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February 20, 2020

Osage County Oil and Gas EIS
BIA Osage Agency
Attn: Superintendent
P.O. Box 1539
Pawhuska, OK 74056

Via Email: osagecountyoilandgaseis@bia.gov

Re: **BIA Osage County Environmental Impact Statement (EIS) Public Comment**

On behalf of Osage Buck Creek LLC I am writing with the purpose of supporting more stringent environmental protection for natural resources within Osage county in regard to oil and gas production and exploration.

We feel strongly that the environmental impact statement needs to address concerns with a long term outlook in mind for all stakeholders in Osage county. For much of the last century the protection of natural resources in Osage county has taken a back seat to the expedition of oil and gas exploration. This endeavor has led to pollution and degradation of thousands of acres of native tallgrass prairie as well as pollution of surface and subsurface waterways and riparian areas. We support the adoption of **Alternative 4** as part of the Environmental Impact Statement (EIS) to serve as a baseline to enhance natural resource protection in Osage county.

Tallgrass Prairie Ecosystem in Osage County

The tallgrass prairie that Osage county is most notably known for has been identified as an ecosystem that is under extreme risk of peril. With only about 4% of the original tallgrass prairie still intact an effort must be made by all resource managers to try and mitigate or limit the physical impacts to the soil, water, and air in order to maintain this valuable ecosystem. It has taken many thousands of years for the tallgrass prairie to develop into the productive grassland, wildlife habitat, and fresh water producing ecosystem that it is and in the last 100 years all of those things have been tarnished due to a lack of regulation for oil production in Osage county. With that in mind we believe that the approach to drafting this EIS should be to keep in mind the long term sustainability and preservation of our unique natural resources in Osage county.

Certainly the tallgrass prairie is economically valuable in the short term due to its viability as grazing land for livestock and the opportunity to extract resources that fuel our world. However, I would argue that the long term economic viability of maintaining Osage county as productive tallgrass prairie is up to all stakeholders to develop a better set of working conditions that ensure more sustainable practices to minimize damages in the future but to also aid in the remediation of damages that have already occurred.

There is also a need to consider social sustainability that goes hand-in-hand with economic stability in Osage county. Ranching and oil and gas production are primary drivers of the economy in Osage county and most all of the populous of the county is directly or indirectly benefitting from one of

these industries. It only seems logical to work on protecting both of these cultures by devising improved and enforceable best management practices (BMPs) that will ensure cleaner and more sustainable oil and gas production as well as preserve property values and the productivity of these lands as agricultural enterprises.

An often overlooked aspect of oil and gas production in the tallgrass prairie is the impact that it has on wildlife that are unique to our ecosystem. In addition to the many mammals and aquatic species that we all enjoy the tallgrass prairie also supports a large population of grassland obligate bird species, both resident birds and migratory birds, as well as endangered species such as the American Burying Beetle. The tallgrass prairie acts as a travel corridor and has been identified as an area of importance for migratory birds as they move from their wintering grounds to their breeding grounds. Many of these migratory species also breed and nest here. However, with every pad site, road, power line, and pipeline that is associated with increased oil and gas exploration the available habitat for breeding, nesting, raising chicks, and wintering birds is decreased. The Greater Prairie Chicken is a species of concern that totally relies on the tallgrass prairie for its home range. Research conducted in Osage county from 2014-2016 (Londe et al. 2019) has shown that Greater Prairie Chickens have a strong propensity to avoid structures such as power lines, pump jacks, tank batteries, and roads and that increased oil and gas operations actually fragment the landscape and provide barriers that these birds avoid which only increases the rate at which their useable habitat is shrinking. Western Osage county represents that last of the unfragmented tallgrass prairie in the state of Oklahoma and therefore is home to what is likely the southernmost population of greater prairie chickens left in the world. As a species of concern for federal and state agencies as well as private landowners it would be a shame to blindly continue to fragment their habitat with increased oil and gas exploration and infrastructure. We propose an amendment be made to the DEIS to include an exclusion of further oil and gas development in areas of highest importance of habitat for the Greater Prairie Chicken. We propose that any area of importance of a 6 or higher from Figure 3-9 on page E-17 of the DEIS be excluded from any further development of oil and gas production to aid in preserving habitat for Greater Prairie Chickens. It's no coincidence that these areas within Osage county are also the most scenic tallgrass prairies left in Oklahoma. Enhanced protection in these areas would effectively protect valuable wildlife habitat, protect sight and sound pollution to these stunning areas, protect surface land and water from pollution, and protect the very last piece of unfragmented tallgrass prairie left in the state of Oklahoma which is important ecologically and economically to the tourism based in Oklahoma and Osage county.

As a ranching enterprise with a strong emphasis on conservation of the tallgrass prairie and the plants and animals that depend on it we are very concerned for the future of greater prairie chickens and other grassland bird species. It is also troubling to see the continual degradation of the tallgrass prairie from brine scars, water pollution, oil contamination, air quality reduction, and general human safety.

The tallgrass prairie is too important economically, socially, culturally, and environmentally to have such short sighted goals that we can't adequately preserve our natural resources within a sustainable and acceptable petroleum and gas extraction plan for Osage county.

Alternative concepts

- Include exclusion of areas of highest importance (6 or higher) of habitat for the Greater prairie Chicken from any further oil and gas development.
- COAs should be enforceable actions with consequences should they not be followed.
- COAs should be readily available to landowners to facilitate more straightforward dealings with oil producers.
- Oil companies and their associates should be required to execute surface damage agreements prior to entry on the property.
- There must be requirements for producers to remediate surface damages caused by oil and gas activities, and requirements to restore the land back to tall grass prairie once oil and gas operations on the lease have ceased.
- There must be enforceable limits and standards governing remediation of brine and petroleum contamination of soil and water.
- Include burying of power lines in the COAs to reduce the wildfire potential and have less intrusion in to areas of importance for greater prairie chickens.
- Include burying of oil and water flow lines in the COAs to reduce the risk of unnecessary leaks.

Conclusion

It is time for the BIA to step up and be a leader in the campaign to protect ALL natural resources in Osage county. For too long there has been a lack of oversight and enforcement of already existing rules for oil and gas exploration and production coupled with a lack of inclusion with landowners and it has created an environment of confusion and frustration for landowners attempting to protect the natural resources. Many landowners representing hundreds of thousands of acres in Osage county are making an effort to preserve their part of the tallgrass prairie ecosystem as a viable business, a home to their families, an oasis for wildlife populations, and a cultural and social model for conservation in today's society. In an effort to protect the natural resources of Osage county great care needs to be taken to ensure the long term sustainability of the people, the land, and wildlife that inhabit the tallgrass prairie. We support the adoption and implementation of **Alternative 4** from the DEIS with further enhanced protection for areas of importance for Greater Prairie Chickens.

Sincerely,

Brody Wallis

Brody Wallis
Osage Buck Creek LLC

Literature Cited

Londe, D.W., S.D. Fuhlendorf, R.D. Elmore, C.A. Davis, J. Rutledge. 2019. Female Greater Prairie-Chicken response to energy development and rangeland management. Ecosphere 10(12):e02982.

