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RESEARCH ARTICLE

Nest site selection and nest survival of Greater Prairie-Chickens near a wind energy facility

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ABSTRACT

Rapid development of wind energy facilities in the Great Plains of North America has raised concerns regarding their potential negative impact on the nesting ecology of Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*). We investigated the effects of a pre-existing, 36-turbine wind energy facility on nest site selection and nest survival of Greater Prairie-Chickens in the unfragmented grasslands of the Nebraska Sandhills, USA. In 2013 and 2014, we monitored 91 nests along a 24-km disturbance gradient leading away from the wind energy facility. We found little evidence of an effect of the wind energy facility on Greater Prairie-Chicken nest site selection and nest survival. Instead, we found that the primary drivers of nest site selection and nest survival were related to landscape and habitat factors. Greater Prairie-Chickens avoided nesting near roads, with 74% of Greater Prairie-Chickens selecting nest sites >700 m from roads. Greater Prairie-Chickens selected nest sites with more than twice the visual obstruction and residual standing dead vegetation of random points. Our results suggest that small wind energy facilities, such as the facility in our study, may have little effect on Greater Prairie-Chicken nest site selection and nest survival. We suggest that livestock grazing and other grassland management practices still have the most important regional effects on Great Prairie-Chickens, but we caution future planners of wind energy facilities to account for the potential negative effect of roads on nest site selection.

Keywords: grouse, habitat selection, Nebraska, nesting ecology, Sandhills, *Tympanuchus cupido pinnatus*, wind farm, wind turbine

Selección del sitio de anidación y supervivencia del nido de *Tympanuchus cupido pinnatus* cerca de un parque de energía eólica

RESUMEN

El rápido desarrollo de los parque de energía eólica en las Grandes Llanuras de América del Norte ha generado preocupación sobre su potencial impacto negativo en la ecología de anidación de *Tympanuchus cupido pinnatus*. Investigamos el efecto de un parque de energía preexistente de 36 turbinas eólicas sobre la selección del sitio de anidación y la supervivencia del nido de *T. c. pinnatus* en los pastizales no fragmentados de las Sandhills de Nebraska. En 2013 y 2014, monitoreamos 91 nidos a lo largo de un gradiente de disturbio de 24 km que se alejaba del parque de energía eólica. Encontramos poca evidencia de un efecto del parque de energía eólica sobre la selección del sitio de anidación y la supervivencia del nido en *T. c. pinnatus*. En cambio, encontramos que las causas principales de la selección del sitio de anidación y la supervivencia del nido se relacionaron con el paisaje y los factores del hábitat. La especie *T. c. pinnatus* evitó anidar cerca de las rutas, con un 74% de los individuos seleccionando sitios de anidación >700 m desde las rutas. Los individuos seleccionaron sitios de anidación con más del doble de obstrucción visual y vegetación residual muerta en pie con relación a puntos elegidos al azar. Nuestros resultados sugieren que pequeños parques eólicos, como el de nuestro estudio, tendrían un efecto menor en la selección del sitio de anidación y en la supervivencia del nido en *T. c. pinnatus*. Sugerimos que el pastoreo del ganado y otras prácticas de manejo de los pastizales se mantienen como los impactos regionales más importantes para *T. c. pinnatus*, pero alertamos a los futuros gestores de los parques de energía eólica para que contemplen los potenciales efectos negativos de las rutas en la selección del sitio de anidación.

Palabras clave: ecología de anidación, Nebraska, parque eólico, Sandhills, selección de hábitat, turbina de viento, *Tympanuchus cupido pinnatus*, urogallo

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INTRODUCTION

Wind energy development has increased at an unprecedented rate in the past decade. The Global Wind Energy Council predicts that wind power could supply up to 17–19% of global electricity demands by 2030 and 25–30% of requirements by 2050 (http://www.gwec.net). The Great Plains of central North America are often targeted for wind energy development due to wide-open landscapes with high wind speeds (Fargione et al. 2012). The increasing presence of wind energy development in the Great Plains may have negative consequences for grassland birds (Smith and Dwyer 2016), which are currently the most rapidly declining avian group in North America (Vickery et al. 2000). Specifically, behavioral avoidance of wind energy facilities may effectively lead to habitat loss, which may lead to decreased nest survival, especially in highly fragmented landscapes (Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011). The potential effects of wind energy facilities in contiguous grasslands have not been assessed.

The Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) is a grassland bird species of conservation concern in North America. Once abundant in 20 U.S. states and 4 Canadian provinces (Svedarsky et al. 2000), the Greater Prairie-Chicken (hereafter, prairie-chicken) is now found in only 11 U.S. states (Westemeier et al. 1998, Svedarsky et al. 2000). Declining populations and contraction of the prairie-chicken's range are primarily due to agricultural development, which has led to loss and fragmentation of nesting habitat (Svedarsky et al. 2000). Currently, Nebraska supports one of the largest remaining prairie-chicken populations in North America, and the Sandhills region of north-central Nebraska provides important nesting habitat (Svedarsky et al. 2000). Yet, prairie-chickens are now designated as a species of highest conservation concern in Nebraska (Schneider et al. 2011). Sandy soils in the region are not suitable for row crop agriculture; instead, the largely unfragmented tracts of Sandhills prairie are used for cattle grazing, which can be compatible with management for prairie-chicken habitat (Anderson 2012). However, wind energy development is projected to increase in the area (Nebraska Energy Office, http://www.neo.ne.gov/) and has the potential to fragment grasslands and negatively affect nesting prairie-chickens.

Although the effects of wind energy facilities on prairie-chickens are largely unknown, and the potential mechanisms driving these effects are poorly understood, sensitivity to and avoidance of anthropogenic structures (Robel et al. 2004, Pruett et al. 2009, LeBeau et al. 2014) are likely important. For example, Matthews et al. (2011) found that low nest and brood survival of prairie-chickens in southeastern Nebraska could be attributed to high predation near the tree lines that dissected the landscape. Raptors are the main predators of prairie grouse, and will often perch in trees when hunting (Lammers and Collopy 2007, Pruett et al. 2009). Thus, prairie grouse may perceive trees and, indeed, tall anthropogenic structures as an indication of an increased threat of predation and avoid them through an adaptive response (Pruett et al. 2009). If prairie-chickens perceive areas with wind turbines as high predation risk areas, females in proximity to wind energy facilities may exhibit a shift in nest site selection in which they avoid nesting near wind energy facilities.

