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RESEARCH ARTICLE

Anthropogenic noise does not surpass land cover in explaining habitat selection of Greater Prairie-Chicken (*Tympanuchus cupido*)

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ABSTRACT

Over the last century, increasing human populations and conversion of grassland to agriculture have had severe consequences for numbers of Greater Prairie-Chicken (*Tympanuchus cupido*). Understanding Greater Prairie-Chicken response to human disturbance, including the effects of anthropogenic noise and landscape modification, is vital for conserving remaining populations because these disturbances are becoming more common in grassland systems. Here, we evaluate the effect of low-frequency noise emitted from a wind energy facility on habitat selection. We used the Normalized Difference Soundscape Index, a ratio of human-generated and biological acoustic components, to determine the impact of the dominant acoustic characteristics of habitat relative to physical landscape features known to influence within–home range habitat selection. Female Greater Prairie-Chickens avoided wooded areas and row crops but showed no selection or avoidance of wind turbines based on the availability of these features across their home range. Although the acoustic environment near the wind energy facility was dominated by anthropogenic noise, our results show that acoustic habitat selection is not evident for this species. In contrast, our work highlights the need to reduce the presence of trees, which have been historically absent from the region, as well as decrease the conversion of grassland to row-crop agriculture. Our findings suggest physical landscape changes surpass altered acoustic environments in mediating Greater Prairie-Chicken habitat selection.

Keywords: acoustic habitat selection, anthropogenic noise, avoidance behavior, prairie grouse, resource selection, soundscape, wind energy, woody encroachment

El ruido antropogénico no sobrepasa a la cobertura del suelo para explicar la selección de hábitat de *Tympanuchus cupido*

RESUMEN

A lo largo del último siglo, al aumento de la población humana y la conversión de los pastizales a la agricultura han tenido severas consecuencias para los números de *Tympanuchus cupido*. Entender la respuesta de *T. cupido* al disturbio humano, incluyendo los efectos del ruido antropogénico y la modificación del paisaje, es fundamental para conservar las poblaciones remanentes debido a que estos disturbios se están volviendo cada vez más comunes en los sistemas de pastizales. En este trabajo, evaluamos el efecto del ruido de baja frecuencia emitido por una instalación de energía eólica sobre la selección de hábitat. Usamos el Índice de Paisaje Sonoro de Diferencia Normalizada, un cociente entre los componentes generados por los humanos y los acústicos biológicos, para determinar el impacto de las características acústicas dominantes del hábitat con relación a los rasgos físicos del paisaje conocidos por influenciar la selección de hábitat dentro del rango de hogar. Las hembras de *T. cupido* evitaron las áreas boscosas y los cultivos en hilera, pero no mostraron selección o evasión de las turbinas eólicas en base a la disponibilidad de estos rasgos a través de sus rangos de hogar. Aunque el ambiente acústico cerca de la instalación de energía eólica estuvo dominado por ruido antropogénico, nuestros resultados muestran que la selección de hábitat acústico no es algo evidente para esta especie. En contraste, nuestro trabajo subraya la necesidad de reducir la presencia de árboles que han estado históricamente ausentes de la región, así como de disminuir la conversión de pastizales a agricultura de cultivos en hilera. Nuestros resultados sugieren que los cambios físicos en el paisaje sobrepasan a los ambientes acústicos alterados para determinar la selección de hábitat de *T. cupido*.

Palabras clave: comportamiento de evasión, energía eólica, ocupación arbórea, paisaje sonoro, ruido antropogénico, selección de hábitat acústico, selección de recursos, urogallo de pradera

INTRODUCTION

The amount of anthropogenic noise in the environment has potential to have as large an impact on habitat selection as vegetation cover types, topographical features, or physical anthropogenic landscape features (Ware et al. 2015, Shannon et al. 2016, Kleist et al. 2017). For example, exposure to chronic, industrial noise from natural gas wells had a larger effect than forest cover on nest box selection for cavity-nesting Ash-throated Flycatchers (*Myiarchus cinerascens*) and Mountain Bluebirds (*Sialia currucoides*) (Kleist et al. 2017). Other recent work suggests that acoustically sensitive bird species can be largely absent from habitats experiencing even slight increases in ambient acoustic conditions from anthropogenic sources (Gasc et al. 2016, Shannon et al. 2016). Collectively, these studies suggest anthropogenic noise may render otherwise suitable habitat unusable, resulting in partial habitat loss (Francis 2015, Ware et al. 2015). Characterizing and managing the acoustic environment, in addition to the dominant physical land cover, should be a component of terrestrial ecosystem management (Kleist et al. 2017). Given the proliferation of anthropogenic noise across landscapes (Barber et al. 2011, Shannon et al. 2016), further investigation of the effect of acoustic disturbance on habitat selection of birds is warranted (Patricelli et al. 2013, Gasc et al. 2016, Mullet et al. 2017).

One example of a species with well-studied physical habitat preferences is the Greater Prairie-Chicken (*Tympanuchus cupido*), a grassland-obligate grouse of conservation concern in North America (Matthews et al. 2013, McNew et al. 2014, Winder et al. 2015, Harrison et al. 2017). Greater Prairie-Chickens are ground-nesting birds that do not forage or roost in wooded areas during the breeding season and explicitly rely on grassland resources (e.g., leaves, seeds, and insects) only available at or near ground level (Johnson et al. 2011). Females nest within 2–3 km of the lek at which successful copulation occurred (Powell et al. 2014, Hovick et al. 2015b, Winder et al. 2015). Although once common throughout the Great Plains of North America, Greater Prairie-Chickens have experienced a precipitous decline due to habitat loss caused by agricultural expansion and are now limited to a small fraction of their original distribution (Johnson et al. 2011). More recently, population reductions have been linked to increased fragmentation of remaining grassland habitats from energy development (Pruett et al. 2009, Hovick et al. 2014). These anthropogenic disturbances are also increasingly exposing Greater Prairie-Chickens to sensory disturbance including anthropogenic noise (Whalen et al. 2019), which has been posited as a likely driver of functional habitat loss (Hovick et al. 2014). Wind turbine noise, for example, is a potential source of sensory disturbance, as it is audible to Greater Prairie-Chickens (Walsh et al. 2015, Whalen 2015). Recently, low-frequency wind turbine noise has been determined to result in adjustment to Greater Prairie-Chicken vocalizations emitted within this distance (Whalen et al. 2018).

To date, research on habitat selection of prairie grouse, including the closely related Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*), has shown avoidance of anthropogenic landscape structures such as power transmission lines and well pads (Pruett et al. 2009, Hovick et al. 2014, Plumb et al. 2019) and natural landscape features including grassland habitat edges (Winder et al. 2015) and trees (Lautenbach et al. 2017). However, little is known about the effects of anthropogenic structures on Greater Prairie-Chicken habitat use beyond the nest and lek locations (Pruett et al. 2009; McNew et al. 2014; Hovick et al. 2015a, 2015b, 2015c). Furthermore, the role of anthropogenic noise on the habitat use of prairie grouse remains unclear because field investigation has not been attempted. Because the presence of low-frequency noise sources (i.e. energy extraction infrastructure) is rapidly expanding across the Great Plains (Northrup and Wittemyer 2013, Allred et al. 2015), the lack of an understanding on the effects of anthropogenic noise intrusion on Greater Prairie-Chicken behavior–habitat relationships is a cause for concern as such low-frequency noise overlaps with their operative acoustic spectrum (Walsh et al. 2015, Smith et al. 2016, Whalen et al. 2018).