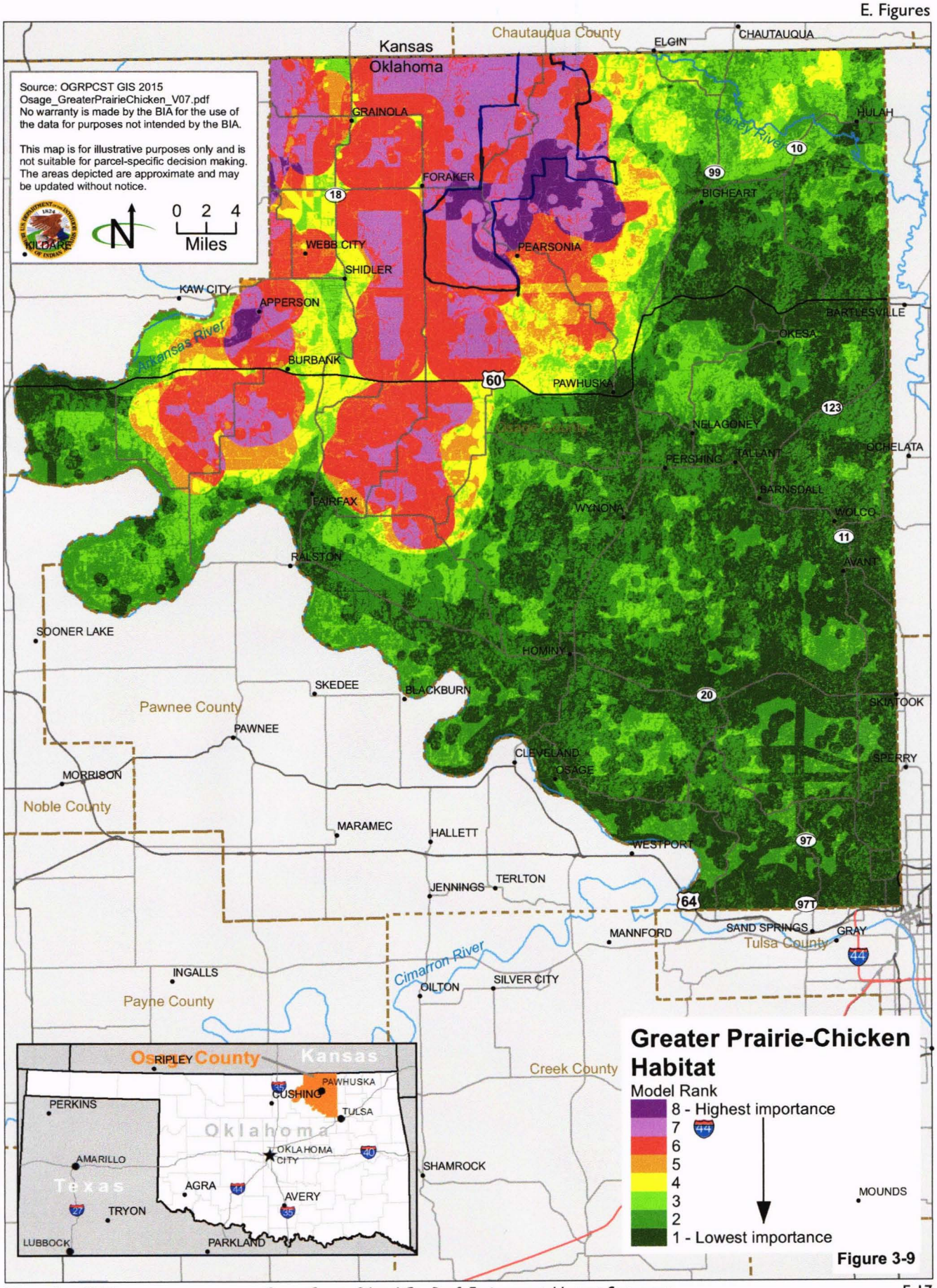
Source: OGRPCST GIS 2015
Osage_GreaterPrairieChicken_V07.pdf
No warranty is made by the BIA for the use of the data for purposes not intended by the BIA.
This map is for illustrative purposes only and is not suitable for parcel-specific decision making. The areas depicted are approximate and may be updated without notice.
0 2 4
Miles
Kansas
Oklahoma
Chautauqua County
ELGIN
CHAUTAUQUA
GRAINOLA
HULAH
Caney River
FORAKER
BIGHEART
WEBB CITY
PEARSONIA
SHIDLER
KAW CITY
APPERSON
BARTLESVILLE
OKESA
Arkansas River
BURBANK
PAWHUSKA
NELAGONEY
OCHELATA
PERSHING
TALLANT
BARNSDALL
FAIRFAX
WYNONA
WOLCO
RALSTON
AVANT
SOONER LAKE
HOMINY
SKEDEE
BLACKBURN
Pawnee County
SKIATOOK
PAWNEE
CLEVELAND
OSAGE
SPERRY
MORRISON
Noble County
MARAMEC
HALLETT
WESTPORT
JENNINGS
TERLTON
MANNFORD
SAND SPRINGS
GRAY
Tulsa County
Cimarron River
INGALLS
OILTON
SILVER CITY
Payne County
Creek County
SHAMROCK
MOUNDS
Greater Prairie-Chicken Habitat
Model Rank
8 - Highest importance
7
6
5
4
3
2
1 - Lowest importance
Osage County
RIPLEY
Kansas
PAWHUSKA
CUSHING
TULSA
PERKINS
Oklahoma
OKLAHOMA CITY
AMARILLO
Texas
AGRA
AVERY
TRYON
LUBBOCK
PARKLAND

Figure 3-9

esa ECOSPHERE

Female Greater Prairie-Chicken response to energy development and rangeland management

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Abstract. Wildlife habitat use is the result of behaviors that occur at multiple spatial and temporal scales. The interactions between these behaviors can often result in complex patterns of selection that can make it challenging to select the most appropriate scale to implement management actions. Greater Prairie-Chickens (*Tympanuchus cupido*), a declining grassland grouse species, face many conservation challenges throughout its distribution, including increased fragmentation from anthropogenic activities (e.g., energy development and altered disturbance regimes). However, much of the literature on this species has focused on a narrow portion of its lifecycle, specifically the breeding season. We examined habitat use of female Greater Prairie-Chickens in a grassland that is managed with prescribed fire and grazing and that has also undergone considerable development for oil and gas production. We developed discrete choice models for four behaviorally distinct life-history stages and two spatial scales to evaluate how rangeland management, energy development, and scale influence habitat use throughout the annual cycle. Additionally, we used cumulative distribution functions to determine response distances to landscape features. We found that time since fire, proximity to woodlands and proximity of lek sites were the most consistent predictors of habitat use during most periods and spatial scales. Greater Prairie-Chickens consistently avoided woodlands and remained relatively close to lek sites during all parts of the year. Selection of time since fire varied through the year with Greater Prairie-Chickens primarily using unburned patches in the lekking and nesting season and recently burned patches in the post-nesting and nonbreeding season. Greater Prairie-Chickens demonstrated a seasonally variable response to energy development, avoiding power lines and areas with a high densities of oil wells by as much as 300–600 m in the lekking, post-nesting, and nonbreeding season. Management actions that promote vegetation 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.

Key words: avoidance; energy development; greater prairie-chicken; landscape heterogeneity; oil development; scale; tallgrass prairie.

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Introduction

Effective management of wildlife species in human-modified landscapes requires a thorough understanding of how spatiotemporal patterns influence a species resource needs and response to its environment (DeCesare et al. 2012, McGarigal et al. 2016). Habitat selection is often considered the result of a series of hierarchal decisions and behaviors that result in a nested pattern with

smaller resource units nested within larger units (Kolasa and Waltho 1998). This nested pattern can make selecting the most appropriate scale to manage a species difficult, as management actions may occur at scales that differ from the scale at which a species responds to its environment (Fuhlendorf et al. 2002, Long et al. 2008). These patterns can be further complicated as individuals transition between life stages, and habitat requirements change as a result of seasonal differences in behavioral patterns, energetic needs, or resource availability (Beier and McCullough 1990, Levin 1992, Aldridge and Boyce 2007, Long et al. 2008). Understanding the role of scale in habitat selection and how these relationships shift across life stages is critical for making sound management decisions. Failing to account for these sources of variation can potentially result in ineffective management practices (Bowyer and Kie 2006).

The Greater Prairie-Chicken (*Typmanuchus cupido*; hereafter, prairie-chicken) is a North American grassland grouse species that has undergone substantial distribution and population declines over the last century and is considered vulnerable by the International Union for Conservation of Nature (Svedarsky et al. 2000, Johnson et al. 2011). Due to the prairie-chicken's large annual home range and dependence on intact grasslands containing a range of vegetation structures necessary to meet all of its life stages (e.g., short stature vegetation for leks [communal courtship displays], dense vegetation for nesting), prairie-chickens are highly sensitive to anthropogenic alterations of grasslands. Both local-scale activities, such as fire and grazing, and landscape-level factors, such as fragmentation from agriculture or anthropogenic infrastructure, can have significant impacts on habitat selection, demographics, and site occupancy of prairie-chickens (Gregory et al. 2011, McNew et al. 2012, 2013). Due to their high conservation value and specific habitat needs, prairie-chickens are an ideal species for evaluating the role spatial and temporal patterns play in habitat selection, particularly in relation to two of the most significant conservation challenges for grasslands, altered disturbance regimes, and fragmentation from human development (Svedarsky et al. 2000, Robbins et al. 2002, Pruett et al. 2009, Fuhlendorf et al. 2017).

Grassland management can have a significant influence on the availability of resources for prairie-chickens (Robbins et al. 2002, McNew et al. 2012, Winder et al. 2017*a*), and management strategies which emphasize the creation of structural heterogeneity have been proposed as a conservation strategy for grassland birds including prairie-chickens (Fuhlendorf et al. 2006). Heterogeneity-based strategies restore structural variation in grasslands through burning portions of the landscape and allowing herbivores to preferentially graze recently burned patches while leaving areas unburned and lightly grazed for one or more years (Fuhlendorf and Engle 2001). As a result, these grasslands are composed of patches of different vegetation structures that are important for prairie-chickens to complete their different life stages (e.g., leks, brood-rearing, and nesting; McNew et al. 2015). While these practices have been in use for some time, they only recently have been put forward as an alternative to traditional management practices that often simplify disturbance regimes and result in structurally homogeneous grasslands (Fuhlendorf and Engle 2001). Understanding prairie-chicken use of heterogeneous grasslands is critical for identifying important resources required throughout their lifecycle, as well as potentially identifying factors that shape prairie-chicken response to other anthropogenic activities in grasslands (Winder et al. 2017*b*).