The evolutionary response by grouse to avoid tall structures may be maladaptive in an anthropogenic landscape, as avoidance of tall structures could lead to functional habitat loss and a subsequent decrease in reproductive success (Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011). Anthropogenic disturbances from wind energy facilities also have the potential to increase the release of the stress hormone corticosterone in birds (Romero and Reed 2005, Sheriff et al. 2011, Wills 2013), which may influence nest survival. When chronic stress causes corticosterone to be released for extended periods of time, reductions in nest attendance and increased egg loss may result (Angelier and Chastel 2009). Alternatively, given that raptors avoid wind energy facilities (Pearce-Higgins et al. 2009, Garvin et al. 2011), there may be a decrease in predation on adult grouse in proximity to wind energy facilities, leading to the potential for an indirect positive effect on prairie-chicken survival and reproductive success (Smith and Dwyer 2016).

Our study was designed to measure the potential effects of an existing wind energy facility in the Nebraska Sandhills on (1) nest site selection and (2) nest survival of prairie-chickens. We hypothesized that female prairie-chickens would avoid the turbines and transmission lines associated with the wind energy facility due to a perceived increase in predation risk (Pruett et al. 2009). Thus, we predicted that females would select nest site locations farther from the wind energy facility. We also predicted that females near the wind energy facility would have lower nest survival compared with those nesting farther away.

We also addressed the effects of habitat variation, weather and temporal factors, and roads on prairie-chicken nest site selection and nest survival. We expected that prairie-chickens would nest in areas with higher residual vegetation and cover than what was generally available on the landscape (Svedarsky 1979, Buhnerkempe et al. 1984, Westemeier et al. 1995, Anderson 2012). We expected that residual vegetation cover from the previous year would increase nest survival (Kirsch 1974, Johnsgard 2002, Davis 2005, Manzer and Hannon 2005), but that weather factors, such as temperature and precipitation, and the temporal factor of nest age at time of discovery would be stronger predictors of nest survival (Davis 2005, Fields et al. 2006, Anderson 2012, Matthews et al. 2013).

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We predicted that roads would have a negative effect on both nest site selection and survival because predator abundance could be higher in these areas (Dijak and Thompson 2000, Winter et al. 2000, Bollinger and Gavin 2004).

METHODS

Study Area

Our study area was centered on a pre-existing wind energy facility (42°27′44″N, 99°55′39″W) located ~10 km south of Ainsworth, Brown County, in the north-central Nebraska Sandhills, USA. The facility was owned and operated by the Nebraska Public Power District and consisted of 36 1.65-MW-capacity wind turbines standing 70 m tall with 40-m-long blades. The facility was constructed across ~44.5 km^2, with roads, turbine foundations, and the substation encompassing approximately 0.2 km^2 (Nebraska Public Power District, http://www.nppd.com). Other infrastructure at the site included maintenance buildings, gravel roads, an electrical substation on the southeast corner of the property, and a transmission line (3-pole wooden support towers, 230 kV) that ran north and south from the substation. The facility had been operational since 2005 (Nebraska Public Power District, http://www.nppd.com). Because our study was conducted 8 yr after construction of the wind energy facility was completed, we were unable to conduct a before–after study design. We collected data along a disturbance gradient (Adaramola 2015), sampling from "control" lek sites far from the wind energy facility and "experimental" lek sites near the facility. Data from our gradient design therefore provided inferences only about the population of prairie-chickens present during our study and their interactions with the wind energy facility. The transmission line in our study site ran along the experimental gradient (Figure 1) and paralleled a main highway. Thus, we were not able to explicitly design our study to test for effects of the transmission line.

The Nebraska Sandhills ecoregion is the most intact remnant prairie of the Great Plains, encompassing ~50,000 km^2 of Nebraska (Schneider et al. 2011, U.S. Fish and Wildlife Service, http://www.fws.gov/mountain-prairie/pfw/ne/ne4.htm), which provided a unique opportunity to assess the effects of wind energy in an unfragmented grassland. The climate is semiarid, with average annual rainfall ranging from 580 mm in the east to <430 mm in the west (Schneider et al. 2011). Temperatures range from lows of ca. −12°C in winter to highs of ~32°C in summer (Schneider et al. 2011). The Sandhills sit above the Ogallala aquifer, which allows for the formation of temporary and permanent shallow lakes and subirrigated meadows in the low-lying areas between the upland grass-stabilized sand dunes. Vegetation varies between meadows and upland sites, with upland sites dominated by mixtures of warm-season tallgrass species, and subirrigated meadows dominated by mixtures of native warm-season grasses and exotic cool-season grasses. Land use surrounding the wind energy facility is predominantly cattle ranching (http://www.fws.gov/mountain-prairie/pfw/ne/ne4.htm). Grassland management practices vary, and may affect nesting habitat (Anderson et al. 2015). Only ~7% of the study area is planted with row crops such as corn and soybeans (U.S. Department of Agriculture National Agricultural Statistics Service, http://www.nass.usda.gov/).

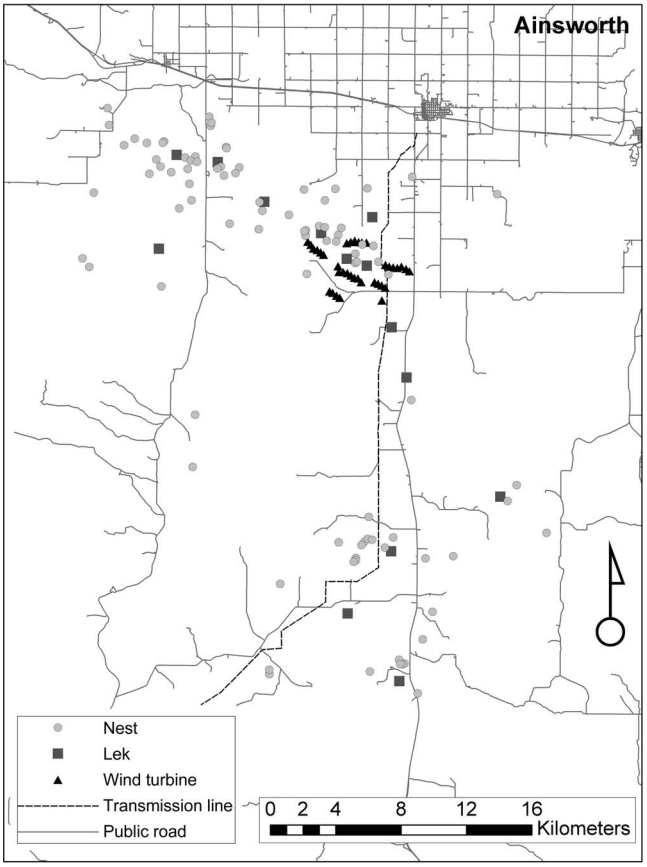


FIGURE 1. Locations of leks and nests of Greater Prairie-Chickens in 2013 and 2014 in relation to roads, the transmission line (230 kV), and the wind energy facility near Ainsworth, Nebraska, USA. Leks ranged in distance from 0.7 km to 23.3 km from the wind energy facility, with 3 leks <1 km from the facility.

