader scales in grasslands where the interaction of fire and grazing is a primary driver of vegetation structure. Increased use of unburned patches during the lekking and nesting season is likely driven by the use of patches with optimal nesting conditions. In landscapes managed with fire and grazing, prairie-chickens primarily use areas two to three years or greater post fire for nesting, as the vegetation structure in these patches likely offer improved visual concealment from predators and optimal thermal conditions (Hovick et al. 2014b, Hovick et al. 2015c, McNew et al. 2015). After nesting, use shifts to recently burned patches during the post-nesting and nonbreeding seasons, which may be driven by selection for patches with sparse litter layers that improve foraging and mobility (Norton et al. 2002, Rumble et al. 1987). However, knowledge of how fire and grazing affects availability of critical resources, such as thermal cover and forage, during brood-rearing and over wintering periods in relation to fire and grazing is lacking and future research should aim to identify resource needs during these periods.

Female prairie-chickens appear to be making selection decisions about energy development at coarse spatial scales, with decisions likely occurring at the level of second order selection, or placement of home ranges within the landscape (Johnson 1980). Compositional analysis suggests that home ranges are placed on the landscape nonrandomly in relation to energy development, with home ranges including areas less than 400 meters from energy infrastructure less than expected based on availability

during most seasons. These results were supported by discrete choice analysis where we analyzed habitat use based on two definitions of availability in order to evaluate different selection processes, differential use within an individual's home range and space use on the wider landscape. Selection patterns were similar between the two definitions of availability; however, selection generally was stronger at the landscape scale. Consideration of multiple spatial scales and definitions of availability during resource selection studies is critical when identifying the scale at which a species may respond to changes in its environment (Fuhlendorf et al. 2002, Boyce et al. 2003).

We found that power lines and high densities of oil wells were the most important energy development related drivers of prairie-chicken habitat use, but the importance of these structures varied during different life stages. Prairie-chickens showed an avoidance of areas of high oil well density and areas near power lines during the post-nest and nonbreeding seasons, two biological periods that have received relatively little attention in the prairie-chicken literature in relation to energy development (Winder et al. 2014a, Winder et al. 2014b). Response to energy development during nesting and lekking periods was limited with nest placement being minimally affect by infrastructure and individuals demonstrating an attraction to areas closer to oil wells within home ranges during the lekking period. Reduced sensitivity to energy development during the lekking and nesting periods may be the result of altered behavior patterns and reduced use of the landscape during these parts of the year. Female prairie-chicken use of the landscape during the early spring is primarily directed toward leks and nest sites, with leks typically being associated with areas of low anthropogenic disturbance (Gregory et al. 2011, Hovick et al. 2015a, Hovick et al. 2015b). Prior selection for locations with limited

disturbance and the restricted use of the landscape may limit individual's exposure to energy development during this period. This is supported by compositional analysis which indicated that similar to other periods prairie-chickens used areas less than 400 meters from oil wells less than expected during the lekking period. Further, in relatively continuous grasslands nest site selection may be primarily driven by section for local scale characteristics, such as predator avoidance or cooler thermal conditions, reducing the importance of landscape level conditions (Hovick et al. 2015c, McNew et al. 2013).

Prairie-chicken response to oil wells was primarily driven by density of wells, but proximity to individual structures was rarely an influential variable, suggesting that while use may still occur on the periphery of oil fields prairie-chickens are avoiding the most heavily developed areas. Similar patterns of avoidance have been observed in other open country grouse (Doherty et al. 2008, Hagen et al. 2011, LeBeua et al. 2017, Walker et al. 2007), and these behaviors have been suggested to be related the avoidance of increased human activity and disturbance that occurs in highly developed areas (Holloran et al. 2015, Lyon and Anderson 2003). Additionally, the spatial scale at which prairie-chickens responded to oil well density varied throughout the year with hens responding most strongly to the smallest spatial scale measured (number of wells within 100 hectares) during the post nesting period but then responding to density of wells at courser spatial scales (number of wells within 350 hectares for within home range selection and number of wells within 400 hectares for landscape level selection) during the nonbreeding season. Differences in spatial scales between the two periods indicate females may be more sensitive to the level of fragmentation of the landscape during the nonbreeding season, and may choose to move to areas further from development. This increased sensitivity

may be the result of the overall larger home ranges during the nonbreeding season which may expose prairie-chickens to development more than in other seasons (Patten et al. 2011).