The impact of anthropogenic noise is thought to be severe when it interferes with cognitive processing leading to distraction, a phenomenon known as "informational masking" (Kidd et al. 2008). Such disturbance may occur when irrelevant stimuli outcompete for limited attentional resources (Rosa and Koper 2018) thus redirecting attention and potentially leaving individuals more susceptible to predation or to missing foraging and mating opportunities (Chan et al. 2010, Francis and Barber 2013, Smith et al. 2017, Kleist et al. 2018). For instance, noise can impair the use of multisensory prey detection and subsequent handling as prey detection and hunting success is not solely limited to visual cues (Maes and de Groot 2003, Leiva et al. 2015). Information masking differs from the more commonly studied energetic masking by pertaining to interference of an animal's cognitive processes instead of an animal's ability to detect a signal due to an overlap of the frequency distribution of the background noise and the signal (Bradbury and Vehrencamp 2011, Rosa and Koper 2018). Regardless of the mechanism, anthropogenic noise may cause avoidance of noisy areas causing displacement (Blickley and Patricelli 2012, Hovick et al. 2014, May 2015). Wind turbines propagate constant, low-frequency noise (Barber et al. 2011, Whalen et al. 2018), which places this acoustic disturbance at the "chronic" end of the "disturbance–behavior interference continuum" (Francis and Barber

2013), such that their presence may displace individuals from otherwise suitable habitat or interfere with essential behaviors such as foraging (May 2015, May et al. 2019).

The impact of low-frequency noise emitted from wind energy facilities on habitat selection when an individual is exposed to this relatively new sensory disturbance is not known (Barber et al. 2011, Hovick et al. 2014, Smith and Dwyer 2016). In contrast, grassland habitat that is lacking trees and tall anthropogenic structures such as transmission lines is commonly selected by prairie grouse because such habitat has lower predation risk (Matthews et al. 2013, Hovick et al. 2014). At our study site, previous work showed no effects of proximity to the wind energy facility on movements of female Greater Prairie-Chickens during the breeding season (Harrison 2015), selection of nest sites (Harrison et al. 2017), and selection of brood-rearing sites (Harrison 2015). However, Whalen (2015) showed that wind and topography caused noise levels near the wind energy facility to vary such that simple distance to turbines was not sufficient to predict local noise levels. Currently, it is not known whether anthropogenic noise affects habitat selection when studied in concert with physical landscape features such as trees and row-crop fields.

We collected field data on female Greater Prairie-Chickens breeding in the general vicinity of a wind energy facility to gain insight into the features of the acoustic and physical grassland environment that influence habitat selection. We aimed to assess whether the soundscape, which is the totality of the sounds occurring at any location within a certain time frame (Qi et al. 2008), surrounding the wind energy facility affected the selection of natural and anthropogenic landscape features by female Greater Prairie-Chickens. Specifically, we developed resource selection functions to examine the effect of proximity to anthropogenic features (e.g., wind turbines, transmission lines, and row-crop agriculture), trees, and topography on habitat selection within home ranges (i.e. third-order selection; Johnson 1980). Next, we evaluated selection of acoustic habitat available to female Greater Prairie-Chickens residing near a wind energy facility. For this analysis, we developed an acoustic surface by interpolating the ground-level acoustic soundscape (level of anthropogenic noise relative to biological sounds, the Normalized Difference Soundscape Index; Qi et al. 2008, Kasten et al. 2012) available to individuals during the breeding season. We included this spatially explicit index of the acoustic environment with the physical landscape characteristics we measured for our resource selection analysis. Because the home range of 53% of our study individuals fell within our acoustic surface, we ran separate analyses for these individuals to evaluate the role of distance to wind turbine and acoustic environment on habitat selection. In addition, we assessed the effects of physical landscape features not associated with the wind energy facility on the entire study population, to demonstrate behavioral–physical habitat relationships are not specific to a single section of the study area.

We hypothesized that female Greater Prairie-Chickens would exhibit selection for both known physical habitat features and areas not exposed to low-frequency anthropogenic noise. As a result, we predicted that Greater Prairie-Chickens would select grassland areas with relatively few anthropogenic structures including power transmission lines and that they would avoid areas near wind turbines. Further, we predicted that treeless grassland would be selected more than wooded areas and that prairie-chickens would avoid row-crop agriculture. If prairie-chickens selected habitat based on the natural soundscape, we predicted an acoustic environment dominated by anthropogenic sound (i.e. machinery) would be a key component of habitat avoidance. We provide the first assessment of the influence of acoustic disturbance on the resource selection of female Greater Prairie-Chickens during the breeding season.

MATERIALS AND METHODS

Study Area

Our study area was located in the vicinity of a preexisting wind energy facility managed by the Nebraska Public Power District (NPPD), located ~10 km south of Ainsworth, Brown County, Nebraska (42°27′44″N, 99°55′39″W; Figure 1) in the Sandhills ecoregion. The facility consists of thirty-six 1.65-MW capacity constant-velocity wind turbines, standing 70 m to the hub with 40 m long blades. The total area of the wind energy facility was 44 km^2. Other infrastructure included maintenance buildings, gravel roads, an electrical substation, and power lines and towers. The facility has been in existence since 2005 (Nebraska Public Power District 2015). Land use surrounding the wind energy facility is predominantly cattle ranching (United States Fish and Wildlife Service 2015).

We created a ~1,130 km^2 study area by fitting a minimum convex polygon to all locations of female Greater Prairie-Chickens (n = 49) monitored during the breeding season (April–July 2013–2014). The area was composed of 88% grassland/prairie, 7% row-crop agriculture (corn and soybeans), 2% woodland, 1% developed area, and 1% water bodies. The landscape supported a road density of 0.49 km of road per km^2 (Raynor et al. 2017a), which is low when compared to a grassland/agriculture system hosting Greater Prairie-Chickens in Kansas with almost 3 times higher road density (1.40 km of road per km^2; Winder et al. 2014). Furthermore, low levels of row-crop agriculture in the area have led to relatively little habitat fragmentation of plant and animal populations (Chaplin et al. 2012). See Online Supplementary Material for further description of the study site.

Trapping Methods and Movement Data

We captured females during March and April of 2013 and 2014 using walk-in traps at 13 lek sites in 2013 and 15 in 2014 (12 leks were considered in both years of the study; Figure 1). We used a disturbance gradient design in which leks were distributed roughly evenly along a 24 km straight-line gradient running perpendicularly away from the wind energy facility, allowing us to sample prairie-chickens from lek sites near and far from the wind turbines to identify at what distance or spatial scale effects occur (Powell et al. 2017); 3 leks were within 1 km of the wind energy facility. Females were tracked using radio/GPS methods, with their locations established on a near-daily basis during the breeding season. See Online Supplementary Material for further description of prairie-chicken tracking methodology.