Field Methods

Trapping and nest monitoring. We captured female prairie-chickens during March and April of 2013 and 2014 using walk-in traps (Schroeder and Braun 1991) and drop-nets at 13 lek sites in 2013 and 15 lek sites in 2014 (12 leks were used in both years of the study). Leks were located along a gradient from 0.7 km to 23.3 km from the wind

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energy facility; 3 leks were within 1 km of the wind energy facility (Figure 1).

We fitted captured females with necklace-style, very high frequency (VHF) radio-transmitters equipped with mortality sensors (Advanced Telemetry Systems, Isanti, Minnesota, USA) or rump-mounted Solar Argos/GPS Platform Transmitter Terminals (PTTs; Microwave Telemetry, Columbia, Maryland, USA). PTT satellite tag locations were recorded 10 times daily in April–July of 2013 and 2014. We located VHF radio-tagged females 5–7 times per week during the nesting season (May 9 to July 31, 2013, and April 24 to July 31, 2014) to monitor nests. VHF radio-tagged females were located using either a truck-mounted 5-element antenna-receiver, or on foot or ATV using hand-held 3-element Yagi antenna-receiver systems (Advanced Telemetry Systems, Isanti, Minnesota, USA). We recorded all nest locations using a handheld Garmin Etrex Vista GPS device (Garmin International, Olathe, Kansas, USA).

We conducted nest checks at least 5 days after the expected clutch completion date to decrease the likelihood of nest abandonment due to disturbance. Upon inspection, we recorded the completed clutch size for all active nests and predicted the nest initiation and hatching dates using egg flotation (Westerskov 1950). We monitored nesting prairie-chickens daily from a distance of >30 m to determine nest fate. We assumed nest failure or abandonment if a female was found off her nest for 3 consecutive days during the nesting period, at which time we visited the nest to confirm its fate. We returned to nests on expected hatching dates when females were no longer attending nests. We considered successful nests as those with at least one hatched chick, as indicated by the presence of hatched egg shells, and failed nests as those that had been depredated, abandoned, or had no hatched eggs.

Microhabitat and macrohabitat sampling. For both active and inactive (depredated or abandoned) nests, we conducted vegetation sampling of microhabitat (nest site) characteristics including vegetation height, cover, and composition to evaluate nest site selection. Vegetation sampling was conducted 5–7 days after nest discovery so that our inferences would correspond to vegetation near the time of nest initiation. All vegetation sampling was conducted from May 1 to June 30 in 2013 and 2014. We placed a 20 cm × 50 cm quadrat on the northern and southern edge of the nest bowl and estimated percent cover of cool-season grasses, warm-season bunch grasses, warm-season rhizomatous grasses, forbs, shrubs, standing dead vegetation, litter, and bare ground at the nest site using methods adapted from Daubenmire (1959). We recorded the height of the tallest live plant and the litter depth in the northeast corner of the quadrat. We measured litter depth under the canopy of residual vegetation resting below 90° of standing live or dead vegetation. We took a visual obstruction reading (VOR) at the nest with a Robel pole (Robel et al. 1970) placed at the center of the nest bowl and recorded from north, south, east, and west at 4 m from the pole. We averaged the 4 measurements for our final VOR reading.

On the same day that we sampled vegetation at nest sites, we also sampled vegetation at 5 additional and randomly selected locations within each pasture containing a known nest. Random locations were placed along a transect leading away from the nest in a random cardinal direction; random locations were located ≥30 m from the nest and from each other (Anderson et al. 2015) to ensure independence and provide a sample of available habitat in the area that we presumed the female assessed when selecting her nest (Powell et al. 2014). All random locations were within the same ecological site and topographic position as the nest (Anderson et al. 2015). Ecological sites were characterized based on distinct soil, climatic, and physiographic characteristics that produce specific plant communities (Natural Resources Conservation Service, https://esis.sc.egov.usda.gov/Welcome/pgReportLocation.aspx?type=ESD). The ecological sites in our study area included choppy sands (steep slopes characterized by exposed sand), sandy highlands (rolling hills with sandy soil), sandy lowlands (level areas with loam to fine sand), and subirrigated meadows (low-lying areas with fine sand and loam that were seasonally inundated with water; https://esis.sc.egov.usda.gov/Welcome/pgReportLocation.aspx?type=ESD). We measured vegetation cover and structure at random locations using the same methods as those used at nest sites.

We recorded macrohabitat (large-scale) characteristics for nests and random locations by mapping landscape features using a Geographic Information System (GIS) in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA). We mapped nest sites, random sites, transmission line location, and wind turbine locations. We obtained data on road locations (highways and county roads) from the Nebraska Department of Natural Resources (http://www.dnr.ne.gov/transportation-data), digital elevation models (10-m resolution) from the U.S. Geological Survey National Elevation Dataset (http://ned.usgs.gov), and ecological site descriptions from the Natural Resources Conservation Service (http://websoilsurvey.nrcs.usda.gov/app/). Using these data, we calculated the distance to the nearest wind turbine, distance to the transmission line, distance to the nearest nest, distance to the nearest road, degree of slope, and ecological site for each nest and random location.

Weather. We recorded daily temperature, precipitation, and growing degree day (GDD) throughout the 2013 and 2014 nesting periods (April–July) from a weather station located 10 km northeast of the wind energy facility

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(Ainsworth Regional Airport, 42°34′45′′N, 99°59′35′′W). Data from the weather station were downloaded via the Northeast Regional Climate Center website (http://www.nrcc.cornell.edu/). We downloaded the monthly Palmer Drought Severity Index (PDSI) from NOAA's (National Oceanic and Atmospheric Administration) National Centers for Environmental Information (https://www.ncdc.noaa.gov/) for the nesting period.

Data Analyses

We assessed the effect of the wind energy facility on nest site selection and nest survival by performing discrete choice conditional logistic regression model analyses using our macrohabitat and microhabitat data (Manly et al. 2002, Therneau and Lumley 2009) and a known-fate nest survival analysis (White and Burnham 1999, Rotella et al. 2004). For all analyses, we created a correlation matrix to test for multicollinearity among covariates and removed covariates to avoid multicollinearity if $r > 0.6$. We investigated whether continuous covariates were nonlinear by creating models in which each covariate (x) was represented in a linear, quadratic ($x + x^2$), and cubic ($x + x^2 + x^3$) model. For the nest survival analysis, we compared distance to the nearest wind turbine as a discrete (nests <1 km or >1 km from the wind energy facility) and a continuous (linear, quadratic, and cubic) function. We used this classification because we found that the home ranges of prairie-chickens captured within 1 km of the wind energy facility were likely to overlap with the footprint of the wind energy facility (Harrison 2015). We conducted model selection using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). We assessed model support using ΔAIC_c and model weights (w_i) as suggested by Burnham and Anderson (2002). We then used the selected form (linear, quadratic, or cubic) of each covariate for model creation and comparison in our analyses of macrohabitat and microhabitat nest site selection and nest survival.