Prairie-chickens were observed to avoid power lines at our study site with avoidance being the strongest during the post nesting and nonbreeding season. Power lines and transmission lines have been implicated in displacement of individuals and as barriers to movement in multiple grouse species (Braun 1998, Pruett et al. 2009, Hagan et al. 2011). Both greater prairie-chickens and the closely related lesser prairie-chicken (*Tympanuchus pallidicinctus*) have been observed to avoid crossing power lines less than would be expected based on normal movement behaviors (Pruett et al. 2007). Avoidance of tall structures by grouse is hypothesized to be the result of predator avoidance behaviors as power lines may offer potential perch sites for avian predators (Knight and Kawashima 1993). However, information on how energy development alters the abundance of avian predators in the region is limited (Smith et al. 2017), and it is unclear if avoidance is driven by the perceived risk of predation or by the presence of actual predators (Dinkins et al. 2014). Regardless, the presence of tall structures such as power lines in otherwise open landscapes results in further fragmentation and reduced landscape connectivity for prairie-chickens.

Similar to previous research, we found that selection for areas close to leks was an important driver of habitat use throughout the year (Winder et al. 2014b, Winder et al. 2015). Proximity of females to leks during periods when females may not be actively using the lek has been suggested as evidence for the hotspot hypothesis which posits that leks will be established in areas with high densities of females or near important

resources used by females (Bradbury et al. 1986). In landscapes managed with the interaction of fire and grazing, lek sites are associated with edges of burn patches, where males have access to recently disturbed areas for displaying and escape and loafing cover in undisturbed areas (Hovick et al. 2015a, Patten et al. 2007). These areas may also represent locations of high female density as females may choose to establish home ranges in heterogeneous locations with easy access to multiple seral stages used to carry out all stages of their lifecycle.

A potential confounding factor at our study site that may influence some of our results is the practice of lek mowing. On some properties at our study site where prairie-chickens were monitored land owners mow areas where males were observed to be displaying the previous spring. On properties where mowing does not occur, leks tend to be associated with recently burned patches where short sparse vegetation is widely available (Hovick et al. 2015a). However, lek mowing can create optimal lekking conditions (short, sparse vegetation) in areas that would otherwise have too dense of vegetation structure for lekking activities, potentially decoupling prairie-chicken reliance on recently burned areas during this period. This may explain the preferential use of unburned areas during the lekking season which appears to contrast with other studies that report preference for burned patches during this period (Hovick et al. 2015a, Patten et al. 2007). However, most previous studies have focused on the actual lek site and male locations, and the increased preference for unburned patches during this period may also be a reflection of female use of unburned patches for loafing cover during the day when they are not actively attending the lek. Further, these results emphasize the importance of heterogeneity for prairie-chickens, as it is apparent that individuals are selecting for

variation in vegetation structure at multiple scales, and that a number of management methods are available to create heterogeneity.

Habitat selection should be viewed as a hierarchal process, where constraints or filters at larger scales limit selection choices and distribution of species at lower scales (Kolasa and Waltho 1998, Fuhlendorf et al. 2017). Selection for time since fire was among the most consistent predictors of space use across seasons, however certain features limited prairie-chicken use of the landscape. These containing features included: trees, power lines and high density oil development. Reintroduction of heterogeneous disturbance regimes into grasslands may be among the best strategies for prairie-chicken conservation as this will maintain grasslands by preventing woody plant encroachment and create a variety of seral stages that can be used as year round habitat. However, efforts to minimize future fragmentation of grasslands from various sources including energy development and woody plant encroachment will ensure the ongoing utility of local management action, and viability of prairie-chicken populations.