Acoustic Surface

To estimate the level of anthropogenic noise dominance within the grassland soundscape, we measured ambient sound levels at prairie-chicken head height (25 cm) at 10 random locations on the landscape, 15 prairie-chicken leks, and from an acoustic sampling grid of 70 systematic locations overlaid on the wind energy facility (Supplemental Material Figure S1; Whalen 2015). Recordings were made with SM2+ audio recorders with omnidirectional microphones (Wildlife Acoustics, Maynard, Massachusetts, USA) mounted on wooden stakes (Whalen 2015). A time-stratified random sampling schedule was followed to record sound for 3 hr between 0100 and 0500 hours at each location on the landscape 3–6 times between March and July in both 2013 and 2014. Acoustic sampling occurred in the early morning as concurrent studies required the isolation of anthropogenic noise to assess the spread of sounds from turbines (Whalen et al. 2019). The acoustic environment encountered by prairie-chickens during the day most likely included more biological acoustic components than we measured while the levels of anthropogenic noise on the landscape likely were similar to those recorded at night. Recordings collected during periods of rain or high winds (above 24 km hr^{-1}) were not used in subsequent analyses. See Online Supplementary Material for descriptions of the methodology used to calibrate acoustic recording equipment. From our acoustic samples (Supplemental Material Figure S1), we used 2 min every 30 min throughout the

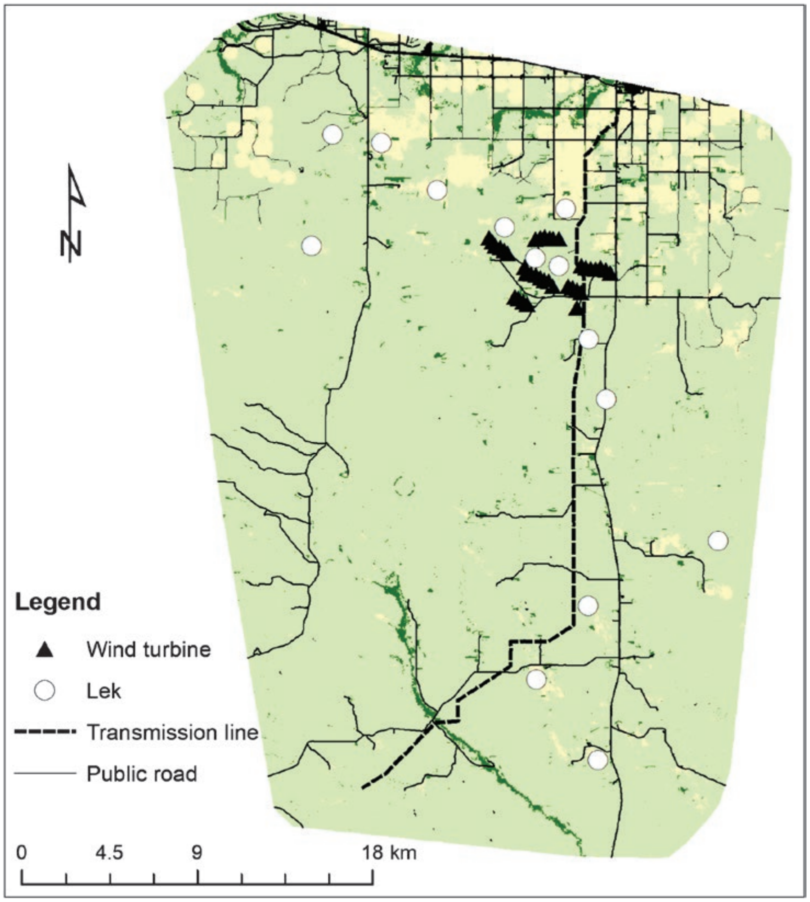

FIGURE 1. Study area and occupied leks targeted for capturing and monitoring female Greater Prairie-Chicken (*Tympanuchus cupido*) near Ainsworth, Brown County, Nebraska. Trees and row-crop agriculture are depicted as dark green and yellow, respectively.

3 hr sampling period to estimate the level of anthropogenic noise within the soundscape. We calculated the Normalized Difference Soundscape Index (NDSI) ratio of human-generated to biological acoustic components using methods described by Qi et al. (2008) and calculated in R package SEEWAVE (Sueur et al. 2019). NDSI employs a simple algorithm to compress acoustic information into an ecological index. The NDSI is calculated as follows:

$$(b-a)\ /\ (b+a);$$

where b is biophonic sound in the range of 2–10 kHz and a is technophonic sound (~0.1–2 kHz; see Kasten et al. 2012). NDSI ranges from −1 to +1 where low values of the index indicate the dominance of lower technophonic frequencies and higher values of the index show dominance of higher biophonic frequencies. We used the NDSI to determine the dominance of these 2 sound types on the landscape. We considered acoustic signals detected from frequencies between 0.100 and 2 kHz as most likely to be anthropogenic noise (technophony) in this landscape, while signals above 2 kHz were considered most likely to be biological sounds (biophony) emitted by organisms such as grassland birds, amphibians, and insects (Gage and Axel 2014). Concurrent work in this landscape demonstrated that wind turbine noise overlaps with the 0.200–2 kHz spectrum (Walsh et al. 2015, Raynor et al. 2017b, Whalen et al. 2018).

After combining data from both years, we performed an interpolation analysis ("kriging") using the Geostatistical Analyst Wizard in ArcView 110.4.1 (ESRI, Redlands, California, USA) to estimate NDSI variation on the landscape at 30 m resolution. This interpolation method used a set of linear regressions to predict values at locations without data, based on data associated with known locations and the degree of spatial dependence between data points (Houlding 2000, Dale and Fortin 2014). We used ordinary kriging and a stable semivariogram with a prediction output and set the lag size to 2,400 m and the number of lags to 12. We used cross-validation to assess the reliability of our model, and our results indicated that prediction error was unbiased; variability in prediction was assessed correctly and predicted vs. measured points fell along a 45° line (Supplemental Material Figure S2). Thus, we considered our estimated soundscape index layer to be a reliable acoustic surface for our landscape-level acoustic habitat selection analysis. See Online Supplementary Material for descriptions of the methodology used to interpolate the acoustic index.

Physical Habitat Covariates

We modified existing 30 m resolution habitat/vegetation layers (National Land Cover Database, 2011; Homer et al. 2012) and a digital land-use map from Smith et al. (2017) by combining similar habitat types to produce a layer with 6 habitat classes. Habitat classes were agriculture, wooded areas comprising upland or riparian woodlands, primary or paved roads, secondary roads (i.e. non-paved roads), the wind energy facility electrical transmission line, and wind turbine locations (Figure 1). We calculated distances from the centroid of all 30 × 30 m used and available pixels to the closest pixel of the habitat classes using the "Euclidean Distance" tool in the Spatial Analyst toolbox in ArcMap 10.5.1 (ESRI, Redlands, California, USA) using methods described by Benson (2013). We estimated slope and elevation from digital elevation models (DEM) in ArcGIS (Table 1); DEM data were estimated at ~9.5 m resolution, but we averaged these data across 30 m used and available pixels for our analyses. Mean NDSI values were estimated from our soundscape layer and used as a classification-based value. These distance- and classification-based values allowed us to compare physical and acoustic resources used by and available to female prairie-chickens while traversing their home range.