Nest site selection analyses. At the macrohabitat scale, we assessed whether prairie-chickens selected nest sites farther away from the wind energy facility rather than sites near the facility by evaluating the effect of distance to the nearest wind turbine. We created 25 a priori discrete choice models relating to predictions of how macrohabitat characteristics may affect nest site selection (Table 1). Our model set evaluated the effects of the following covariates on nest site selection: distance (m) to the nearest wind turbine (McNew et al. 2014), distance (m) to the transmission line (Pitman et al. 2005, Gillian et al. 2013, Hansen et al. 2016), distance (m) to the nearest road (Dijak and Thompson 2000, Winter et al. 2000, Bollinger and Gavin 2004), distance (m) to the nearest neighboring nest, ecological site (Anderson et al. 2015, but see Doherty et al. 2011), and degree of slope of the nest site (Anderson 2012, Matthews et al. 2013). We included distance to the nearest nest to investigate effects of neighboring females on nest site selection.

TABLE 1. Comparison of competing discrete choice models in the full a priori model set examining Greater Prairie-Chicken macrohabitat nest site selection by females breeding in the vicinity of a wind energy facility near Ainsworth, Nebraska, USA, in 2013 and 2014. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c). K is the number of model parameters; ΔAIC_c is the difference in AIC_c score relative to the highest-ranked model; w_i is the Akaike weight, which indicates relative support for the model; and CW is the cumulative w_i. Ecosite = ecological site of the nest (sands, sandy, or subirrigated), Nest = distance to nearest neighboring nest (m), Road = distance to nearest road (m), Slope = the degree of slope of the nest site, Trans = distance to transmission line (m), and Turbine = distance to nearest wind turbine (m). A superscript 2 after a covariate represents a quadratic term and a superscript 3 represents a cubic term.

Model	K	ΔAIC_c	w_i	CW
Road^3 + Nest^2	5	0.00 [a]	0.34	0.34
Slope + Nest^2	3	0.57	0.26	0.60
Trans^2 + Nest^2	4	1.14	0.19	0.79
Nest^2	2	2.51	0.10	0.89
Global	12	4.15	0.04	0.93
Slope + Ecosite + Nest^2	5	4.58	0.03	0.97
Ecosite + Nest^2	4	5.83	0.02	0.98
Nest^2 + Turbine^2	4	6.43	0.01	1.00
Slope + Road^3	4	24.02	<0.01	1.00
Slope	1	24.10	<0.01	1.00
Trans^2 + Slope	3	25.21	<0.01	1.00
Slope + Turbine^2	3	25.83	<0.01	1.00
Road^3	3	27.22	<0.01	1.00
Road^3 + Turbine^2	5	27.30	<0.01	1.00
Trans^2	2	27.32	<0.01	1.00
Turbine^2	2	27.86	<0.01	1.00
Slope + Ecosite + Road^3	6	28.05	<0.01	1.00
Slope + Ecosite	3	28.08	<0.01	1.00
Trans^2 + Road^3	5	28.44	<0.01	1.00
Trans^2 + Turbine^2	4	28.67	<0.01	1.00
Ecosite	2	29.46	<0.01	1.00
Slope + Ecosite + Turbine^2	5	29.86	<0.01	1.00
Ecosite + Road^3	5	30.06	<0.01	1.00
Trans^2 + Ecosite	4	30.24	<0.01	1.00
Ecosite + Turbine^2	4	31.21	<0.01	1.00

[a] $AIC_c = 198.09$.

We assessed selection for microhabitat vegetation structure and composition at nest sites to account for potential differences in habitats used by females nesting at varying distances from the wind energy facility. For the microhabitat analysis, we created 11 a priori discrete choice models based on previous knowledge of prairie-chicken nesting habitat selection (Svedarsky 1979, Buhnerkempe et al. 1984, Westemeier et al. 1995, Anderson 2012, Matthews et al. 2013; Table 2). We investigated the effect of the following covariates on nest site selection: visual obstruction reading (VOR, dm), litter depth (cm),

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TABLE 2. Comparison of competing discrete choice models in the full a priori model set investigating Greater Prairie-Chicken microhabitat nest site selection by females breeding near Ainsworth, Nebraska, USA, in 2013 and 2014. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c). *K* is the number of model parameters; ΔAIC_c is the difference in AIC_c score relative to the highest-ranked model; and w_i is the Akaike weight, which indicates relative support for the model. CS = cool-season grasses (%), FORB = forbs (%), LD = litter depth (cm), LIT = litter (%), SD = standing dead vegetation (%), SHR = shrubs (%), VOR = visual obstruction reading (dm), WSB = warm-season bunch grasses (%), WS = all warm-season grasses (%), and WSR = warm-season rhizomatous grasses (%). A superscript 2 after a covariate represents a quadratic term and a superscript 3 represents a cubic term.

Model	*K*	ΔAIC_c	w_i
$VOR^3 + LIT + SD + LD^3$	8	0.00 [a]	0.98
Global	18	7.65	0.02
$VOR^3 + SD$	4	25.56	<0.01
$CS + WS + FORB + SHR^3 + VOR^3$	9	40.52	<0.01
VOR^3	3	49.13	<0.01
SD	1	112.03	<0.01
$WSB^3 + SHR^3$	6	209.05	<0.01
SHR^3	3	212.42	<0.01
$SHR^3 + FORB + CS + WS$	6	216.79	<0.01
FORB	1	222.04	<0.01
$WSR + CS + FORB$	3	225.68	<0.01

[a] $AIC_c = 97.66$.

and percent cover of cool-season grasses, forbs, shrubs, litter, standing dead vegetation, warm-season bunch grasses, warm-season rhizomatous grasses, and combined warm-season bunch and rhizomatous grasses. Two other covariates, bare ground cover (%) and live vegetation height (cm), were considered for analysis, but were correlated with litter and VOR, respectively, and thus were not included in the a priori model set.

For all discrete choice analyses, the nest site was considered the sampling unit, and was compared with corresponding random locations as described above. We included a global model in all analyses, but were unable to include a null model because our discrete choice models had no intercept.