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Table 1. Explanatory variables to in model habitat use of Greater Prairie-Chickens during the lekking, nesting, post-nest, and non-breeding seasons in Osage County, Oklahoma between 2014 and 2016.

Covariate	Description
Environmental Variables	
Lek	Distance from prairie-chicken location to capture lek
Woodlands	Distance from prairie-chicken location to nearest woodland
Time Since Fire (TSF)	Time since fire measured in 12 month intervals
tsf.0	Patches 0 to 12 months post fire. Reference category during analysis
tsf.1	Patches 13 to 24 months post fire.
tsf.2	Patches 25 to 36 months post fire
tsf.3	Patches greater than 36 months post fire
Development Variables	
Oil Well	Distance from prairie-chicken location to nearest active well pad or tank battery
Power line	Distance from prairie-chicken location to nearest power line
Road	Distance from prairie-chicken location to nearest primary road, defined as county roads greater than 8 meters wide
Oil Density	Number of wells within a specified buffer around a point. Buffered area starts at 1 km^2 and increases by 0.5 km^2 up to 5 km^2

Table 2. Mean value and standard deviation (in parenthesis) of used and available locations used in each analysis used to describe Greater Prairie-Chicken habitat use in Osage County, Oklahoma between 2014-2016. All distance variables measured in kilometers. Density of oil wells was measured at nine scales but only the smallest scale (Density 1, wells within 1 km^2) and largest scale (Density 2, wells within 5 km^2) are presented. Time since fire measured in months.

Period	Availability		Oil Wells	Power lines	Roads	Woodlands	Lek	Density 1	Density 2	Time Since Fire (Months)
Lekking Period	Movement Buffer	Used	1.07 (0.7)	0.94 (0.53)	1.2 (0.93)	3.98 (1.64)	0.94 (0.47)	0.99 (2.83)	1.12 (1.93)	26.5 (22.5)
		Available	1.2 (0.84)	0.93 (0.59)	1.15 (0.86)	3.8 (1.8)	1.15 (0.57)	1.22 (3.08)	1.15 (2.04)	23.4 (24.5)
	Home Range	Used	1.05 (0.69)	0.94 (0.53)	1.26 (0.93)	3.98 (1.65)	0.95 (0.47)	1 (2.85)	2.82 (1.94)	25.2 (22.19)
		Available	1.20 (0.78)	0.98 (0.57)	1.23 (0.92)	4.0 (1.57)	0.98 (0.54)	0.96 (2.82)	2.85 (1.99)	22.8 (19.78)
Post-nesting Period	Movement Buffer	Used	1.3 (0.70)	0.99 (0.49)	1.34 (0.94)	3.9 (1.53)	1.16 (0.70)	0.42 (1.29)	0.93 (1.65)	16.9 (19.4)
		Available	1.3 (0.77)	0.99 (0.59)	1.31 (0.91)	3.86 (1.60)	1.24 (0.73)	0.77 (2.32)	0.99 (1.85)	19.2 (21)
	Home Range	Used	1.23 (0.70)	0.98 (0.49)	1.30 (0.94)	3.99 (1.55)	1.11 (0.67)	0.62 (2.21)	1.86 (1.81)	18.8 (19.3)
		Available	1.28 (0.75)	0.99 (0.552)	1.34 (0.94)	3.88 (1.51)	1.28 (0.78)	0.66 (1.86)	2.21 (1.78)	18.9 (20.5)
Nonbreeding Period	Movement Buffer	Used	1.81 (0.93)	1.175 (0.62)	1.16 (0.92)	3.00 (1.7)	1.31 (0.93)	0.24 (0.93)	0.4 (0.98)	26.9 (48.7)
		Available	1.72 (0.98)	1.10 (0.70)	1.12 (0.89)	2.91 (1.80)	1.51 (0.98)	0.52 (1.79)	0.6 (1.34)	28.2 (48.8)
	Home Range	Used	1.89 (0.90)	1.18 (0.63)	1.19 (0.92)	3.08 (1.7)	1.34 (0.93)	0.16 (0.78)	1.55 (0.86)	28.8 (28.8)
		Available	1.78 (1.02)	1.09 (0.69)	1.19.91 (0.93)	3.12 (1.75)	1.52 (1.06)	0.43 (1.55)	0.78 (1.3)	28.9 (26.1)
Nesting Period	2 Kilometer buffer	Used	1.11 (0.89)	1 (0.52)	1.02 (0.85)	2.91 (1.47)	0.97 (0.55)	1 (3.28)	1.06 (1.96)	27.92 (16.67)
		Available	1.25 (0.98)	1.1 (0.69)	1.15 (0.87)	2.7 (1.45)	1.21 (0.71)	1.31 (3.32)	1.31 (2.19)	19.92 (18.19)