Use and Availability

To make inference concerning the habitat choices that individual birds made, we evaluated female prairie-chicken habitat selection within the home range, or at the third order of Johnson's (1980) hierarchy of habitat selection by constructing resource selection functions (RSF). Thus, our inferences with regard to resource selection must be viewed in the context of our third-order, within–home range analyses. We compared locations used by prairie-chickens to those available within their breeding season home range following a use-vs.-availability design (Boyce et al. 2002). We identified 30 m pixels (30 × 30 m) on the landscape outside of a 100 m diameter circle centered on females' nest locations. In so doing, we selected locations that were likely associated with foraging, roosting, or brood rearing rather than nesting. Used and available locations within a 100 m diameter of a nest were not included in our analysis. Therefore, locations >50 m from a nest and within the outer limits of each individual's home range were included in our analysis. We restricted our analysis to females with at least 30 total locations collected over the breeding season of which at least 20 were not associated with a nest. We considered all data collected from April to July. We chose to focus our analyses on locations away from the nest because selection at the nest sites was quantified previously (Harrison et al. 2017) and because resource selection away from the nest site is critical for survival and reproduction during this important period of the annual cycle (Winder et al. 2014).

To estimate habitat availability within each home range, we estimated 95% fixed kernel home ranges with the plug-in estimator to determine bandwidth (Sheather and Jones 1991) using the package adehabitatHR in R (Calenge and Fortmann-Roe 2013, R Development Core Team 2019) and telemetry data for each prairie-chicken.

We estimated home ranges for 49 female prairie-chickens with telemetry data (mean number of locations: 178; range: 32–1,188) collected across 1–4 mo in both 2013 and 2014 (mean monitoring days: 85; range:18–95). We systematically subsampled 30 m pixels throughout each home range (resulting in a mean of 1,060 pixels km^{-2}) to estimate the availability of resources for each individual (Benson 2013, Benson et al. 2016). We calculated distances to landscape features from the centroid of all 30 m pixels designated as used by or available to female prairie-chickens. We classified the slope and elevation values associated with used and available pixels. To determine if home range size was estimated without bias concerning sampling effort (Winder et al. 2014), we used analysis of covariance (ANCOVA) to test whether home range size was a product of the number of individual locations, tag type, or their interaction.

Resource-Selection Models

We modeled resource selection within home ranges with generalized linear mixed regression models (GLMMs) implemented in the R 3.3.2 package lme4 with a binary (0 = available, 1 = used) response variable. Resource selection functions were estimated with use–availability logistic regression (design III data; Thomas and Taylor 2006) with random intercepts for each individual to mitigate the effects of unbalanced sampling design and the lack of independence between used locations from the same individual (Gillies et al. 2006). Before resource-selection modeling, we rescaled values for all fixed effects by subtracting their mean and dividing by 2 standard deviations following Gelman et al. (2008) to improve the fit of the model and to allow for the direct comparison of the effect size of each predictor variable.

We conducted 2 sets of resource selection analyses: (1) females from the study site (Figures 1 and 2), and (2) only females with home ranges near the wind energy facility (Figures 3 and 4). For the first analysis, we used a suite of covariates (Table 1) to develop 15 models that considered physical habitat characteristics known to influence habitat selection, and we applied the models to data from all females in our study site. This analysis did not consider potential effects of the wind energy facility on habitat selection of Greater Prairie-Chickens. We evaluated the effect of topography (slope and elevation) and proximity to trees, transmission line, and row-crop agricultural land on resource selection. We included distance to capture lek into all a priori environmental models in an attempt to spatially control habitat selection patterns, as the lek at which a female prairie-chicken breeds likely influences selection patterns (Hovick et al. 2015a). We investigated whether continuous covariates were nonlinear by creating logistic regression models in which each covariate (x) was

TABLE 1. Influence of environmental variables on Greater Prairie-Chicken resource selection near Ainsworth, Nebraska, USA, 2013–2014. Influential fixed effects, based on 95% confidence intervals, shown in bold. Estimates (±SE) are derived from model-averaging of the set of 2 models <2 ΔAIC_c of the top model for whole study area ($n = 49$ individuals) and from set of 6 models <2 ΔAIC_c of the top model for the 26 individuals with a home range encapsulated by the predicted acoustic surface. Units for lek, trees, transmission line, row crop, and wind turbine are distances to those features (m). Units for Normalized Difference Soundscape Index (NDSI) range from −1 to +1.

Variable	β	95% LCL	95% UCL	Mean (±SD) used value	Mean (±SD) available value
Whole study area					
Intercept	**−2.20**	**−2.26**	**−2.14**	–	–
Lek	**−0.06**	**−0.10**	**−0.03**	1,962 (1,777)	2,062 (1,723)
Slope	**−0.03**	−0.06	0.00	2° (2)	2° (2)
Trees	**0.23**	**0.19**	**0.28**	633 (379)	600 (446)
Trees^2	**−0.14**	**−0.17**	**−0.11**	–	–
Transmission	**−0.08**	**−0.14**	**−0.02**	3,890 (4,118)	4,031 (4,106)
Transmission^2	**0.05**	**0.02**	**0.07**	–	–
Row crop	**0.07**	**0.03**	**0.12**	619 (474)	576 (468)
Row crop^2	−0.01	−0.03	0.01	–	–
Acoustic surface					
Intercept	**−2.11**	**−2.19**	**−2.03**	–	
Lek	**−0.07**	−0.13	0.00	1,741 (1,113)	1,785 (1,173)
Slope	−0.03	−0.06	0.01	2° (2)	2° (2)
Trees	**0.25**	**0.19**	**0.30**	605 (315)	571 (357)
Trees^2	**−0.33**	**−0.39**	**−0.28**	–	–
Transmission	−0.06	−0.14	0.01	2,486 (2,037)	2,571 (2,156)
Transmission^2	**−0.10**	**−0.18**	**−0.02**	–	–
Row crop	0.01	−0.04	0.07	645 (474)	606 (464)
Row crop^2	**0.03**	**0.00**	**0.06**	–	–
Wind turbine	0.08	−0.02	0.18	3,467 (5,109)	3,472 (5,132)
Wind turbine^2	−0.04	−0.10	0.03	–	–
NDSI	0.01	−0.03	0.06	−0.49 (0.22)	−0.49 (0.23)

represented by a linear and quadratic term ($x + x^2$). Many of the covariates were highly correlated (Pearson's correlation analysis $|r| \geq 0.6$); however, we did not allow 2 highly correlated covariates in the same model.

NDSI was highly correlated with distance to nearest wind turbine (r = 0.87), indicating anthropogenic noise within the grassland soundscape decreased with increasing distance from the nearest wind turbine, although prevailing wind directions did result in lower noise in areas close to turbines. This correlation precluded the acoustic surface and distance to nearest wind turbine from being included in the same model for our analysis of individuals with home ranges within our acoustic surface. We found moderate correlation between distance to nearest primary road and distance to capture lek (r = 0.66), distance to nearest transmission line and secondary road (0.62), and elevation and distance to row-crop agricultural land (0.62). Thus, we maintained the effect of capture lek in all models and also retained the effect of distance to transmission line. We used an information criterion approach to compare Akaike information criterion corrected for small sample size ($\mathrm{AIC_c}$) scores between models.