In addition to altered disturbance regimes, energy development is increasing in many grassland systems (McDonald et al. 2009), which has the potential to affect biodiversity in these systems (Sawyer et al. 2006, Aldridge and Boyce 2007, Northrup and Wittemyer 2013, Jones et al. 2015). Prairie-chickens and other grouse species have been shown to be highly susceptible to energy development (Hovick et al. 2014*a*). In addition to direct mortality of grouse from collisions with some types of infrastructure (Wolfe et al. 2007, Zeiler and Grunschachner-Berger 2009), many grouse species also avoid or are displaced by energy infrastructure (Aldridge and Boyce 2007, Hovick et al. 2014*a*, Winder et al. 2014*b*). Research on prairie-chicken response to energy development has focused primarily on wind energy and has shown that response to development is influenced by time of year, and the type of infrastructure (Winder et al. 2014*a*,

2014*b*, 2015). At present, there are relatively few studies investigating prairie-chicken response to other types of energy development such as oil and gas (Hovick et al. 2015*b*). As many parts of the prairie-chicken's distribution are expected to experience continued fragmentation from development, understanding the factors that determine prairie-chicken response to energy development will be critical for guiding future development as well as potential mitigation approaches.

In order to better understand the importance of spatial scale and temporal patterns in shaping the response of prairie-chickens to anthropogenic activities and energy infrastructure, we examined habitat use of prairie-chickens in a grassland landscape that is managed for heterogeneity through the application of fire and grazing and has been developed for oil and gas production. Our objective was to identify patterns of use or avoidance of different landscape features including time since fire patches and oil and gas infrastructure by female prairie-chickens and to determine how these patterns of selection may change through time and across spatial scales. In order to accomplish this objective, we used locations from Global Position System (GPS) transmitters deployed on adult female prairie-chicken to evaluate habitat use during four behaviorally distinct life-history stages: lekking, nesting, post-nesting, and the nonbreeding periods. We focused on female prairie-chickens in this study as decisions about habitat selection by females can influence nest and reproductive success which can in turn influence population dynamics (Boyce and McDonald 1999). We used resource selection functions to determine the relative importance of different factors for prairie-chicken habitat selection and cumulative distribution functions (CDFs) to estimate the distance that prairie-chickens either avoided or were attracted to features related to oil and gas infrastructure. Our study aims to identify how female prairie-chickens interact with a multi-use grassland and improve our understanding of the spatial ecology of a species of conservation concern.

Study Site

Our study took place on several private properties in Osage County, Oklahoma, including The Nature Conservancy's Tallgrass Prairie Preserve, from 2014 to 2016. The study site is located in the southernmost extent of the Flint Hills Ecoregion, which contains some of the largest remaining intact tracts of tallgrass prairie (With et al. 2008). The 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*), switchgrass (*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.

Energy development at our study site primarily consisted of traditional pump jack style oil wells powered by both electrical power lines and on-site generators. Most wells were approximately 6–8 m tall, but a few contained taller structures. A single 138-Kv transmission line is located on the southern edge of the study site, but few of the satellite-marked prairie-chickens encountered this structure over the course of this study, and thus, our study focused on the shorter electrical distribution lines (both 7.2 and 14.4 kV lines) that were typically about 10 m in height. The density of features associated with energy development at the study site was 0.41 km of power lines per km^2, 0.33 km of county roads per km^2, and 0.98 oil wells per km^2 with oil well density ranging from 0 to 14 wells per km^2.

Our study site is managed for heterogeneity using prescribed fire and grazing. In general, fire is applied on a rotational basis where only a portion of the landscape is burned annually, leaving the remainder of the landscape unburned. Approximately, 51%, 42%, and 45% percent of the study area was burned in 2014, 2015, and 2016, respectively. The average size (±1 SE) of prescribed burns was 227.5 ha (13.5), with prescribed burns ranging from 20 ha to 1125 ha. Burn patches were distributed throughout the 35,098-hectare study area and were intermixed with patches that were left unburned in a given year resulting in a mosaic of different vegetation structures across the landscape. The majority of prescribed fires took place in the spring (March–May) before the start of the growing season. The

fire return interval was approximately 2–4 yr, and due to the extensive use of prescribed fire, nearly the entire field site had been burned within the preceding 4–5 yr of our study, with relatively few patches having been unburned for longer periods. We monitored prairie-chickens primarily on privately owned land that is managed for livestock and grazed seasonally with cattle. However, one property included a single pasture that was grazed year-round with bison (*Bison bison*). Stocking rates are light to moderate throughout the area (2–2.5 AUM/ha). Cattle and bison are allowed to graze on burned areas of the pastures preferentially.

Methods

Capture and monitoring Prairie-Chickens

We captured prairie-chickens on leks between mid-March and late-April using standard walk-in funnel traps (Schroeder and Braun 1991). We aged and determined gender for each captured prairie-chicken based on plumage and secondary sex characteristics (Henderson et al. 1967). We marked all captured prairie-chickens with uniquely numbered metal leg bands and equipped females 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 m. From 1 March to 31 August, 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 (1 September to 28 February), we programmed transmitters to collect one location approximately every two hours from 6:00 to 19:00 and two nocturnal locations at 0:00 and 1:00. We monitored hens remotely by downloading GPS locations from the ARGOS server as data became available. We only included females in the subsequent analysis due to the limited number of locations from males at our study site.

We monitored female locations daily during the spring for nesting activity using GPS satellite locations. Once a female's activity became localized to a small area for three or more days, we located nests by ground searching the area corresponding to the transmitter error around GPS points where the female had localized. We flushed females only once during the incubation period to record clutch size and the Universal Transverse Mercator coordinates of the nest. To determine nest fate, we only revisited a nest after the female was determined to have departed the nest based on GPS locations.

We separated prairie-chicken locations into four behaviorally distinct periods (lekking, nesting, post-nesting, and nonbreeding seasons) to account for changes in resource use throughout the year. Individuals could transition between periods independently, resulting in considerable temporal overlap for some periods among individuals (e.g., some individuals can begin and end the nesting period sooner or later than others depending on nest initiation and failure dates). The lekking period began on 15 March of each year, corresponding to the earliest date hens begin attending leks, and ended when an individual began incubating a nest. We defined the nesting period as the period from the start of nest incubation for each hen to when each nest hatched or failed. We only used nest locations for analysis during the nesting period. The post-nesting breeding season encompasses all locations after a hen's nest hatched or failed until 14 September, which corresponds to the approximate timeframe the last broods were breaking up for the fall/winter season. Preliminary analysis revealed little difference in habitat selection between hens with and hens without broods, so all hens were pooled during the period for the final analysis. The nonbreeding season encompassed the remainder of the year (15 September–14 March) and included all nonbreeding activities.

Acquisition of GIS data

For each year of the study, we developed habitat variables related to grassland management, energy development, and the environment for the lekking, nesting, post-nesting, and nonbreeding season (Table 1). We determined the timing and distribution of prescribed fires and wildfires from GIS (geographic information systems) layers acquired from land managers on properties where we tracked prairie-chickens. To measure the use of different vegetation patches that result from fire and grazing, we converted time since fire layers into four discrete categories: 0–12 months since fire, 13–24 months since fire,

Table 1. Explanatory variables used to model habitat use of Greater Prairie-Chickens during the lekking, nesting, post-nesting, and nonbreeding seasons in Osage County, Oklahoma, between 2014 and 2017

Covariate	Description
Energy development	
Oil well	Distance to nearest active well pad or tank battery
Power line	Distance to the nearest power line
Road	Distance to the nearest primary road
Oil density	The number of wells within a specified buffer around a point. The buffered areas start at 1 km^2 and increase by 0.5 km^2 up to 5 km^2
Grassland management	
Time Since Fire (TSF)	Categorical variable for time since fire measured in 12-month intervals
tsf-0–12	Patches 0–12 months post-fire. Reference category during analysis
tsf-13–24	Patches 13–24 months post-fire
tsf-25–36	Patches 25–36 months post-fire
tsf->36	Patches >36 months post-fire
Distance to patch edge	Distance to the nearest edge between two time since fire patches
Environmental	
Lek	Distance to lek where a hen was captured or likely bred in a season
Woodlands	Distance the nearest woodland patches >0.5 ha
Elevation	Absolute distance above sea level in meters
Slope	Measured in degrees values range from 0 to 90
Topographic Position Index (TPI)	Relative landscape location within a neighborhood with a 400-meter radius. Values range from −1 to 1 (−1 = drainage or valley, 1 = ridge or hilltop).