Nest survival analysis. We performed a known-fate nest survival analysis to investigate whether the wind energy facility and/or other habitat, weather, or observer variables affected nest survival (White and Burnham 1999, Rotella et al. 2004, Shaffer 2004). We created and analyzed 27 a priori known-fate models relating to predictions of the effects of single or combined covariates on nest survival (Table 3). We included the following covariates in our known-fate models: distance (m) to nearest wind turbine, distance (m) to transmission line, distance (m) to nearest road (Dijak and Thompson 2000, Winter et al. 2000, Bollinger and Gavin 2004), VOR, litter depth, Growing Degree Day (GDD) units of the previous year,

TABLE 3. Comparison of competing known-fate models in the full a priori model set analyzing Greater Prairie-Chicken nest survival near Ainsworth, Nebraska, USA, 2013–2014. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c). *K* is the number of model parameters; ΔAIC_c is the difference in AIC_c score relative to the highest-ranked model; w_i is the Akaike weight, which indicates relative support for the model; and Dev is the model deviance. Age = nest age at discovery (0 = first day of incubation), Ecosite = ecological site of nest (sands, sandy, or subirrigated), FORB = forbs (%), GDD = growing degree day, GRASS = all live cool- and warm-season grasses (%), LD = litter depth (cm), LIT = litter (%), PDSI = monthly Palmer Drought Severity Index, Road = distance to nearest road (m), SD = standing dead vegetation (%), SHR = shrubs (%), Trans = distance to transmission line (m), Turbine = distance to nearest wind turbine (m), and VOR = visual obstruction reading (dm). A superscript 2 after a covariate represents a quadratic term and a superscript 3 represents a cubic term.

Model	*K*	ΔAIC_c	w_i	Dev
$FORB^3 + Age$	5	0.00 [a]	0.21	418.12
$Trans + Age$	3	1.33	0.11	423.48
$SHR + FORB^3 + Age$	6	1.87	0.08	417.98
$Trans + Road + Age$	4	2.66	0.06	422.80
$Road + Age$	3	2.73	0.05	424.88
$Trans + Turbine + Age$	4	3.31	0.04	423.45
$Ecosite + Age$	4	3.31	0.04	423.45
$GRASS + FORB^3 + SHR + Age$	7	3.89	0.03	417.97
$SD + Age$	3	4.06	0.03	426.21
$SHR + Age$	3	4.10	0.03	426.25
$Ecosite + Turbine + Age$	5	4.17	0.03	422.29
$Ecosite + Road + Age$	5	4.25	0.03	422.37
Constant	1	4.31	0.02	430.47
$Road + Turbine + Age$	4	4.33	0.02	424.46
$Trans + Road + Turbine + Age$	5	4.43	0.02	422.56
$VOR^2 + Age$	4	4.62	0.02	424.76
$LD + Age$	3	4.63	0.02	426.78
$GDD + Age$	3	4.68	0.02	426.83
$LIT + Age$	3	4.72	0.02	426.87
$PDSI + Age$	3	4.73	0.02	426.88
$Turbine + Age$	3	4.75	0.02	426.90
$GRASS + Age$	3	4.77	0.02	426.92
$VOR^2 + SHR + FORB^3 + Age$	8	4.96	0.02	417.03
$VOR^2 + SD + Age$	5	5.18	0.02	423.30
$LIT + SD + Age$	4	6.06	0.01	426.19
$VOR^2 + GRASS + Age$	5	6.62	0.01	424.75
$VOR^2 + LD + LIT + Age$	6	8.06	<0.01	424.16

[a] $AIC_c = 428.16$.

Palmer Drought Severity Index (PDSI) of the month the nest was initiated, ecological site, nest age at time of discovery, and percent cover of live cool and warm-season grasses, standing dead vegetation, forbs, shrubs, and litter. Two other variables, live vegetation height and the discrete grouping of nests either near (<1 km) or far from (>1 km) the wind energy facility, were considered, however were not included in the a priori model set: live vegetation height was correlated with both VOR and percent cover of cool- and warm-season grasses, and the discrete grouping

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of nests near and far from the facility had less support than the continuous variable of distance to the nearest wind turbine. We incorporated weather, temporal, and vegetation structure and composition covariates in our analysis because they have been shown to be associated with nest survival (Kirsch 1974, Svedarsky 1988, Johnsgard 2002, Davis 2005, Manzer and Hannon 2005, Fields et al. 2006, Fisher and Davis 2010, Anderson 2012, Matthews et al. 2013). We included ecological site in our analysis due to varying vegetation structure and composition found at each site, which may influence nest survival (Anderson 2012). We included nest age at time of discovery to investigate whether there was an observer effect on nest survival, and included this covariate in all models except the constant nest survival model.

We conducted model selection for the nest site selection analyses and nest survival analysis using AIC_c, w_i, and ΔAIC_c (Burnham and Anderson 2002). Our macrohabitat nest site selection analysis was relatively simple, with 6 covariates of interest and a balanced model set (Arnold 2010), so we considered the evidence of the cumulative weights of covariates in model rankings. In cases of low model certainty, we were prepared to use unconditional model averaging for the model set within the top 90% (cumulative $w_i = 0.90$; Burnham and Anderson 2002, Rehme et al. 2011).We performed discrete choice microhabitat and macrohabitat selection analyses using the survival package (Therneau and Lumley 2009) in R 3.2.0 (R Foundation for Statistical Computing, Vienna, Austria), and conducted the known-fate nest survival analysis in program MARK (White and Burnham 1999, Rotella et al. 2004). All coefficient estimates and means are reported ± standard errors (SE). We considered evidence for an effect to be strong when 95% confidence intervals did not encompass zero.

RESULTS

We captured and tagged 78 female prairie-chickens, 38 in 2013 and 40 in 2014. We fitted 32 captured females with VHF radio transmitters in each year, totaling 64 radio-tagged females. We attached PTT satellite tags to 6 females in 2013 and 8 females in 2014. We located 91 nests, ranging in distance from 0.13 km to 24.10 km from the nearest wind turbine. Of the 91 nests, ~17% were within 1 km of the lek at which the nesting female was captured, 52% within 2 km, and 91% within 5 km. Of 42 females whose first nests failed, 62% ($n = 26$) attempted to nest a second time. There were 5 third nesting attempts. The average clutch size was 11.07 eggs (SE = 0.39, $n = 56$) for first nests, 9.91 eggs (SE = 0.56, $n = 24$) for second nests, and 10.00 eggs for third nests (SE = 1.53, $n = 3$). Of the 91 nests, 36% were successful ($n = 33$).

TABLE 4. Unconditionally model averaged estimates (β) and standard errors (SE) of covariates within the top 90% (cumulative $w_i = 0.90$) of discrete choice models of Greater Prairie-Chicken macrohabitat nest site selection (Table 1).