Our second set of analyses was limited to a subset of 26 individuals with home ranges encapsulated entirely by our acoustic surface of NDSI. Within this subset of 26 females, we tested the role of the dominance of anthropogenic noise and a linear and nonlinear effect of distance to wind turbine on resource selection. We created 31 models evaluating topography, acoustic habitat, and distance to various physical landscape features including nearest wind turbine, tree, transmission line, and agricultural land.

To test the predictive ability of our models in both the focused and study-wide analyses, we used *k*-fold cross validation implemented in lme4 (Bates et al. 2015) as described by Boyce et al. (2002). Specifically, we used data from 80% of the individuals in our sample as our training set to construct a model that was then used to predict the relative probability of use of the remaining 20% (test data). This procedure was repeated 5 times until all data had been administered as both training and test data. Next, we ran Spearman rank correlations to assess relationships between the frequency of cross-validated used habitat locations and 10 probability bins of equal size expressing the range of predicted values. A model with good predictive ability is expected to show a strong correlation with higher numbers of used habitat locations falling into higher probability bins (Boyce et al. 2002).

Following model validation, we used results from our second analysis to make habitat selection predictions for the average prairie-chicken residing within our interpolated acoustic surface. We placed a 30 × 30 m grid within the 100% minimum convex polygon across all home ranges on the landscape (Figure 3A) to make a predictive map. We calculated relative use values from the top model containing informative predictors and placed them into 4 quartiles: 0–25, 26–50, 51–75, and 76–100% using percentiles to represent progressively selected habitats.

To avoid misinterpretation, we use the terms selection or avoidance throughout to indicate (1) that used locations were significantly closer to, or farther from, distance-based resources variables (habitat types, land-use types) than available locations; or (2) that values of classification-based resource variables (elevation, slope, and NDSI) were significantly higher, or lower, at used locations relative to available locations within the home range. We concluded selection or avoidance of resource variables when 95% confidence intervals of fixed beta coefficients did not overlap zero (Ware et al. 2015, Kleist et al. 2017), indicating a nonrandom relationship between the subject variable and use.

RESULTS

Home range size for each individual averaged 31.5 ± 8.1 km^2 (mean ± SE). Home range size was estimated without bias with respect to sampling effort because the home range was not related to the number of individual locations (ANCOVA; F = 1.57, df = 1 and 47, P = 0.22), collar type (F = 0.23, df = 1 and 47, P = 0.64), or the interaction between these factors (F = 0.22, df = 2 and 46, P = 0.64).

We found variation in the NDSI acoustic surface near the wind energy facility (Figure 3B). Areas near the turbines had more negative indices indicating proportionally higher levels of low-frequency sounds. The acoustic surface varied locally; generally, prevailing winds from the northwest and the topography of the grass-stabilized dunes appeared to dampen the spread of low-frequency sounds.

In our study-wide analysis (Figure 1; n = 49 females), model fit for models with resource variables was considerably better than the null model ($\Delta\mathrm{AIC_c}$ = 213.8 for Null model; Table 1), indicating that the resource variables provided significant information concerning resource selection by Greater Prairie-Chickens. Two of the 15 models had substantial empirical support with $\Delta\mathrm{AIC_c} < 2.0$ (Supplemental Material Table S1), so we model-averaged coefficients across the 2 top models (Table 1). Across the study area, significant quadratic terms indicated selection during the breeding season within the home range tended to decrease within 1,000 m of the nearest tree (Figure 2A) and selection decreased for locations between 5,000 and 12,000 m of the nearest transmission line (Figure 2B). Prairie-chickens avoided row-crop fields within the home range (Figure 2C), tended to avoid steeper slopes (Figure 2D), and selected sites closer to their leks (Figure 2E). The best resource-selection model, the global model, had good predictive ability as the frequency of cross-validated locations within probability bins was moderately correlated with bin ranks (xr_s = 0.71).

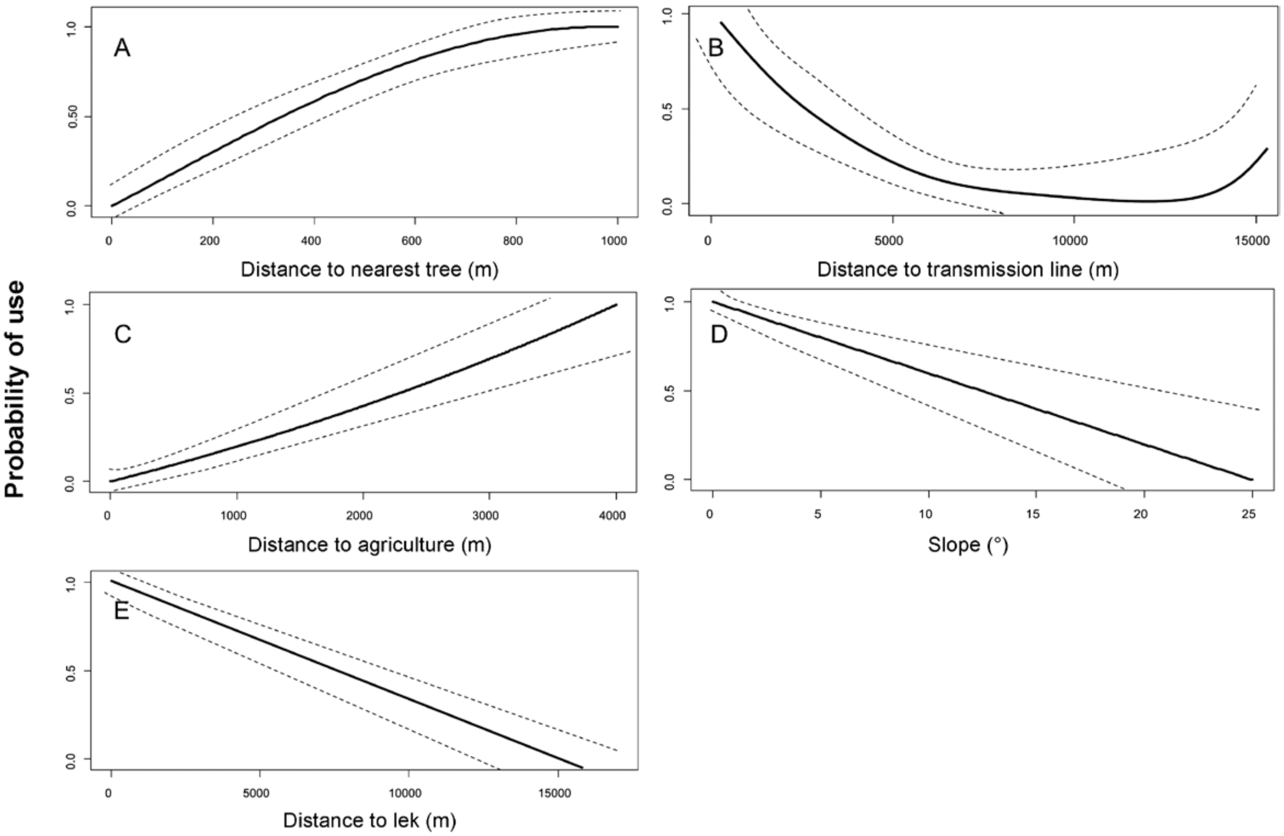

FIGURE 2. Relative probability of use (with 95% confidence intervals) in relation to (**A**) distance to nearest tree, (**B**) distance to nearest transmission line, (**C**) distance to nearest agricultural land, (**D**) slope, and (**E**) distance to capture lek for female Greater Prairie-Chickens in the grasslands of eastern Nebraska Sandhills during the breeding season; *n* = 49 individuals across whole study area. Relative probability of 0.5 is neutral selection (not selected or avoided).