25–36 months since fire, and patches that were >36 months since fire. All time since fire categories >36 months post-fire were combined due to their relatively limited availability, and the fact that previous research at our study site has shown that biomass accumulation generally plateaus after 36 months resulting in structurally similar patches (Fuhlendorf et al. 2006, 2009). We used the 0- to 12-month category as the reference category in subsequent analyses (Therneau 2015), meaning the estimated use of the remaining patches is relative to the use of patches 0–12 months post-fire. We selected the 0- to 12-month category as our reference level because this is the most common time since fire on the landscape due to the extensive use of prescribed fire as a management tool in the Flint Hills Ecoregion (Robbins et al. 2002). Additionally, as the distance to the edges of time since fire patches have been shown to be an important variable for prairie-chicken habitat use in other studies (Patten et al. 2007, Hovick et al. 2015*a*), we calculated the Euclidian distance to the nearest time since fire patch edge across the landscape for each year.

We manually digitized the location of all oil facilities (pump jacks, gas wells, and tank batteries), power lines, county roads from the National Agricultural Imagery Program (NAIP), acquired in 2015, and GIS layers were updated based on landowner and county records in addition to being ground-truthed in 2015 and 2016. We log-transformed all distance variables to model the decreasing effect of a feature with increasing distance (Dzialak et al. 2012). Additionally, we calculated the density of oil wells, power lines, and roads at a prairie-chicken locations at multiple scales. We measured the density by buffering a prairie-chicken location and dividing the number of wells or length of road or power lines by the area of the buffer. Buffers ranged from 100 to 500 ha, increasing incrementally by 50 ha (Plumb et al. 2019). However, as all three density measurements were highly correlated (Pearson's $r > |0.7|$), we only considered density of oil wells during model development.

Additionally, we measured a number of environmental variables that are known to influence grouse habitat use. We calculated absolute elevation and slope using a 10-meter resolution digital elevation map (U.S. Geological Survey 2015). We calculated the Topographic Position Index (TPI) across the landscape by dividing the elevation at each cell by the average elevation of all cells within a 400-meter neighborhood. TPI maps ranged from −1 to 1 with sites with TPI values close to 1 representing ridges or high points and sites with TPI values close to −1 representing low points or valleys (Guisan et al. 1999). We manually digitized all patches of continuous woodlands >0.5 ha using aerial imagery from the NAIP acquired in 2015. Similar to development variables, we log-transformed distance to trees. Tree cover was the only additional vegetation or land cover metric considered as our study site is composed of a relatively continuous grassland,

with few other cover classes outside of areas developed for oil and gas and the crosstimber woodlands. Further, time since fire and grazing are the primary drivers of vegetation structure and composition at our study site so we felt that the use of the time since fire covariates and a single cover class for woodlands would sufficiently capture broad-scale variation in the plant community (Fuhlendorf et al. 2006, Hovick et al. 2015*c*).

Discrete choice models

We used discrete choice models to evaluate prairie-chicken resource use during the lekking, nesting, post-nesting, and nonbreeding seasons. Discrete choice models assume selection is the result of a decision between a finite set of habitat units that are available to an individual at a given time (i.e., choice set). In this study, we defined a choice set as three random locations and one used location. We chose to use discrete choice analysis because it allows the resource units available to an individual to change with time, which was necessary to account for the 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 our analysis using Cox proportional hazard mixed models, where lek sites were included as a random intercept using the COXME package in program R (Therneau 2015, Brooke et al. 2016). In this analysis, we presumed that individual responses to landscape features would be uniform, and thus examined population-level responses to landscape features. This corresponds to a type I resource selection study as defined by Thomas and Taylor (2006). However, we used lek sites as a random variable to account for the fact that individuals have strong fidelity to their lek sites, and there may be variation in habitat conditions around individual leks that may not be included in our models. For all models, we performed a likelihood ratio test to determine whether a random effect improved model fit over a fixed effect only model.

We analyzed prairie-chicken resource use at two scales that correspond to the second-order and third-order selection as defined by Johnson (1980). For second-order selection (e.g., selection of home ranges into the broader landscape), we defined availability as a circular buffer around each used location with radii corresponding to the average cumulative distance moved by an individual in a 24-h period for each period (lekking = 1755 m, post-nesting = 905 m, nonbreeding = 1755 m; Boyce et al. 2003). We defined a choice set for second-order selection as a single used point and three random points drawn from within the circular buffer associated with that used location. For availability at the third-order scale of selection (e.g., selection within a home range), we selected choice sets from within an individual's home range for the lekking, post-nesting, or nonbreeding period. We calculated home ranges using Brownian bridge movement models (BBMM; Horne et al. 2007) using the BBMM package in program R (Nielsen et al. 2013). We used 99% home ranges to capture the entire extent of an area used by prairie-chickens (Plumb et al. 2019).

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. 2015*b*). Based on previous literature that found that the majority of nests occur within 2 km of lek sites (McNew et al. 2013, Hovick et al. 2015*b*), we selected available locations from a 2-kilometer buffer around lek sites.

Model development

As we considered 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 correlated variables ($r > |0.70|$) were excluded from the same model.

Based on the literature, we separated habitat variables into four groups representing environmental variables, grassland management (i.e., time since fire), oil well density variables, and proximity to energy development variables

(Table 1; Hovick et al. 2015*a*, 2015*b*, Winder et al. 2014*b*, 2017*b*). To account 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 then 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 whether grassland management, proximity to energy development, and density of oil wells influenced prairie-chicken habitat use, we added each variable from these three suites to the best-supported environmental model for each period. We considered variables as influencing selection if they substantially improved model fit (models performed better than 2 AICc units than the base environmental 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 and grassland management-related 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 90% confidence intervals that did not overlap zero.

We calculated the 90% confidence intervals using bootstrap methods that treated the individual as the sampling unit (Manly et al. 2002). By resampling the population at the individual level and using a higher value of α (0.1), we attempted to account for non-independence among choice sets within individuals and provide more conservative estimates of habitat selection. To calculate the bootstrap confidence intervals, we randomly resampled with replacement choice sets associated with individual prairie-chickens and refitted the top model for each scale and period 500 times (Manly et al. 2002). We then calculated percentile confidence intervals from the resulting distribution of the coefficients estimated from the bootstrap sample distribution.

Model validation

To evaluate model fit, we performed k-fold cross-validation using methods described by Boyce et al. (2002) by randomly assigning each choice set (one used location and three associated available locations) to 10 equal-sized groups. For each iteration, we withheld one group as a test set and refitted the top model for each scale and period with the remaining nine training sets. Using the coefficients estimated from the training sets, we predicted the probability of use for used locations in the test group. We divided the resulting predictions into ten equal-sized classes based on percentiles, with class 1 having the lowest probability of use and class 10 having the highest probability of use. We then compared the number of used locations in each class to the class rank using Spearman's rank correlation coefficient (r_s). We repeated this procedure for all ten validation sets, and the average Spearman's rank coefficients from the ten iterations are presented for the top model for each scale and period.

We generated predictive surfaces for the average prairie-chicken in each season for the two scales of selection to visualize the results of the discrete choice analysis. We placed a 90 × 90 m grid over the study area and calculated the probability of use for each cell from the covariates of the top model in each season and scale. As the distribution of time since fire patches changes from year to year, we used prescribed fire data from 2015 to generate maps. Weather and habitat variables were uniform throughout the study period, so we selected 2015 to make predictions as this was the midpoint of our study. We then classified relative use into five quantiles ranging from lowest predicted use to the highest predicted use.

Thresholds of avoidance

We used CDFs to determine prairie-chicken response thresholds to oil and gas infrastructure. Cumulative distribution functions provide a graphical method of evaluating selection–neutral–avoidance behavior with continuous variables and large data sets (Dunkin et al. 2009, Tanner et al. 2015) and are conceptually similar to Manly's selection ratios (Manly et al. 2002). Specifically, CDFs allow for thresholds of selection/avoidance to be determined through the interpretation of the shape of the distribution function. Selection behaviors relative to features on the landscape can be described by subtracting the relative cumulative frequency of the observed relocations ($G[x]$) from the cumulative frequency of randomly distributed points ($F[x]$) over the same study area ($G[x]$)-$F[x]$; Dunkin et al. 2009).

This method provides a graphical index of selection behavior as the slope of the resulting curve describes how the distribution of animal relocations differs from if an animal's locations were distributed randomly relative to features on the landscape. For example, a negative slope (slope < 0) indicates an avoidance as random points are accumulating faster than observed relocations over a specified distance. Similarly, if the slope is positive (slope > 0), random points are accumulating slower than observed points, suggesting there are more animal locations within a given distance from a feature than would be expected if relocations were randomly distributed across the landscape.