Table 3. Top three discrete choice models and the null used to describe greater prairie-chicken habitat use during the lekking, nesting, post-nesting, and nonbreeding season in Osage County, Oklahoma between 2014 and 2016. Habitat selection was evaluated at definitions of availability for the lekking, post-nesting, and nonbreeding season, selection based on a movement buffer, and selection from within an individual's home range. Availability was defined by a single 2 kilometer buffer for the nesting period. Models with the lowest ΔAICc were considered the best model for each period. Models are presented with the number of parameters (K) and model log-likelihood score.

Season	Model	ΔAICc	K	Log Likelihood
Lekking	*Movement Buffer*			
	TSF- Woodlands+ Lek	0	3	-1040.27
	TSF+ Lek	24	2	-1053.12
	TSF-Woodlands	141.363	2	-1063.12
	Null	154.46	1	-1115.97
	Home Range			
	TSF+ Oil	0	3	-1077.66
	TSF-Power lines	12.08	3	-1083.7
	TSF	14.296	2	-1084.6
	Null	32.558	1	-1097.94
Nesting	*2 km Buffer*			
	TSF	0	2	-37.33
	TSF- Woodlands+ Leks	3.28	4	-36.16
	Null	6.38	1	-44.36
Post-nesting	*Movement Buffer*			
	TSF- Woodlands+ Lek- Power Lines- Well Density	0	5	-3429.55
	TSF- Woodlands+ Lek- Power Lines- Well Density- Roads	2.09	6	-3431.95
	TSF- Woodlands+ Lek- Power Lines- Roads	53.544	5	-3457.72
	Null	385.49	1	-3630.70
	Home Range			
	TSF- Woodlands+ Lek- Power Lines	0	5	-4444.56
	TSF- Woodlands+ Lek- Power Lines- Oil Well Density	1.47	6	-4444.81
	TSF- Woodlands+ Lek- Oil Well Density	33.24	5	-4463.52
	Null	239.59	1	-4570.61
Nonbreeding	*Movement Buffer*			
	TSF- Woodlands+ Lek- Power Lines- Oil well Density- Roads	0	7	-4646.52
	TSF- Woodlands+ Lek- Power Lines- Oil well Density	9.58	6	-4652.31
	TSF- Woodlands+ Lek- Power Lines- Oil well Distance	26.91	6	-4663.62
	Null	877.43	1	-5093.24
	Home Range			
	TSF- Woodlands+ Lek- Power Lines- Oil Well Density	0	6	-4549.15
	TSF- Woodlands+ Lek- Power Lines- Oil Well Density- Roads	0.745	7	-4547.78
	TSF- Woodlands+ Lek- Power Lines- Distance to Oil Wells	51.12	6	-4574.35
	Null	539.8	1	-4825.69

Table 4. Beta coefficients, odds ratio, standard error, and confidence intervals for the lekking period models describing availability based on a movement based buffer and within home range selection for greater prairie-chickens monitored in Osage County, Oklahoma between 2014 and 2016.