In our second analysis within our acoustic surface (Figure 3, *n* = 26 females), distance to the nearest wind turbine or acoustic environment (NDSI) were present in 4 of the top 6 models ($\Delta AIC_c < 2.0$) describing resource selection of females within their home range (Table S2). The model assessing distance to nearest wind turbine (Turbine + Turbine^2) was ranked third with substantial support ($\Delta AIC_c < 2.0$); however, female prairie-chickens did not select or avoid areas proximate to wind turbines within their home range (Figure 4A), as 95% confidence intervals of the linear term overlapped zero (Table 1). The NSDI effect was present in the fourth-ranked model, although the evidence for prairie-chickens to select sites characterized by biological sound was weak, as 95% confidence intervals overlapped zero. Similar to individuals across the entire study area, prairie-chickens with home ranges completely within our acoustic landscape avoided locations near trees and row-crop agriculture (Figure 4B, D). Significant quadratic terms indicated decreasing selection for locations within ~500 m of trees and ~1,000 m of row crops. Spatially, we predicted the relative probability of selection to be low around trees (Figure 3C). Based on predictive mapping, the proportions of cells within wooded, row-crop agriculture, and grassland land cover classifications with greater than 50% predicted use were 13, 37, and 56, respectively. The best resource-selection model, the full environmental model without distance to turbine or NDSI, had predictive capability as the frequency of cross-validated locations within probability bins was moderately correlated with bin ranks ($\bar{x}r_s = 0.75$).

DISCUSSION

We found little evidence to support a substantial effect of the acoustic environment or proximity to wind turbines on prairie-chicken habitat selection, at least when compared to physical habitat characteristics known to influence habitat selection in the broader study area. The relative probability of use increased quickly over short distances with regard to distance to nearest tree, while other effects were manifested over larger spatial scales (Figure 2). Importantly, the strong correlation found between distance to wind turbine and noise did not impact our findings because neither landscape component influenced habitat selection; thus,

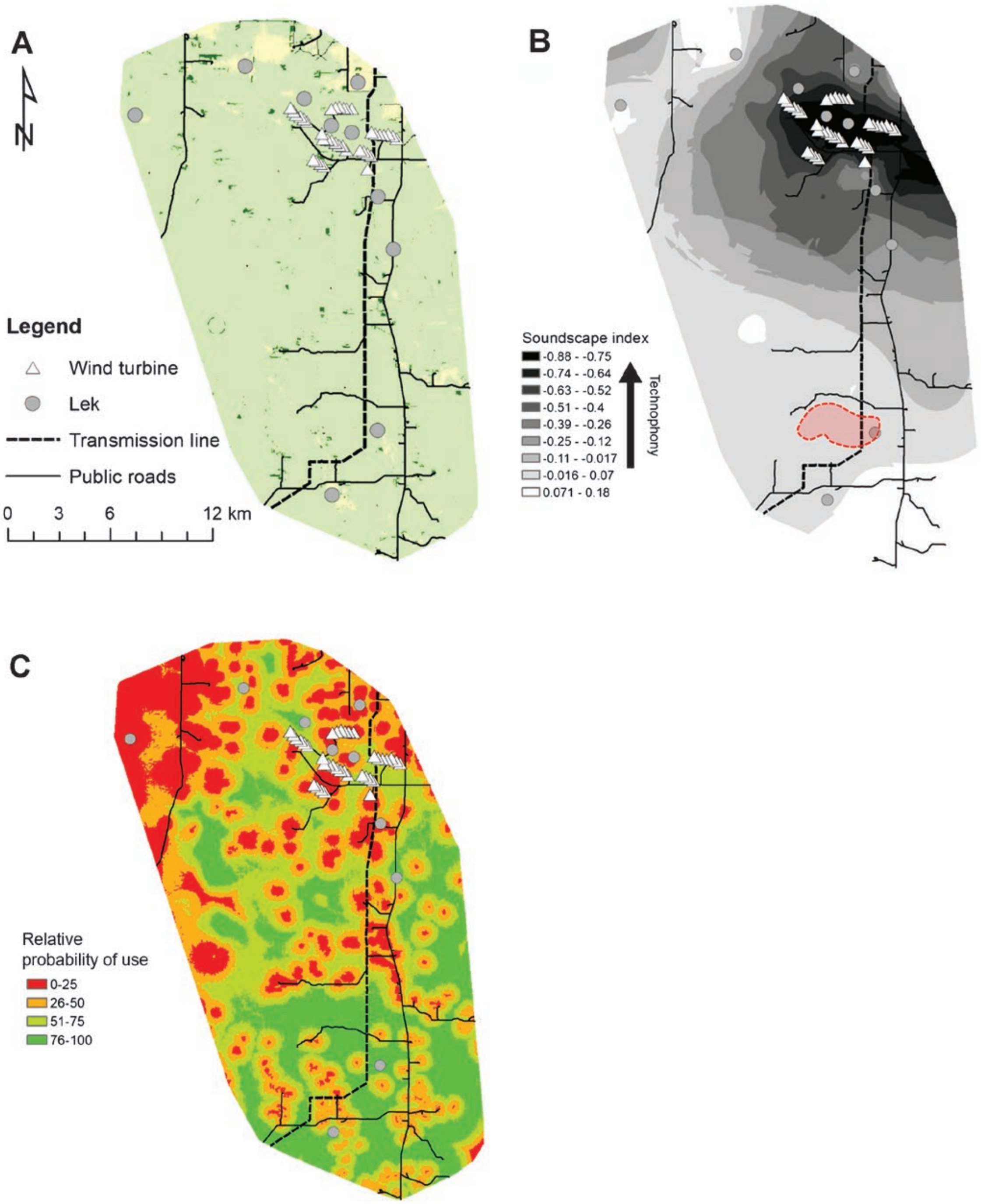

FIGURE 3. (**A**) Study area within acoustic sampling area and occupied leks targeted for capturing and monitoring female Greater Prairie-Chicken near Ainsworth, Brown County, Nebraska. Trees and row-crop agriculture are depicted as dark green and yellow, respectively. (**B**) Acoustic surface depicting normalized soundscape difference (NDSI); example home range is depicted with red dashed line and shading. (**C**) Predicted levels of prairie-chicken habitat selection for within the acoustic surface. We made predictions using a resource selection function model developed for the acoustic surface area. Relative probability of use predicted by generalized linear mixed model of resource selection is depicted.