To test for avoidance thresholds for different types of infrastructure throughout the year, we calculated separate CDFs for each infrastructure type during each biological period and determined at what point response to a feature changes based on where the slope of the CDF curve changed. To ensure our estimates were comparable to the discrete choice analysis, we used a similar definition of availability for each biological period to draw random locations for the CDF analysis. This was done by merging the circular buffers used to define available for the second-order discrete choice models to create a single polygon that encompassed the same spatial extent for each biological period. We choose to only compare the results of the CDF analysis to the second-order discrete choice models, because we felt the broader definition of available for the second-order models was more appropriate for estimating landscape-level avoidance thresholds compared to the narrower definition of available used for the third-order discrete choice analysis. For each season, we generated three random points for every prairie-chicken location within the availability polygon and calculated the Euclidian distance (m) from random and used locations to the closest oil well, power line, and road. For the lekking, post-nesting, and nonbreeding seasons, we calculated the $(G[x]-F[x])$ function based on prairie-chicken and random locations for every 50-m interval (0–49.999 m, 50–99.99 m, etc.). Due to our small sample size of nest sites, we used 100-m intervals for the nesting season CDF analysis to reduce the number of distance bins with no recorded prairie-chicken nests. We repeated this process thirty times for each structure in a season and took the mean CDF value for each distance interval to create an average CDF curve (Martin et al. 2012, Tanner et al. 2015).

To estimate the location of avoidance thresholds, we used segmented linear regression to estimate the approximate point at which the slope of the CDF curve changes. Segmented regression allows the relationship between a response variable (CDF value) and an explanatory variable (distance to feature) to be described by two or more linear segments that are connected at one or more change points (Muggeo 2008). We classified the response of female prairie-chickens to development based on the slope of the first linear segment, with negative slopes indicating avoidance, positive slopes indicating an attraction, and slopes with confidence intervals that included 0 as showing no response. In cases where female prairie-chickens were determined as either avoiding or being attracted to a feature, we used the change point and associated confidence intervals to estimate the approximate distance at which a prairie-chicken's response to a structure type changed. As our interest was specifically in identifying prairie-chicken response thresholds to different landscape features, we restricted the interpretation and discussion of CDF curves to the initial shape of the curve near the feature and not subsequent fluctuations in response direction.

As CDF models are relatively new in the literature, we validated the threshold estimates from the CDF curves using a procedure analogous to segmented regression to estimate avoidance thresholds within the context of a resource selection framework (Boulanger et al. 2012). To estimate avoidance thresholds for each type of infrastructure during each period, we created a suite of new threshold variables where we set all distances greater than or equal to the predicted threshold as equal to the threshold value. For example, to test for a threshold at 500 m from power lines, we set all distances >500 m from power lines as equal to 500 m. To determine the optimal threshold value for each structure in a biological period, we created a threshold variable for every 50-meter increment between 50 and 1000 m. The individual threshold variables were then added to the top model for each period, and models with threshold variables were then

ranked using AICc. The threshold variable contained in the model with the lowest AICc was considered the best for describing prairie-chicken response to an infrastructure type. We only performed this analysis using models based on the second-order level of selection to ensure our results were comparable with the CDF analysis.

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-nesting period, and 23 individuals to the nonbreeding season analyses. These individuals contributed 805, 2619, and 3674 GPS locations to the lekking, post-nesting, and nonbreeding analyses, respectively. We included 38 nests (33 first attempts and five renests) in the nest-site selection analysis. Nest success was 48% and 40% for first attempts and renests.

Habitat selection

The spatial scale and biological period influenced the results of the discrete choice analysis, with different variables being selected as important, resulting in different levels of predicted use across the landscape in each season and scale (Fig. 1). The top models for second-order selection (availability defined by circular movement buffers) typically differed from models describing third-order selection (availability defined by individual's home ranges) in the same period by the addition of one or more variables typically related to oil and gas development. Through most periods and scales, female prairie-chickens showed a consistent attraction to lek sites, selected high values of Topographic Position Index (TPI) and elevation while avoiding wooded areas (Fig. 1; Tables 2–5). Distance to oil wells and density of oil wells were highly correlated for all periods and scales ($r \geq |0.7|$), so we only considered these variables in separate models.

Lekking period.—The environmental model for the lekking period at the second-order scale included distance to woodlands, distance to associated lek, TPI, and elevation (Table 2). The inclusion of power lines and time since fire offered a substantial improvement over the environmental model for this period (ΔAICc = 40.95). Prairie-chickens used all time since fire patches that were >13 months post-fire more than patches 0–12 months post-fire at the second-order level (Table 2). Additionally, prairie-chickens showed an avoidance of power lines during this period (β = 0.13, 90% CI = 0.064–0.19). The second-best model for this period and scale contained only the environmental variables and time since fire (ΔAICc = 4.58).

The environmental model for the third-order level of selection during the lekking period contained elevation, and TPI (Table 2). The addition of time since fire and distance to oil wells resulted in substantial improvements over the environmental model (ΔAICc = 12.72). Similar to the model for second-order availability, prairie-chickens used all patches that were >13 months post-fire more than recently burned areas (0–12 months post-fire; Table 2). Additionally, the probability of use increased in areas of prairie-chicken home ranges that were relatively close to oil wells (β = −0.20, 90% CI = −0.31 to −0.09; Table 2). The next best performing model contained only elevation, TPI, and time since fire (ΔAICc = 6.9).

The model describing availability at the second-order selection performed well with new data during cross-validation (average r_s = 0.89), while the model for third-order selection did not have as high of predictive power for this period and should be interpreted with caution (r_s = 0.6). Further, the two models differ in how they suggest female prairie-chickens respond to oil and gas infrastructure with the second-order model showing avoidance of power lines and the third-order model showing an attraction to oil wells.

Nest-site selection.—The top model describing prairie-chicken nest-site selection contained the variables time since fire, distance to woodlands, and Topographic Position Index (Table 3). Similar to the lekking period, female prairie-chickens avoided woodlands (β = 0.78, 90% CI = 0.53–2.04) and preferred to use area with high TPI (β = 3.82, 90% CI = 0.45–8.28) when selecting nest sites. Female prairie-chickens showed a trend toward using patches >13 months post-fire for nest sites compared to recently disturbed patches, with nests preferentially being placed in patches 25–36 months post-fire and patches >36 months post-fire (Table 3). The inclusion of

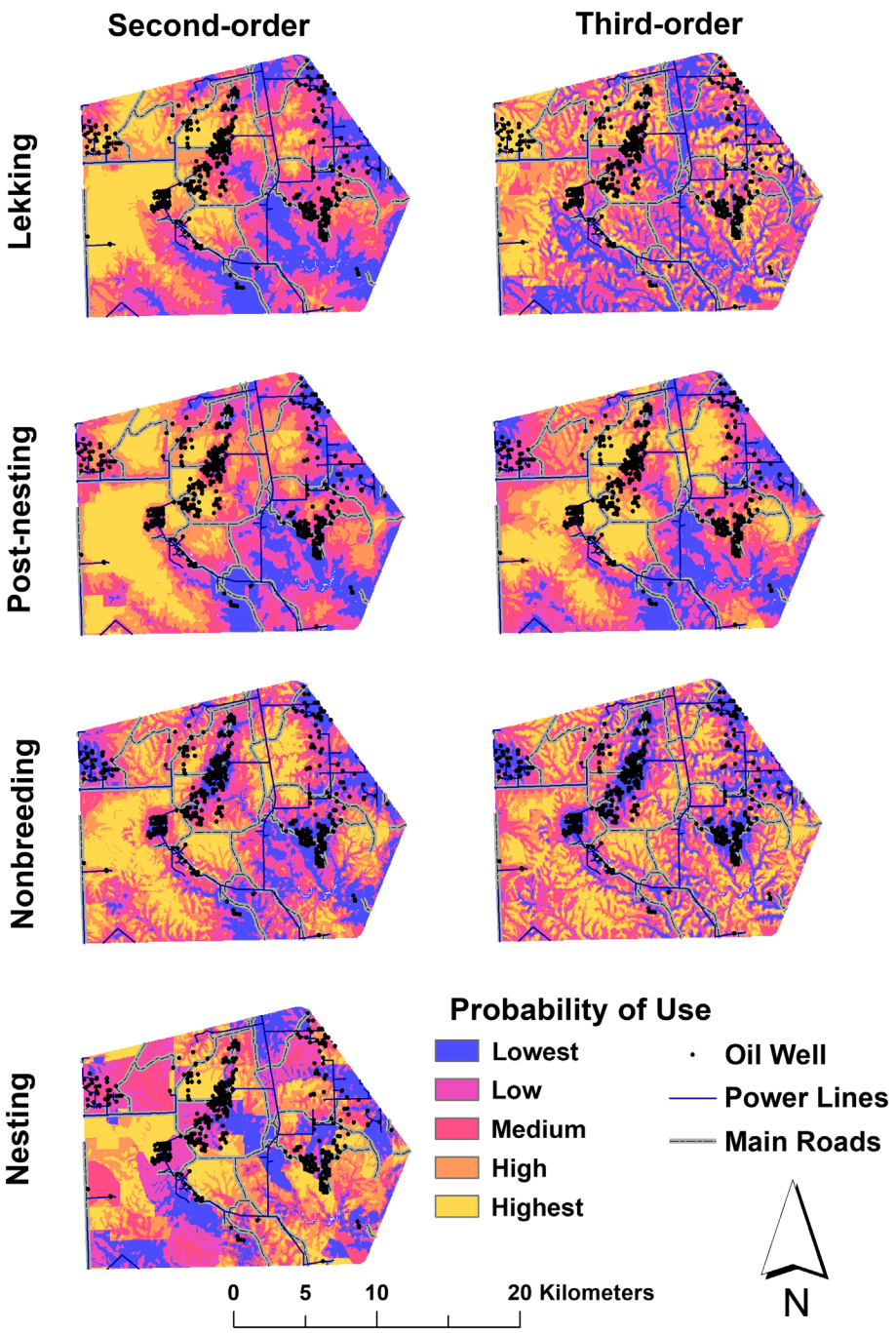

Fig. 1. Predicted probability of use by Greater Prairie-Chickens during four behavioral periods at two spatial scales in Osage County, Oklahoma, between 2014 and 2016. Predictive surfaces for each season were derived from beta coefficients from separate discrete choice models for each scale and period. The availability at the second-order scale was based on circular movement buffers (equal to the average cumulative daily distance moved in a period) around individual locations, while available at the third-order scale was based on actual home ranges of individual Greater Prairie-Chickens.