Covariate	β	SE
Slope	−0.0537	0.0278
Nest	−0.0023	0.0010
$Nest^2$	<0.0001	<0.0001
Road	0.0027	0.0011
$Road^2$	<−0.0001	<0.0001
$Road^3$	<0.0001	<0.0001
Trans	−0.0004	0.0002
$Trans^2$	<0.0001	<0.0001

Macrohabitat Nest Site Selection

We found none of the covariates to be correlated (all r values were <0.6), so we used all covariates in the analysis. In our initial analysis comparing linear vs. nonlinear forms of covariates, we found support for quadratic, nonlinear effects of distance to the transmission line, distance to the nearest nest, and distance to the nearest wind turbine. Distance to the nearest road was supported as a cubic, nonlinear effect, while slope was a linear effect.

We found extremely weak support for an effect of distance to the nearest wind turbine on nest site selection. The model assessing the effect of distance to the nearest wind turbine (Turbine + $Turbine^2$) was ranked 16th (Table 1), with low model support and weak effect ($\Delta AIC_c = 27.86$, $w_i < 0.01$; $\beta_{turbine} = 0.0002 \pm 0.0002$, $\beta_{turbine}{}^2 = <-0.0001 \pm <0.0001$). The top model representing nest site macrohabitat selection included the effects of distance to the nearest road and distance to the nearest nest ($\Delta AIC_c = 0.00$, $w_i = 0.34$; Table 1). The second-best model had a $\Delta AIC_c = 0.57$, and 4 models were within the top 90% (cumulative $w_i = 0.90$). Relative selection for potential nest sites tended to decrease between ~600 m and 1,400 m of the nearest neighboring nest (model-averaged $\beta_{nest} = -0.0023 \pm 0.0010$, $\beta_{nest}{}^2 = <0.0001 \pm <0.0001$; Table 4, Figure 2G), within ~700 m of the nearest road (model-averaged $\beta_{road} = 0.0027 \pm 0.0011$, $\beta_{road}{}^2 = <-0.0001 \pm <0.0001$, $\beta_{road}{}^3 = <0.0001 \pm <0.0001$; Table 4, Figure 2A), and >1,500 m from the transmission line (model-averaged $\beta_{trans} = -0.0004 \pm 0.0002$, $\beta_{trans}{}^2 = <0.0001 \pm <0.0001$; Table 4, Figure 2B).

Microhabitat Nest Site Selection

Percent cover of bare ground and litter were negatively correlated ($r = -0.88$), so we used the litter covariate for further analysis and removed bare ground. Live vegetation height and VOR were also correlated ($r = 0.72$), so we used the VOR covariate for further analysis and removed vegetation height. Our initial analyses provided support for VOR, litter depth, and percent cover of shrubs and

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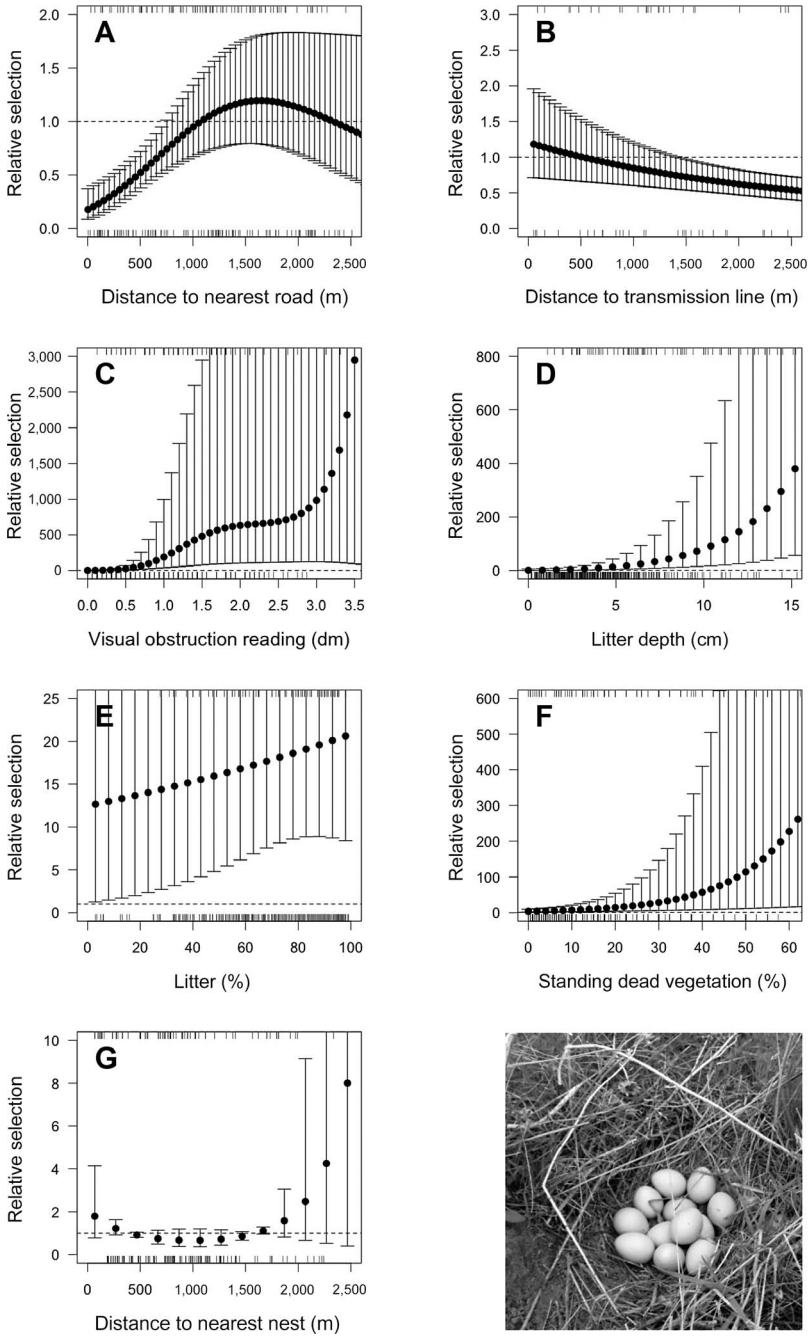


FIGURE 2. Relative selection (with 85% confidence intervals) for potential Greater Prairie-Chicken nest sites (typical nest pictured) in relation to (**A**) distance to the nearest road, (**B**) distance to the transmission line, (**C**) visual obstruction reading, (**D**) litter depth, (**E**) percent litter cover, (**F**) standing dead vegetation, and (**G**) distance to the nearest neighboring nest for females breeding in the vicinity of a wind energy facility near Ainsworth, Nebraska, USA, in 2013 and 2014. Selection is significant for values >1, indicated by the dotted line. Rugs (tick marks) on the top axis represent used nest sites and rugs on the bottom axis represent random sites.

warm-season bunch grasses as cubic, nonlinear effects, and all other effects as linear.