we confidently conclude that neither factor had a detectable impact on our study population. Previously, no studies of prairie grouse acoustic habitat selection have been conducted, so there is little information about prairie grouse distribution relative to the spatial arrangement of the acoustic environment for comparison. Outside of studies conducted under laboratory conditions, few investigations on the impact of anthropogenic noise on free-ranging

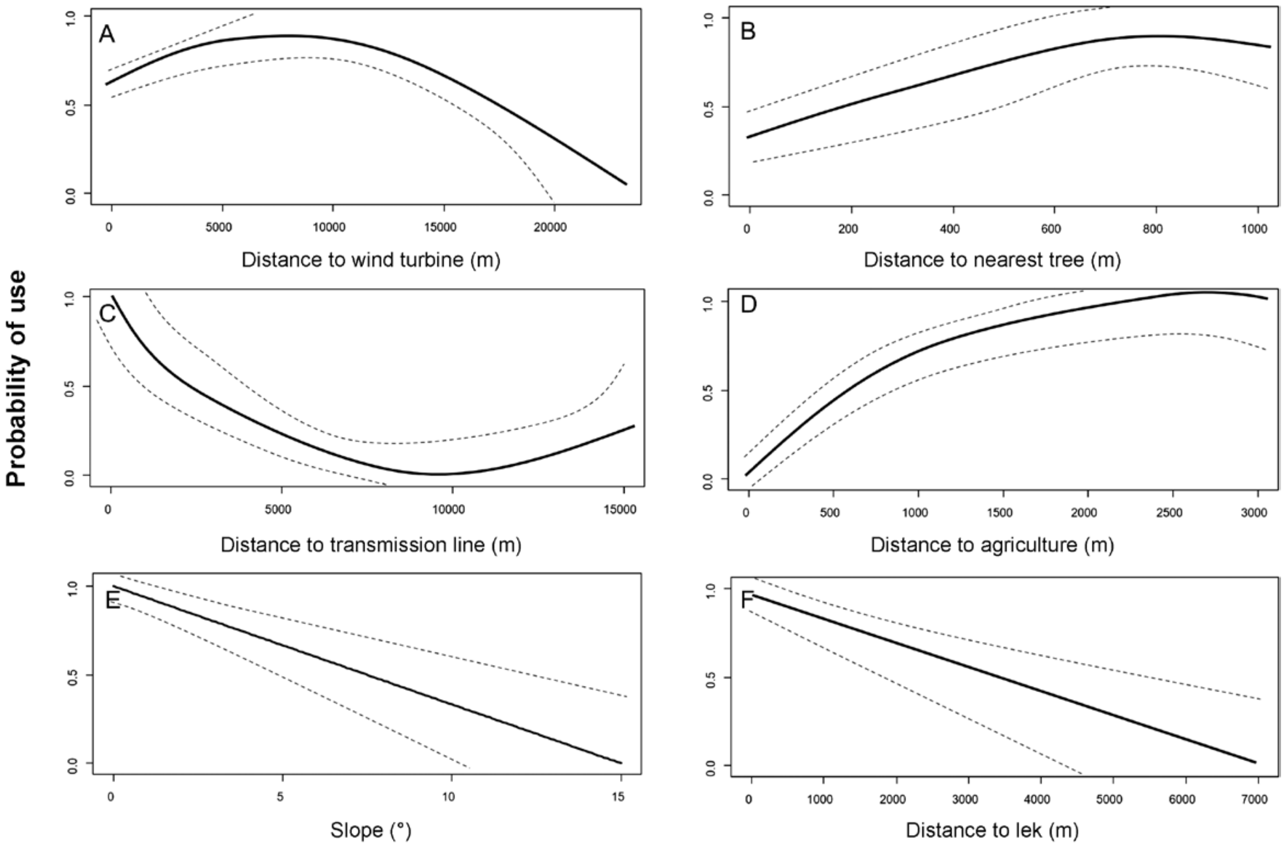

FIGURE 4. Relative probability of use (with 95% confidence intervals) in relation to (**A**) distance to nearest wind turbine, (**B**) distance to nearest tree, (**C**) distance to nearest transmission line, (**D**) distance to nearest row-crop agricultural land, (**E**) slope, and (**F**) distance to capture lek for female Greater Prairie-Chickens in the grasslands of eastern Nebraska Sandhills in the breeding season; *n* = 26 individuals with home ranges encapsulated by acoustic surface. Relative probability of 0.5 is neutral selection (not selected or avoided). Slope and distance to wind turbine were not influential variables in the model selection results.

gallinaceous birds have been undertaken (see Francis 2015, Proulx et al. 2019). An exception is work investigating the relationships between natural gas extraction activities and Greater Sage-Grouse (*Centrocercus urophasianus*) lek attendance and activity. Blickley et al. (2012a) found that male Greater Sage-Grouse attendance at leks declined when exposed to playback of experimental anthropogenic noise (i.e. roads and natural gas drilling), while stress levels of males that remained on a disturbed lek were ~17% higher than individuals on control leks (Blickley et al. 2012b). Thus, we contribute to the small body of information on habitat use of a ground-dwelling gallinaceous bird species by evaluating an unseen but inherent component, wind turbine noise, of many grassland ecosystems that can play a significant part in the way individuals interact with their surroundings. Such assessments are important for understanding unknown, novel phenomena that may influence the reproductive success of species of conservation concern (Barber et al. 2010, 2011; Francis and Barber 2013, Northrup and Wittemyer 2013).

Birds breeding in heterogeneous landscapes select habitat by cueing in on an assortment of factors from landscape features and social information to the occurrence of natural enemies. Our results indicate that multiple factors influence the location of Greater Prairie-Chickens within their breeding season home range in the largely unfragmented grassland in the eastern Nebraska Sandhills. Our work adds to recent efforts focused on the effects of the oil and gas industry on ground-dwelling grassland songbirds showing that anthropogenic noise is not nearly as important for habitat use as other landscape components (Nenninger and Koper 2018, Daniel and Koper 2019). Species traits unrelated to communication systems have been posited by Francis (2015) to predispose some organisms to be more (or less) sensitive to noise. For example, birds that nest within cavities, or on or near the ground, might be less exposed to anthropogenic noise because vegetation near the ground may attenuate noise more quickly compared to positions at greater distances above ground (Wiley and Richards 1978). Foraging and loafing-site location may also play a role (Francis 2015, Mason et al. 2016). Boundary or sound reflection effects can increase the attenuation of low-frequency sounds within a few meters from the ground (e.g., Wiley & Richards 1978); thus, birds that forage or loaf on or near the ground may experience lower sound levels in noisy environments than birds that forage at more considerable distances above the ground. Therefore, we surmise this species is (1) unaffected by turbine noise due to boundary effects or (2) has habituated itself to the acoustic environment since the construction of the wind energy facility. All explanations suggest this species is an acoustic habitat generalist that can occupy both noisy and natural acoustic habitat types (Mullet et al. 2017).