Table 2. Beta coefficients, odds ratios, standard errors, and confidence intervals for lekking period models describing availability at the second-order selection (based on movement-based buffer) and third-order selection (within home range selection) for Greater Prairie-Chickens monitored in Osage County, Oklahoma, between 2014 and 2016

Habitat variable	β	Hazard ratio	Standard error	90% CI	
				Lower	Upper
Second-order					
Distance to Lek	−0.32	0.72	0.07	−0.42	−0.25
Distance to woodland	0.72	2.05	0.14	0.495	0.94
Topographic Position Index	1.99	7.32	0.42	1.38	2.66
Elevation	0.022	1.02	0.005	0.015	0.03
Power lines	0.13	1.14	0.05	0.064	0.19
Time Since Fire†					
0–12 months post-fire	0				
13–24 months post-fire	0.55	1.73	0.14	0.31	0.76
25–36 months post-fire	1.08	2.94	0.19	0.80	1.36
>36 months post-fire	0.30	1.36	0.14	0.096	0.47
Third-order					
Topographic Position Index	1.94	6.94	0.39	1.36	2.61
Elevation	0.006	1.01	.003	0.001	0.01
Distance to oil wells	−0.20	0.82	.063	−0.31	−0.09
Time since fire†					
0–12 months post-fire	0				
13–24 months post-fire	0.61	1.84	0.15	0.37	0.82
25–36 months post-fire	0.41	1.50	0.18	0.098	0.75
>36 months post-fire	0.29	1.34	0.16	0.06	0.56

† Beta coefficients interpreted relative to the reference category 0–12 months post-fire.

time since fire provided a substantial improvement over the environmental model that contained TPI and distance to woodlands (ΔAICc = 12.47). The model containing distance to associated lek was also competitive with the top model (ΔAICc = 0.89); however, the 90% confidence intervals for distance to lek overlapped zero (β = −0.59, 90% CI = −1.62–0.26). Results from model validation for nest sites suggested that the top model only had moderate predictive value (r_s = 0.44). However, this may be in part due to our small sample size (38 nests), which may have resulted in high variance in prediction results for test data sets during cross-validation.

Post-nesting period.—The environmental model for the second-order during the post-nesting period contained TPI, elevation, distance to associated lek, and distance to woodlands (Table 4). The addition of time since fire resulted in a

Table 3. Beta coefficients, odds ratios, standard errors, and confidence intervals for nest-site selection model for Greater Prairie-Chickens monitored in Osage County, Oklahoma, between 2014 and 2016

Habitat variable	β	Hazard ratio	Standard error	90% CI	
				Lower	Upper
Topographic Position Index	3.82	45.63	2.19	0.45	8.28
Distance to woodlands	0.78	2.184	0.38	0.53	2.04
Time Since Fire†					
0–12 months post-fire	0				
13–24 months post-fire	3.48	32.42	1.94	1.81	22.04
25–36 months post-fire	4.53	92.96	2.04	2.64	38.08
>36 months post-fire	4.60	99.62	1.97	2.97	37.11

† Beta coefficients interpreted relative to the reference category 0–12 months post-fire.

Table 4. Beta coefficients, odds ratios, standard errors, and confidence intervals for the post-nesting period models describing availability at the second-order selection (based on movement-based buffer) and third-order selection (within home range selection) for Greater Prairie-Chickens monitored in Osage County, Oklahoma, between 2014 and 2016

Habitat variable	β	Hazard ratio	Standard error	90% CI	
				Lower	Upper
Second-order					
Distance to Lek	−0.11	0.90	0.05	−0.18	−0.05
Distance to Woodlands	0.89	2.45	0.17	0.72	1.07
Topographic Position Index	1.05	2.86	0.24	0.71	1.41
Elevation	0.03	1.03		0.02	0.03
Oil Well Density (1.5 km^2)	−0.15	0.86	0.05	−0.18	−0.12
Distance from Power Lines	0.43	1.54	0.05	0.36	0.51
Distance to Primary Road	0.06	1.06	0.03	0.03	0.09
Time Since Fire†					
0–12 months post-fire	0				
13–24 months post-fire	−1.08	0.34	0.09	−1.23	−0.94
25–36 months post-fire	−0.69	0.50	0.11	−0.84	−0.54
>36 months post-fire	−1.25	0.29	0.13	−1.46	−1.04
Third-order					
Distance to Lek	−0.49	0.61	0.03	−0.55	−0.43
Distance to Woodlands	0.31	1.36	0.08	0.19	0.44
Topographic Position Index	1.46	4.32	0.16	1.22	1.69
Distance from Power Lines	0.19	1.21	0.03	0.14	0.23
Time Since Fire†					
0–12 months post-fire	0				
13–24 months post-fire	−0.32	0.73	0.07	−0.42	−0.21
25–36 months post-fire	0.064	1.07	0.07	−0.05	0.18
>36 months post-fire	0.061	1.06	0.08	−0.08	0.19

† Beta coefficients interpreted relative to the reference category 0–12 months post-fire.

substantial improvement over the environmental model (ΔAICc = 143.7) and showed female prairie-chickens used patches that were 0–12 months post-fire more than any other time since fire category (Table 4). The inclusion of oil and gas infrastructure resulted in substantial improvements over the environmental model as well (ΔAICc = 325.6), indicating female prairie-chickens avoided areas close to power lines (β = 0.43, 90% CI = 0.36–0.51), primary roads (β = 0.06, 90% CI = 0.03–0.09), and areas of high oil well density at the 1.5 km^2 scale (β = −0.15, 90% CI = −0.18 to −0.12; Table 4). The second-best model for the post-nesting period for the second-order contained distance to oil wells rather than oil well density (ΔAICc = 44.08).

The environmental model for the post-nesting period at the third-order level of selection included distance to woodlands, distance to leks, and TPI (Table 4). The inclusion of time since fire and distance to power lines improved on the environmental model for this scale (ΔAICc = 68.47). Female prairie-chickens used areas 13–24 months post-fire less than patches that were 0–12 months post-fire, 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 patches 0–12 months post-fire based on availability within home ranges (Table 4). Female prairie-chickens showed an avoidance of power lines within their home range during this period (β = 0.19, 90% CI = 0.14–0.23). The next best performing model contained oil well density instead of distance to power lines (ΔAICc = 33.3).

The top model for the second-order had high predictability with new data (r_s = 0.93). Similar to the lekking period cross-validation, the model for the third-order selection did not perform as well at predicting habitat use (r_s = 0.7). The second-order model suggested a stronger avoidance

Table 5. Beta coefficients, odds ratio, standard error, and confidence intervals for nonbreeding season models describing availability at the second-order selection (based on movement-based buffer) and third-order selection (within home range selection) for Greater Prairie-Chickens monitored in Osage County, Oklahoma, between 2014 and 2016

Habitat variable	β	Hazard ratio	Standard error	90% CI	
				Lower	Upper
Second-order					
Distance to Lek	−0.39	0.68	0.04	−0.46	−0.32
Distance to Woodlands	0.73	2.06	0.06	0.59	0.85
Topographic Position Index	4.02	55.9	0.18	3.72	4.30
Slope	−0.04	0.96	0.005	−0.05	−0.03
Distance to Burn Unit Edge	0.07	1.07	0.01	0.05	0.09
Oil Well Density (4 km^2)	−0.31	0.73	0.03	−0.37	−0.26
Distance to Power Lines	0.37	1.45	0.03	0.33	0.42
Distance to Roads	0.07	1.06	0.02	0.02	0.10
Time Since Fire†					
0–12 months post-fire	0				
13–24 months post-fire	−0.57	0.57	0.10	−0.67	−0.46
25–36 months post-fire	−0.05	0.95	0.11	−0.18	0.08
>36 months post-fire	−0.40	0.67	0.13	−0.51	−0.29
Third-order					
Distance to Lek	−0.23	0.79	0.03	−0.30	−0.17
Distance to Woodlands	0.09	1.09	0.02	0.05	0.14
Topographic Position Index	4.14	62.7	0.18	3.86	4.39
Slope	−0.04	0.96	0.005	−0.05	−0.03
Distance to Burn Unit Edge	0.05	1.05	0.009	0.04	0.06
Oil Well Density (3.5 km^2)	−0.29	0.75	0.03	−0.36	−0.25
Distance to Power Lines	0.33	1.38	0.03	0.28	0.37
Time Since Fire†					
0–12 months post-fire	0				
13–24 months post-fire	−0.71	0.49	0.07	−0.82	−0.60
25–36 months post-fire	−0.07	0.94	0.08	−0.19	0.08
>36 months post-fire	−0.24	0.79	0.06	−0.33	−0.15

† Beta coefficients interpreted relative to the reference category 0–12 months post-fire.

of energy development compared to the third-order model, with female prairie-chickens avoiding roads and high densities of oil wells in addition to power lines at the second-order scale.