The top model of the discrete choice analysis for nest site microhabitat selection included the effects of litter depth, VOR, and percent cover of litter and standing dead vegetation ($\Delta AIC_c = 0.00$, $w_i = 0.98$; Table 2). VOR, percent litter cover, percent standing dead vegetation cover, and litter depth were selected at higher levels at nest sites than at random locations. Means for VOR, percent litter cover, percent standing dead vegetation cover, and litter depth at nest sites were 1.31 ± 0.07 dm, 75 ± 2%, 27 ± 2%, and 9.12 ± 0.57 cm, respectively. Means for VOR, percent

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TABLE 5. Covariate estimates (β) and standard errors (SE) from the top discrete choice model of Greater Prairie-Chicken microhabitat nest site selection (Table 2).

Covariate	β	SE
VOR	9.1777	2.8708
VOR^2	−4.1053	1.8637
VOR^3	0.6206	0.3645
LIT	0.0051	0.0194
SD	0.0692	0.0274
LD	0.7250	0.5046
LD^2	−0.0371	0.0644
LD^3	0.0011	0.0025

litter cover, percent standing dead vegetation cover, and litter depth at random locations were 0.55 ± 0.03 dm, 74 ± 1%, 12 ± 1%, and 3.79 ± 0.13 cm, respectively. Relative selection for potential nest sites increased with VOR >∼0.2 dm ($\beta_{VOR} = 9.1777 \pm 2.8708$, $\beta_{VOR}{}^2 = -4.1053 \pm 1.8637$, $\beta_{VOR}{}^3 = 0.6206 \pm 0.3645$; Table 5, Figure 2C), litter depth >∼2 cm ($\beta_{LD} = 0.7250 \pm 0.5046$, $\beta_{LD}{}^2 = -0.0371 \pm 0.0644$, $\beta_{LD}{}^3 = 0.0011 \pm 0.0025$; Table 5, Figure 2D), percent cover of litter >∼20% ($\beta_{LIT} = 0.0051 \pm 0.0194$; Table 5, Figure 2E), and percent cover of standing dead vegetation >∼1% ($\beta_{SD} = 0.0692 \pm 0.0274$; Table 5, Figure 2F).

Nest Survival

The daily nest survival estimate from the constant model was 0.9609 (SE = 0.0050). The survival estimate for the 25-day incubation period was 0.3689 (SE = 0.0480). Live vegetation height was correlated with VOR ($r = 0.67$) and percent cover of live cool- and warm-season grasses ($r = 0.72$), so we used the covariates VOR and percent cover of grasses and removed vegetation height. We found support for percent forb cover as a cubic, nonlinear effect, VOR as a quadratic, nonlinear effect, and all other effects as linear. The linear, continuous description of distance to the nearest wind turbine had more support than the discrete grouping of nests near and far from the wind energy facility, so the continuous covariate was used in our model comparisons.

We found no evidence of an effect on nest survival of the turbines or the transmission line associated with the wind energy facility. The model including distance to the nearest wind turbine and nest age at time of discovery ranked 21st, with little support ($\Delta AIC_c = 4.75$, $w_i = 0.02$; Table 3). The model-averaged estimate of the effect of distance to the nearest wind turbine also provided no support for an effect of the wind energy facility on nest survival ($\beta_{turbine} = <0.0001 \pm <0.0001$; Table 6). There was considerable model uncertainty in our assessment of nest survival. The top nest survival model included percent cover of forbs and nest age at discovery ($\Delta AIC_c = 0.00$, $w_i = 0.21$, $\hat{c} = 4.92$; Table 3). The second-best model had a $\Delta AIC_c = 1.33$, and 20 models were within the top 90% (cumulative $w_i = 0.90$).

TABLE 6. Unconditionally model averaged estimates (β) and standard errors (SE) of covariates within the top 90% (cumulative $w_i = 0.90$) of known-fate models of Greater Prairie-Chicken nest survival (Table 3).

Covariate	β	SE
Age	0.0388	0.0295
FORB	0.0563	0.0750
$FORB^2$	−0.0033	0.0044
$FORB^3$	<0.0001	0.0001
Road	<0.0001	0.0001
Ecosite (sandy)	−0.0557	0.1038
Ecosite (subirrigated)	−0.0446	0.0888
SHR	0.0021	0.0066
SD	0.0002	0.0004
Turbine	<0.0001	<0.0001
VOR	−0.0219	0.0454
VOR^2	0.0062	0.0129
LD	0.0002	0.0008
GDD	−0.0001	0.0004
LIT	<0.0001	0.0002
GRASS	<0.0001	0.0002
Trans	<0.0001	<0.0001

None of the model-averaged coefficients showed evidence of an effect on nest survival (Table 6).

DISCUSSION

We found little evidence to support an effect of the wind energy facility on prairie-chicken nest site selection or nest survival. Instead, we found that the primary drivers of nest site selection were habitat and landscape factors (Figure 2). Nest site selection and survival in grasslands without wind turbines are driven largely by spatial and temporal patchiness of vegetation cover created by land use and grazing management (Anderson 2012, Matthews et al. 2013). The distribution of roads may also be critical in planning any developments in areas of contiguous grassland habitat. Current interest in wind energy development has sparked a flurry of research into direct and indirect effects at a local level of wind turbines, roads, and transmission lines (Smith and Dwyer 2016). But, the proportion of prairie-chickens and other grassland birds in the largely unfragmented Sandhills region affected by wind energy development is relatively insignificant when compared with the proportion of grassland birds affected by grazing and other grassland management practices, even if the density of wind energy facilities has increased substantially in the region. Management for heterogeneity of vegetation structure among and within pastures is critical for prairie-chickens (Powell et al. 2014, Anderson et al. 2015).

Responses to the Wind Energy Facility

Our findings suggest no negative impacts of the wind energy facility on female prairie-chicken nest site

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selection and nest survival in our unfragmented landscape. McNew et al. (2014) also found no effect of proximity to wind turbines on nest site selection or survival in a fragmented landscape in Kansas, USA. Thus, there is no evidence, to date, to suggest that prairie-chickens nesting in proximity to wind energy facilities change their patterns of nest site selection or that wind energy facilities affect their nest survival. Winder et al. (2014, 2015), in a study concurrent with that of McNew et al. (2014), reported some effects of a wind energy facility on space use and lek persistence using a before–after study design. However, we found no effects of the wind energy facility on space use of females in work concurrent with this study (Harrison 2015). Landscape context appears to be critical in any assessment of the effects of wind energy facilities on prairie-chickens. A study of Greater Sage-Grouse (*Centrocercus urophasianus*) in Wyoming, USA, found no effect of a wind energy facility on nest site selection (LeBeau et al. 2017a) or lek counts (LeBeau et al. 2017b) in 2 concurrent studies. However, displacement of birds by wind energy facilities has been found for other taxa, including geese (Larsen and Madsen 2000), ducks (Loesch et al. 2013), raptors (Pearce-Higgins et al. 2009, Garvin et al. 2011), shorebirds (Pearce-Higgins et al. 2009, 2012, Niemuth et al. 2013), and songbirds (Pearce-Higgins et al. 2009, Stevens et al. 2013, but see Hale et al. 2014, Johnson 2016). The causes of spatial displacement of these taxa near wind energy facilities may include habitat loss, anthropogenic noise, tall structures, or changes in predator abundance (Smith and Dwyer 2016), but the mechanisms are poorly understood.