A potential drawback to our study design was the use of nocturnal recordings in our NDSI calculation. Employment of only nocturnal sounds in creating our acoustic surface may lead to an underestimation of the role of daytime biophonic sounds in our soundscape index, and thus a misrepresentation of the acoustic environment that a prairie-chicken experiences during the day. Although our spatial layer was useful for assessment of resource use along a relative gradient of technophony, it is possible that the additional biophonic information during the day may have reduced the effect of the technophony. This represents an area for future research as we seek to understand how animals use acoustic information. Further experimental investigation of acoustic habitat selection of prairie grouse living within close proximity to wind energy facilities may help clarify the mechanisms behind the response of this species to acoustic disturbance. Although grassland birds have evolved in an acoustically heterogeneous environment with natural noise from wind and other elements, they may have also evolved adequate behavioral plasticity to compensate for environmental noise (Curry et al. 2018).

Trees are generally considered a negative factor influencing demographic rates of Greater Prairie-Chickens because they provide raptor nesting sites and hunting perches as well as cover for meso-carnivores (Johnson et al. 2011, Hovick et al. 2015c). Low selection coefficients from RSFs indicated that topography, acoustic environment, distances to capture lek, agricultural land, the transmission line, and wind turbines had less influence on prairie-chicken locations than the distance to the nearest tree. Moreover, distance to trees was the most important variable for both spatial extents under evaluation. Comparable results for trees, agriculture, capture lek, and topography have been shown for prairie grouse elsewhere in the Great Plains (Matthews et al. 2013; Winder et al. 2014, 2015). For example, Lautenbach et al. (2017) determined proximity to trees supersedes topography as the most active driver of habitat avoidance both on and off the nest by female Lesser Prairie-Chickens in Kansas. Likewise, in Oklahoma and southeastern Nebraska, proximity to trees reduced the probability of nest-site selection for Greater Prairie-Chicken (Matthews et al. 2013, Hovick et al. 2015c). Although the Sandhills region has experienced less invasion by trees, such as eastern redcedar (*Juniperus virginiana*), than areas farther south in the Great Plains of North America, recent work indicates this region is highly susceptible to conversion from grassland to woodland without changes to current regional land management policies (Donovan et al. 2018, Roberts et al. 2018). Our predicted surface (Figure 3C) of habitat selection throughout the study site was highly influenced by isolated patches of trees, and areas of the landscape without trees had large areas predicted to be highly selected during the breeding season. Our finding that avoidance of trees was the most reliable predictor of within-home range habitat selection is a cause for concern because the grasslands in the range of Greater Prairie-Chickens are threatened by tree invasion, especially in the Nebraska Sandhills region (Donovan et al. 2018, Roberts et al. 2018). Furthermore, our results for Greater Prairie-Chickens agree with those from other studies of ground-dwelling grassland birds that have demonstrated negative effects of vertical structures on habitat use, not anthropogenic noise (Nenninger and Koper 2018).

Although encroachment by trees has replaced conversion of grassland to row-crop agriculture as the primary cause of contemporary grassland fragmentation and degradation in the Great Plains (Lautenbach et al. 2017), attention to the effect of agricultural land on prairie grouse habitat use is warranted. Row crops can act as a habitat sink relative to natural grassland, and an understanding of behavior–habitat relationships is paramount to conserving appropriate habitat (Patten and Kelly 2010). Our data demonstrate prairie-chickens in the Nebraska Sandhills avoid agricultural lands in the breeding season. This finding complements recent studies south of the Sandhills that show prairie-chickens avoid row-crop agriculture even at study areas where ~90% of land cover is prairie (Matthews et al. 2013, Winder et al. 2015).

The apparent selection of the wind energy facility's transmission line does not support the argument that tall structures can indirectly cause functional habitat loss by behavioral avoidance (Walters et al. 2014). We found selection for transmission lines, which corresponds to findings at our study area of nest-site selection within 1,500 m of the transmission line from Harrison et al. (2017). Two females nested very near to the transmission line and within the wind energy facility, which is the most likely reason for apparent selection of the transmission line. However, more research is needed to determine whether transmission lines impact prairie-chicken breeding ecology because a recent decade-long study of Greater Sage-Grouse, a species of grouse that also inhabits open grasslands, found transmission lines negatively impacted numerous behaviors (e.g., nest-site selection, brood-site selection) and demographic rates (e.g., nest survival, recruitment, and population growth) (Gibson et al. 2018). Populations of Common Ravens (*Corvus corax*) nesting on power poles have grown in abundance in Nevada and are implicated in reducing demographic rates of sage-grouse living near power transmission lines (Gibson et al. 2018). Although avoidance became evident ≥1,500 m from the transmission line in our study and a second-order evaluation of nest-site selection by Harrison et al. (2017), we encourage caution in the interpretation of the decline in site selection at such distances. It is possible that correlated topography patterns at certain distances (e.g., valleys, hills) may have been responsible for these results.

CONCLUSION

Within their home range, we found little evidence to support an effect of the noise generated by the wind energy facility on prairie-chicken habitat selection during the breeding season. Our findings parallel work by Harrison et al. (2017) at the nest-site level that found no negative impacts of the wind energy facility on female prairie-chicken nest-site selection and nest survival. This evaluation at 2 spatial scales extends our understanding of how anthropogenic disturbance influences the process of resource selection. Our current results should be linked with analyses of resource selection by prairie-chickens during other seasons, such as the post-breeding period and during winter, to provide a more comprehensive understanding of how prairie-chickens use the landscape along the burgeoning energy development–grassland gradient in the Great Plains. Furthermore, whether prairie-chickens acclimate to wind energy facilities remains an important yet unanswered question. For instance, a study in Kansas, which spanned breeding seasons before and after wind energy facility construction, provided evidence for avoidance of wind turbines during the 3 yr post-construction (Winder et al. 2014). More temporally extensive evaluations could determine if the reduction in avoidance occurs as individuals or populations acclimate to the presence of wind energy facilities (May 2015, May et al. 2019).

For species of conservation concern in landscapes impacted by anthropogenic noise, there is still much work to be done to explore the potential for behavioral avoidance of noisy habitat and how the acoustic dimension of the environment potentially regulates habitat use. We suggest that next steps should include experiments designed to explore the role of noise in obscuring social cues that might influence conspecific assessment of habitat quality (Patricelli et al. 2013), how noise alters vigilance–foraging tradeoffs (Ware et al. 2015, Mason et al. 2016), and how noise interferes with various stages of the breeding process (Kleist et al. 2017, 2018) such as pairing success (Smith et al. 2016) or incubation and nestling provisioning rates and rhythms (Ng et al. 2019).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Condor: Ornithological Applications* online.

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Ethics statement: This research was approved by the University of Nebraska–Lincoln's Institutional Animal Care and Use Committee (permit no. 901).

Author contributions: All authors conceived the idea, design, and experiment. E.J.R. formulated the questions, conducted the research, analyzed the data, and wrote the manuscript. C.E.W. and J.O.H. collected the data and designed the methods. A.J.T., J.B.F., and W.H.S. analyzed the data, reviewed and revised the manuscript. M.B.B., J.A.S., and L.A.P. reviewed and revised the manuscript, supervised the study, and designed the methods. L.A.P. and M.B.B. contributed substantial materials, resources, or funding.

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