Nonbreeding season.—The environmental model for second-order selection during the nonbreeding season included distance to lek, distance to woodlands, TPI, and slope (Table 5). The addition of fire-related variables and energy development variables offered a substantial improvement over the environmental model (ΔAICc = 476.8). Patches burned in the previous 12 months were used preferentially over patches that were 13–24 months post-fire and >36 months post-fire, but the 90% confidence interval for patches 24–36 months post-fire included zero (Table 5). Additionally, female prairie-chickens appeared to avoid time since fire patch edges during the nonbreeding season (β = 0.07, 90% CI = 0.05–0.09). Female prairie-chickens avoided areas close to power lines (β = 0.37, 90% CI = 0.33–0.42), areas close to roads (β = 0.06, 90% CI = 0.02–0.1), and selected areas with lower densities of wells within 4 km^2 (β = −0.31, 90% CI = −0.37 to −0.26). The second-best model contained distance to oil wells instead of the density of wells (ΔAICc = 56.1).

The environmental model describing third-order selection during the nonbreeding season was similar to the second-order model in that it contained distance to associated lek, distance to woodlands, TPI, and slope (Table 5). The addition of time since fire and energy development variables greatly improved model fit over the environmental model (ΔAICc = 285.32). Prairie-chickens showed a trend toward using patches

0–12 months post-fire more than any other times since fire, but the 90% confidence intervals for patches 25–36 months post-fire included zero (Table 5). Distance to time since fire patch edge was also supported as an important variable with female prairie-chickens avoiding areas close to edges ($\beta = 0.05$, 90% CI = 0.04–0.06). At the third-order scale, female prairie-chickens avoided power lines ($\beta = 0.33$, 90% CI = 0.28–0.37) and areas with high numbers of oil wells at the 3.5 km^2 scale ($\beta = -0.29$, 90% CI = −0.36 to −0.25; Table 5). The second-best performing model indicated avoidance of roads, but the confidence interval for roads included zero (ΔAICc = 0.45, road $\beta = 0.02$, 90% CI = −0.01–0.04).

Both models for the nonbreeding season performed well under cross-validation and provided similar levels of accuracy when predicting use for new prairie-chicken locations (second-order $r_s = 0.89$; third-order $r_s = 0.85$). The two nonbreeding season models differed by the inclusion of distance to roads in the second-order model and different oil well density variables.

Thresholds of avoidance

Lekking period.—The CDF curves developed for the lekking period indicated female prairie-chickens avoided power lines but showed a neutral response to oil wells and roads during the lekking season (Fig. 2a–c). The change point estimated by segmented regression for power lines during the lekking period indicates an avoidance threshold at approximately 573 m (95% CI = 546–599). The 95% confidence intervals for the initial slope estimated by segmented regression for the CDF curves for roads and oil wells during this period both overlapped zero (Appendix S1: Table S1). The CDF curves provided similar results to the discrete choice models that incorporated threshold variables. The discrete choice models estimated an avoidance threshold at 700 m for power lines and no threshold from roads and oil wells (Appendix S1: Table S2–S4).

Nest-site selection.—The CDF curves for nest sites indicate little response to oil and gas infrastructure (Fig. 2d–f). The CDF curves for all three features showed a neutral to a negative response to energy development, with the 95% confidence intervals for the initial slope estimated by the segmented regression including 0 for all three curves (Appendix S1: Table S1). The discrete choice models that included threshold variables suggested a similar response to infrastructure, with no threshold variables offering any improvement over the original model for nest-site selection (Appendix S1: Table S2–S4).

Post-nesting period.—The CDF analysis indicated that female prairie-chickens avoided power lines, roads, and oil wells during the post-nesting period (Fig. 2g–i). The CDF curves for all three structures showed an initially negative trend up to the change point (Appendix S1). The avoidance distance for power lines and oil wells was estimated at 288 m (95% CI = 256–320) and 325 m (95% CI = 306–344), respectively. The avoidance threshold for roads during the post-nesting period was much smaller, with female prairie-chickens avoiding roads by 74 m (95% CI = 64–83). Similarly, the avoidance thresholds selected by the discrete choice method indicted female prairie-chickens avoided oil wells and power lines by 400 m and roads by 100 m during the post-nesting season (Appendix S1: Table S2–S4).

Nonbreeding season.—Cumulative distribution function curves developed for the nonbreeding season indicate that female prairie-chickens avoided all three structures during this period (Fig. 2j–l). Female prairie-chickens showed a negative response to power lines up to 481 m (95% CI = 451–510). The change point for the CDF curve developed for roads in the nonbreeding season indicated the avoidance thresholds were approximately 88 m (95% CI = 73–93). While the CDF curve for oil wells showed a negative slope for oil wells, no threshold was identified, suggesting that oil fields may influence female prairie-chickens up to 1000 m away during the nonbreeding season (Fig. 2g). The avoidance thresholds selected by the discrete choice models indicted female prairie-chickens avoided power lines by 550 m and roads by 100 m during the nonbreeding season (Appendix S1: Table S2–S4). Similar to the CDF analysis, no threshold below 1000 m was identified for oil wells during the nonbreeding season.

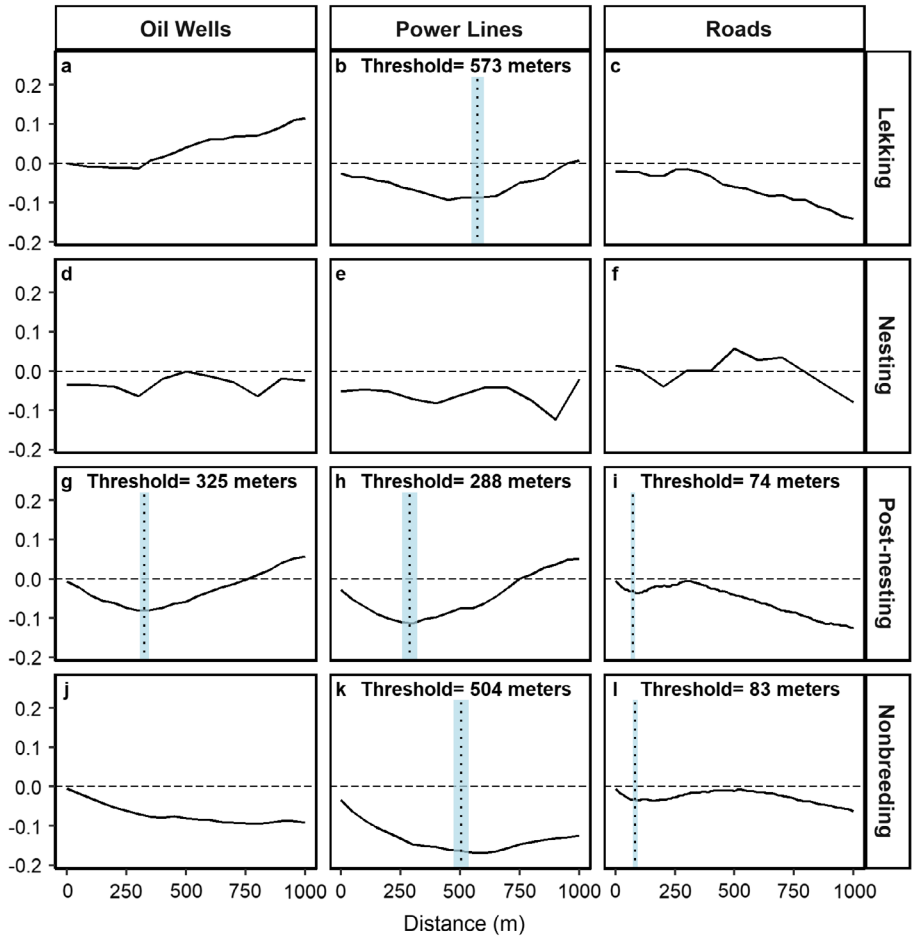

Fig. 2. Cumulative distribution functions describing the distribution of Greater Prairie-Chicken locations relative to oil and gas infrastructure (column labels) during four behaviorally distinct life stages (row labels) in Osage County, Oklahoma, USA, during 2014–2016. Positive initial slopes indicate an attraction to a feature, while negative initial slopes indicate avoidance of a feature. Avoidance thresholds estimated by segmented regression are indicated by the vertical dashed lines (blue region indicates confidence intervals for each threshold estimate).