In contrast to our results, others have reported negative effects of anthropogenic features on the nesting dynamics of other grouse species. Pitman et al. (2005) found negative impacts of anthropogenic features, such as wellheads, buildings, transmission lines, center-pivots, and roads, on nest site selection by Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*). LeBeau et al. (2014) reported negative effects of wind energy facilities on nest survival of Greater Sage-Grouse (but see LeBeau et al. 2017a). It seems likely that differences in responses are due to the type of energy development and level of disturbance. Prairie grouse are possibly more sensitive to oil and gas infrastructure than wind energy facilities because of either noise or activity levels. Alternatively, Greater Prairie-Chickens may be less sensitive to anthropogenic disturbance from energy development than other prairie grouse species that are often investigated in oil and gas infrastructure studies, such as Greater Sage-Grouse (Holloran 2005, Aldridge and Boyce 2007, LeBeau et al. 2014). Studies of other taxa have found little evidence of an effect of wind energy facilities on nest survival (Red-winged Blackbirds [*Agelaius phoeniceus*]: Gillespie and Dinsmore 2014; McCown's Longspurs [*Rhynchophanes mccownii*]: Mahoney and Chalfoun 2016).

Our study focused on a wind energy facility with fewer turbines (36 turbines, distributed in 4- to 7-turbine strings along ridge tops) than the 67-turbine facility in the Winder et al. (2014, 2015) study, and the transmission line in our study may have been smaller than transmission lines in other research. Such differences in the scale and size of development may have contributed to the lack of an effect on nest survival and nest site selection in our study. Effects on nesting ecology may be seen near larger wind energy facilities that have a greater footprint on the landscape. However, prairie-chickens nested in the midst of the wind energy facility and along the transmission line during our study, which created the potential for effects on nest survival to be apparent.

Our finding that prairie-chickens did not avoid nesting near wind turbines contrasts with suggestions by Pruett et al. (2009) that prairie-chickens may avoid wind turbines because of perceived risk. Although prairie-chickens in our study apparently did not perceive wind turbines as potential perching points for raptors or symbolic of other risks, it is possible that female prairie-chickens in proximity to the wind energy facility may have altered their predator avoidance behavior or foraging strategies during the nesting period to make them less susceptible to predation. Smith et al. (2016) reported changes in male behavior near the wind energy facility that may have been related to less need for predator avoidance. We encourage future studies of nesting behavior in the context of energy development to evaluate the ability of females to adjust their life history strategies (Martin 1995).

Responses to Roads and the Transmission Line

Greater Prairie-Chicken nest site selection was higher for sites farther from roads, with 74% of Greater Prairie-Chickens selecting nest sites >700 m from roads. Similar to our results (Figure 2A), Lesser Prairie-Chickens have also been found to avoid roads during nesting (Robel et al. 2004, Pitman et al. 2005), although the mechanism for avoidance has not been determined. Habitat edges such as roads are known to increase predator abundance (Dijak and Thompson 2000), and nest predation has been found to be higher near roads (Pescador and Peris 2007). Thus, prairie-chickens may avoid nesting near roads to decrease the likelihood of predation. Alternatively, prairie-chickens may avoid roads due to noise. Roads in our study site included 2 highways and smaller, secondary roads, and it is highly likely that traffic volume influenced nest site selection near roads. Vehicles ranging from small cars to large semi-trailer trucks frequently moved along the roads in our study site, and truck noise could be heard up to ~1.6 km away (J. O. Harrison personal observation). Development of wind energy facilities is often accompa-

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nied by the construction of roads. Our findings suggest that larger wind energy facilities with a dense network of roads may cause prairie-chickens to select nest sites farther from the facility due to avoidance of roads, which could affect the demographics of prairie-chicken populations near wind energy facilities. We encourage future research to focus on the mechanisms deterring prairie-chickens from nesting near roads.

Nest site selection was not lower near the transmission line in our study site. However, nest site selection did decline at distances >1,500 m from the transmission line (Figure 2B), and we believe that this result was caused by correlated habitat distribution patterns and nesting patterns around the transmission line. Thus, we encourage caution in the interpretation of a decline in nest site selection in the region >1,500 m from the transmission line. We note that several females nested very close to the transmission line during our study (Figure 1), and we found no effects of the transmission line on nest survival. Our results contrast with those of Pitman et al. (2005), who found that Lesser Prairie-Chickens avoided nesting within ~400 m of transmission lines. Avoidance of transmission lines may be due to predation threat, as corvids and raptors have been reported to frequently use high-voltage transmission lines for perching (Worley 1984) or nesting (Coates et al. 2014). Perceived predation threat did not deter prairie-chickens from nesting near the transmission line in our study. In sum, Lesser Prairie-Chickens appear to be more sensitive than Greater Prairie-Chickens to the presence of anthropogenic structures such as transmission lines.

Responses to Microhabitat

Prairie-chickens in our study nested in sites with high amounts of cover and residual vegetation. The importance of vegetation cover is supported by similar studies across the prairie-chicken's range (Hamerstrom et al. 1957, Tester and Marshall 1962, Jones 1963, Svedarsky 1979, Buhnerkempe et al. 1984, Westemeier et al. 1995, Anderson 2012). Anderson (2012) reported an optimal VOR between 10.0 and 22.5 cm in the eastern Sandhills, with a mean VOR of 10.8 cm, which is similar to the mean VOR at nest sites in our study of 13.1 cm. The Sandhills region has more sparse vegetation than tallgrass prairie regions (our study mean VOR at random sites = 5.5 cm), which affects selection for nesting and brood habitat (Powell et al. 2014, Anderson et al. 2015). Prairie-chickens in our study nested in areas with twice the cover of residual standing dead vegetation as random sites, which may inhibit predator detection (Svedarsky 1979, Westemeier et al. 1995, Anderson 2012). Our study suggests that heterogeneity of vegetation structure among and within pastures is critical for prairie-chicken nesting habitat (Powell et al. 2014, Anderson et al. 2015), which will inform range-wide prairie-chicken management decisions.

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