	β	Odds Ratio	Standard Error	95% CI Lower	95% CI Upper
Movement Buffer					
Distance to Lek	-0.451	0.637	0.071	-0.594	-0.309
Distance to Woodland	0.904	2.469	0.193	0.518	1.289
Time Since Fire[a]					
tsf.0	0				
tsf.1	0.646	1.908	0.139	0.367	0.925
tsf.2	1.038	2.824	0.183	0.673	1.404
tsf.3	0.299	1.348	0.138	0.022	0.575
Home Range					
Distance to Oil Wells	-0.227	0.797	0.061	-0.349	-0.105
Time Since Fire[a]					
tsf.0	0				
tsf.1	0.636	1.889	0.145	0.347	0.926
tsf.2	0.342	1.408	0.179	-0.016	0.701
tsf.3	0.267	1.306	0.155	-0.043	0.576

[a] Beta coefficients interpreted in relation to the reference category tsd.0 (0-12 months post fire). Time since fire categories are tsf.1= 13-24 months post fire, tsf.2= 25-36 months post fire, and tsf.3= >36 months post fire.

Table 5. Beta coefficients, odds ratio, standard error, and confidence intervals for the nesting period model for Greater Prairie-Chickens monitored in Osage County, Oklahoma between 2014 and 2016.

	β	Odds Ratio	Standard Error	95% CI Lower	95% CI Upper
Time Since Fire[a]					
tsf.0	0				
tsf.1	0.89	2.44	0.83	-0.76	2.54
tsf.2	2.07	7.91	0.90	0.28	3.86
tsf.3	2.24	9.36	0.78	0.67	3.80

[a] Beta coefficients interpreted in relation to the reference category tsd.0 (0-12 months post fire). Time since fire categories are tsf.1= 13-24 months post fire, tsf.2= 25-36 months post fire, and tsf.3= >36 months post fire.

Table 6. Beta coefficients, odds ratio, standard error, and confidence intervals for the post-nesting period models describing availability based on a movement based buffer and within home range selection for Greater Prairie-Chickens monitored in Osage County, Oklahoma between 2014 and 2016.

	β	Odds Ratio	Standard Error	95% CI Lower	95% CI Upper
Movement Buffer					
Distance to Lek	-0.226	0.797	0.051	-0.328	-0.125
Distance to Woodlands	0.989	2.689	0.155	0.679	1.299
Oil Well Density (1 km^2)	-0.146	0.864	0.022	-0.190	-0.103
Distance from Power Lines	0.347	1.415	0.045	0.256	0.438
Time Since Fire					
tsf.0[a]	0				
tsf.1	-0.869	0.419	0.096	-1.061	-0.677
tsf.2	-0.610	0.543	0.107	-0.823	-0.396
tsf.3	-1.222	0.295	0.126	-1.474	-0.970
Home Range					
Distance to Lek	-0.497	0.608	0.038	-0.572	-0.422
Distance to Woodlands	0.299	1.349	0.083	0.132	0.466
Distance from Power Lines	0.183	1.201	0.032	0.120	0.247
Time Since Fire					
tsf.0[a]	0				
tsf.1	-0.315	0.730	0.072	-0.458	-0.172
tsf.2	0.019	1.019	0.072	-0.125	0.163
tsf.3	0.028	1.029	0.082	-0.136	0.192

[a] Beta coefficients interpreted in relation to the reference category tsd.0 (0-12 months post fire). Time since fire categories are tsf.1= 13-24 months post fire, tsf.2= 25-36 months post fire, and tsf.3= >36 months post fire.

Table 7. Beta coefficients, odds ratio, standard error, and confidence intervals for the nonbreeding period models describing availability based on a movement based buffer and within home range selection for Greater Prairie-Chickens monitored in Osage County, Oklahoma between 2014 and 2016.