Discussion

By studying prairie-chicken habitat use in a grassland managed for structural heterogeneity that has also undergone development for oil and gas production, we were able to assess the relative importance of rangeland management and energy development for female prairie-chicken habitat use. We found habitat use was influenced by scale and seasonal period for most variables considered. Time since fire was one of the most consistent predictors of habitat use, but the use of different time since fire patches varied across periods. Prairie-chickens avoided areas near woodlands throughout the year, emphasizing the potential for tree encroachment into grasslands to fragment the landscape for prairie-chickens. However, the response of female prairie-chickens to energy development was complex, with the relative importance of different types of structures varying across life stages. Notably, female prairie-chickens appeared to be the most sensitive to oil and gas development during the post-nesting and nonbreeding seasons, two life stages that have received limited attention in the literature for many grassland birds.

Spatial scale was an important factor in determining prairie-chicken response to variables

included in our analysis. The second-order and third-order models frequently differed by the inclusion of one or more variables at the second-order level of selection. This suggests that the variables considered in our analysis influence the structure of the landscape at broad spatial scales, and prairie-chickens are likely responding to these features through home range placement rather than altering movements within their home ranges. This is further supported by the fact that the models developed at the second-order scale tended to more accurately predict prairie-chicken habitat use compared to models developed at the third-order scale. Additional variables, such as fine-scale vegetation structure or composition measurements, may be needed to predict within home range selection more accurately. These results emphasize the need for the consideration of multiple spatial scales and definitions of availability during resource selection studies in order to best identify the scale at which a species may respond to changes in its environment (Fuhlendorf et al. 2002, Boyce et al. 2003).

Time since fire was among the most consistent drivers of habitat use for prairie-chickens, with the importance of different time since fire patches varying through the year. Selection in our study was similar to patterns described in previous research, with female prairie-chickens selecting patches that were 2–3 yr post-fire in the lekking and nesting period, then shifting use to patches that were burned in the previous 12 months during the post-nesting and nonbreeding seasons (McNew et al. 2015, Winder et al. 2017*b*). Differential use of time since fire patches throughout the year likely reflects the changing needs during each life stage, such as the need for cooler thermal sites and greater cover from predators during the nesting season (Hovick et al. 2014*c*), or improved foraging opportunities during the post-nesting and nonbreeding season (Norton et al. 2010). Despite these shifting preferences, prairie-chicken habitat use was centered around leks in all seasons, emphasizing the importance of landscapes that have a variety of seral stages juxtaposed near each other to accommodate the various life-stage requirements of prairie-chickens. Much of the research on the effects of heterogeneity-based management of grasslands has focused on the breeding season (Churchwell et al. 2008, Hovick et al. 2015*b*, 2015*c*, McNew et al. 2015), but our results add to the growing body of literature that demonstrates that grassland heterogeneity is critical throughout the entire annual cycle (Hovick et al. 2014*b*, 2017, Winder et al. 2017*b*).

Prairie-chickens showed a consistent avoidance of woodlands during all life stages. These results are similar to previous research that have found prairie-chickens avoid nesting and establishing leks in areas with high tree cover (Merrill et al. 1999, McNew et al. 2012, Hovick et al. 2015*b*). The application of frequent fires is a critical component of grassland maintenance, as fire limits tree invasion into grasslands (Bond and Keeley 2005). However, due to a history of fire suppression, much of the Great Plains is threatened with invasion by eastern redcedar (*Juniperus virginiana;* Engle et al. 2008) and other woody plants, potentially impacting remaining prairie-chicken populations (Merrill et al. 1999, Fuhlendorf et al. 2002, McNew et al. 2012). The use of heterogeneity-based management practices offers an important management strategy for grasslands as it allows for the frequent burning of grasslands, preventing tree encroachment, while leaving portions of the landscape unburned in a given year as wildlife habitat.

Prairie-chicken response to energy development was variable across life stages with female prairie-chickens showing minimal avoidance of energy development during the nesting period, while avoiding power lines during the lekking, post-nesting, and nonbreeding seasons and avoiding high densities of oil wells and roads during the post-nesting and nonbreeding season. Response to infrastructure has been suggested to be related to avoidance of increased human activity in areas of high-density development (Lyon and Anderson 2003, Holloran et al. 2015) or avoidance of potential perch sites for predators (Knight and Kawashima 1993). Understanding the mechanisms that drive displacement of female prairie-chickens will aid in assessing prairie-chicken response to future development in different locations and different infrastructure types. Additional work is needed to understand the specific mechanisms that cause grouse avoidance of energy infrastructure; however, as roads, wells, and power lines frequently occur together in our study area, it may be challenging to disentangle structure-

specific mechanisms driving avoidance behaviors.

Notably, while distance to oil wells was supported as being a potentially important predictor of prairie-chicken habitat use during the post-nesting and nonbreeding seasons at the second-order level of selection, density-related variables consistently provided better estimates of prairie-chicken habitat use suggesting prairie-chickens may be more sensitive to the number and spatial arrangement of wells rather than distance to wells. Similar patterns have been observed in other grouse species (Holloran et al. 2015). Further, the scale that female prairie-chickens responded to oil well density varied with season, with females responding most to smaller scales in the post-nesting season (second-order = number of wells within 1.5 km) compared to the nonbreeding season (second-order = number of wells with 4 km, third-order = number of wells within 3.5 km). Additionally, the magnitude of effect was stronger in the nonbreeding season where the addition of a single oil well per km^2 reduced probability of use by 27% compared to a 14% lower probability of use for the post-nesting season.

Similar to the discrete choice models, results of our threshold analysis indicated female prairie-chickens avoided power lines throughout most of the year and avoided roads and oil wells primarily during the post-nesting and nonbreeding season. Avoidance distances differed across the season, but avoidance distances based on CDF curves generally estimated avoidance thresholds up to 300–600 for power lines, 300 m to as much as 1000 m for oil wells, and approximately 80–100 m from roads. While the CDF curves appeared to estimate smaller avoidance thresholds compared to the discrete choice analysis, the general agreement of the two methods provides a viable range of avoidance distances and increase confidence that these thresholds have biological significance to prairie-chickens. The differences in response distance to specific types of infrastructure, such as oil wells or power lines, in different seasons, emphasize the need for consideration of time of year and life stage when considering the impacts of energy development.

Cumulative distribution function curves offer a relatively simple and concise means of evaluating the distribution of an animal's locations around a discrete point (in this case oil and gas infrastructure) and can provide thresholds of avoidance or attraction that can inform predictive model parameterization such as discrete choice and become testable hypotheses in multivariate models. Because they are univariate, CDFs used alone may provide an overly simplistic representation of selection in that they fail to account for the difference in habitat and the influence of other landscape features on habitat selection. For this reason, we suggest that results of the CDF analysis be considered as conservative estimates of prairie-chicken avoidance thresholds, and should be interpreted within the context of models that account for the interaction of multiple variables in habitat selection, such as discrete choice analysis.

Conclusions

Our results demonstrate that prairie-chicken habitat use varied across behavioral periods and with the spatial scale with regard to a number of landscape features at our study site. Time since fire, avoidance of woodlands, and an attraction to lek sites were consistent drivers of space use across spatial scales and throughout the year, while prairie-chicken's response to oil and gas infrastructure was more variable. In particular, oil and gas development appeared to be more influential at the second-order level of selection, suggesting these features may impact prairie-chicken more through home range placement rather than movement within home ranges. Further, prairie-chicken's appeared to be more sensitive to anthropogenic structures in the post-nesting and nonbreeding seasons, avoiding a greater variety of structures, high densities of oil wells, and roads during these periods. Reintroduction of fire and grazing regimes that promote grassland heterogeneity may be among the best strategies for prairie-chicken conservation as these strategies will create a variety of seral stages that can be used as habitat throughout the year and will maintain grasslands by preventing woody plant encroachment. However, minimizing future fragmentation of grasslands from various sources, including oil and gas development and tree encroachment, will ensure the ongoing utility of local management actions. Further, an examination of multiple spatial scales and

behavioral periods is critical for developing a full understating of prairie-chicken response to anthropogenic activities in grasslands. Our results emphasize the importance of a more comprehensive approach to habitat selection studies, as the use of multiple spatial scales and periods allowed us to identify patterns of avoidance, particularly for oil and gas infrastructure, that may not have been apparent under more restricted investigations.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2982/full