	β	Odds Ratio	Standard Error	95% CI Lower	95% CI Upper
Movement Buffer					
Distance to Lek	-0.385	0.681	0.035	-0.455	-0.314
Distance to Woodlands	0.652	1.920	0.061	0.531	0.774
Oil Well Density (4 km^2)	-0.318	0.728	0.030	-0.378	-0.257
Distance to Power Lines	0.363	1.438	0.031	0.301	0.425
Distance to Roads	0.060	1.062	0.018	0.023	0.097
Time Since Fire					
tsf.0[a]	0				
tsf.1	-0.575	0.563	0.071	-0.717	-0.433
tsf.2	0.010	1.010	0.085	-0.161	0.181
tsf.3	-0.403	0.669	0.065	-0.533	-0.273
Home Range					
Distance to Lek	-0.241	0.786	0.029	-0.298	-0.183
Distance to Woodlands	0.095	1.100	0.026	0.044	0.147
Oil Well Density (3.5 km^2)	-0.304	0.738	0.028	-0.361	-0.247
Distance to Power Lines	0.322	1.380	0.029	0.265	0.379
Time Since Fire					
tsf.0[a]	0				
tsf.1	-0.693	0.500	0.069	-0.830	-0.556
tsf.2	-0.024	0.976	0.078	-0.180	0.131
tsf.3	-0.281	0.755	0.056	-0.392	-0.169

[a] Beta coefficients interpreted in relation to the reference category tsd.0 (0-12 months post fire). Time since fire categories are tsf.1= 13-24 months post fire, tsf.2= 25-36 months post fire, and tsf.3= >36 months post fire.

Table 8. Compositional analysis results for 400 meter intervals from oil wells during the lekking, post-nesting and nonbreeding periods for greater prairie-chickens in Osage County, Oklahoma from 2014-2016. Table values are the difference in the log ratios between two patch types and associated standard errors. Positive values indicate preference for the patch category described by the column. Ranks show order of decreasing preference (1= most preferred, 5 least preferred).

Lekking Period

	Rank	0-400	400-800	800-1200	1200-1600	>1600
0-400	3	0				
400-800	1	2.61 ±0.09 *	0			
800-1200	2	1.21 ±0.15	-.44 ±0.11	0		
1200-1600	4	-.37 ±0.23	-1.54 ±0.21	-1.85 ±0.14 *	0	
>1600	5	-1.8 ±0.24	-2.96 ±0.22 *	-3.52 ±0.18 *	-3.68 ±0.1 *	0

Post-nesting Period

	Rank	0-400	400-800	800-1200	1200-1600	>1600
0-400	5	0				
400-800	3	2.15 ±0.09*	0			
800-1200	1	3.44 ±0.15*	2.5 ±0.13*	0		
1200-1600	2	1.36 ±0.25	0.65 ±0.24	-1.33 ±0.13	0	
>1600	4	0.44 ±0.28	-0.2 ±0.29	-1.95 ±0.2*	-1.52 ±0.14	0

Nonbreeding Period

	Rank	0-400	400-800	800-1200	1200-1600	>1600
0-400	5	0				
400-800	3	2.83 ±0.11 *	0			
800-1200	1	2.88 ±0.14 *	1.91 ±0.04 *	0		
1200-1600	2	2.49 ±0.15 *	1.02 ±0.07	-0.36 ±0.04	0	
>1600	4	1.29 ±0.21	-.19 ±0.16	-0.85 ±0.14	-1.01 ±0.1	0

* Significantly different at P> 0.05 based on t-tests

Table 9. Compositional analysis results for 400 meter intervals from power lines during the lekking, post-nesting and nonbreeding periods for greater prairie-chickens in Osage County, Oklahoma from 2014-2016. Table values are the difference in the log ratios between two patch types and associated standard errors. Positive values indicate preference for the patch category described by the column. Ranks show order of decreasing preference (1= most preferred, 5 least preferred).

	Rank	0-400	400-800	800-1200	1200-1600	>1600
Lekking Period						
0-400	4	0				
400-800	1	3.24 ±0.1 *	0			
800-1200	2	1.78 ±0.17	-0.22 ±0.1	0		
1200-1600	3	0.74 ±0.24	-0.81 ±0.19	-0.92 ±0.14	0	
>1600	5	-0.95 ±0.25	-2.58 ±0.22 *	-2.85 ±0.19 *	-3.24 ±0.13 *	0
Post-nesting Period						
0-400	4	0				
400-800	2	3.34 ±0.1 *	0			
800-1200	1	3.21 ±0.13 *	1.84 ±0.04 *	0		
1200-1600	3	1.12 ±0.21	-0.71 ±0.16	-1.29 ±0.14	0	
>1600	5	-0.5 ±0.26	-2.29 ±0.21 *	-2.88 ±0.19 *	-3.13 ±0.12 *	0
Nonbreeding Period						
0-400	5	0				
400-800	4	3.34 ±0.1 *	0			
800-1200	2	3.21 ±0.13 *	1.84 ±0.04 *	0		
1200-1600	1	1.12 ±0.21 *	-0.71 ±0.16 *	-1.29 ±0.14	0	
>1600	3	-0.5 ±0.26	-2.29 ±0.21	-2.88 ±0.19	-3.13 ±0.12	0

* Significantly different at P> 0.05 based on t-tests.

Table 10. Compositional analysis results for 400 meter intervals from roads during the lekking, post-nesting and nonbreeding periods for greater prairie-chickens in Osage County, Oklahoma from 2014-2016. Table values are the difference in the log ratios between two patch types and associated standard errors. Positive values indicate preference for the patch category described by the column. Ranks show order of decreasing preference (1= most preferred, 5 least preferred).

Lekking Period

	Rank	0-400	400-800	800-1200	1200-1600	>1600
0-400	4	0				
400-800	2	1.89 ±0.09 *	0			
800-1200	1	2.22 ±0.15 *	1.36 ±0.12	0		
1200-1600	3	0.02 ±0.25	-0.64 ±0.25	-1.95 ±0.17 *	0	
>1600	5	-0.48 ±0.3	-1.04 ±0.3	-2.06 ±0.23 *	-1.07 ±0.14	0

Post-nesting Period

	Rank	0-400	400-800	800-1200	1200-1600	>1600
0-400	5	0				
400-800	1	1.9 ±0.1 *	0			
800-1200	4	0.57 ±0.18	-0.8 ±0.11	0		
1200-1600	2	0.67 ±0.25	-0.14 ±0.2	0.42 ±0.15	0	
>1600	3	0.35 ±0.34	-0.24 ±0.3	0.05 ±0.28	-0.22 ±0.21	0

Nonbreeding period

	Rank	0-400	400-800	800-1200	1200-1600	>1600
0-400	3	0				
400-800	2	1.97 ±0.03 *	0			
800-1200	1	1.74 ±0.09 *	1.2 ±0.07	0		
1200-1600	4	-0.12 ±0.17	-0.53 ±0.16	-1.58 ±0.11	0	
>1600	5	-0.73 ±0.26	-1.03 ±0.24	-1.66 ±0.2	-1.02 ±0.16	0

* Significantly different at P> 0.05 based on t-tests.

Table 11. Compositional analysis results for patches of different times since disturbance for the post nesting period for greater prairie-chickens in Osage County, Oklahoma from 2014-2016. Table values are the difference in the log ratios between two patch types and associated standard errors. Positive values indicate preference for the patch category described by the column. Ranks show order of decreasing preference (1= most preferred, 5 least preferred).

	Rank	0-12 months	13-24 months	25-36 months	>36 months
0-12 months	1	0			
13-24 months	2	-2.28 ± 1.05*	0		
25-36 months	3	-2.86 ± 1.01*	-0.57 ± 1.3	0	
>36 months	4	-4.97 ± 1.11*	-2.68 ± 1.31*	-2.11 ± 1.28	0

* Significantly different at P> 0.05 based on t-tests.

VITA

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