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Space use by female Greater Prairie-Chickens in response to wind energy development

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Abstract. Wind energy development is targeted to meet 20% of U.S. energy demand by 2030. In Kansas, optimal sites for wind energy development often overlap with preferred habitats of Greater Prairie-Chickens (*Tympanuchus cupido*), a lek-mating species of prairie grouse with declining populations. Our goal was to use movement data from radio telemetry to investigate patterns and drivers of seasonal space use by female prairie-chickens during pre- and post-construction periods at a wind energy facility in northcentral Kansas. We developed individual and population level resource utilization functions (RUFs) for four time periods: the 6-month breeding and nonbreeding seasons during the pre-construction stage (2007–2008; $n = 28$ and 14 females), and the same two seasons during a post-construction period (2009–2011; $n = 102$ and 37). RUFs relate non-uniform space use within a home range to landscape metrics in a multiple regression framework. We selected ten predictor variables that described land cover, habitat patchiness, anthropogenic disturbance, and social behavior of prairie-chickens. We documented two behavioral responses of females to wind energy development during the breeding season: (1) mean home range size increased approximately two-fold, and (2) space use had a positive relationship with distance to turbine, which indicated female avoidance of wind turbines. A parallel study of demographic rates in our study population found no negative effects of wind energy development on prairie-chicken fecundity or survival, but persistent avoidance of wind energy development could result in the local extirpation of prairie-chicken populations at our study site. Our primary ecological finding was that distance to lek was the strongest predictor of space use during all treatment periods, with relatively high use of areas at short distances from leks in 79% of female home ranges. Thus, lek site surveys should be effective for identifying prairie grouse habitat preferences and monitoring population dynamics when more intensive demographic studies are not feasible. Our study is the first application of resource utilization function techniques to a wildlife population in response to energy development, and our results provide new quantitative insights into the spatial ecology of an upland gamebird of conservation concern.

Key words: grouse; home range; landscape metrics; lek; northcentral Kansas; resource utilization function; spatial ecology; *Tympanuchus cupido*; utilization distribution; wind turbine.

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INTRODUCTION

Environmental and socioeconomic concerns have led the U.S. Department of Energy to develop new targets for domestic use of energy resources. Wind energy development is targeted to fulfill 20% of the U.S. energy demand by 2030, a goal that requires a 29-fold increase from the installed capacity in 2007 (Arnett et al. 2007, DOE 2008). The potential effects of wind energy development on wildlife, especially migratory birds and bats, have received increased attention over the past decade (Drewitt and Langston 2006, Arnett et al. 2007, Kuvlesky et al. 2007, Smallwood and Thelander 2008, Pearce-Higgins et al. 2012). A review of published studies estimated that wind turbines and associated infrastructure are responsible for ~10,000–40,000 bird fatalities per year in the U.S., an average of 2.19 fatalities per year per turbine (Erickson et al. 2001). Direct mortality rates associated with wind energy development may be low and unlikely to affect population viability for most bird species (Osborn et al. 2000), but some taxa may be sensitive and more susceptible to population-level effects (Hunt et al. 1998, Smallwood and Thelander 2008). Indirect effects of wind energy development are poorly understood, but behavioral avoidance, alteration of habitat quality, or changes in trophic interactions might have important implications for population responses to energy development, and could be more pervasive than direct effects of collision mortality (Gill et al. 1996, Leddy et al. 1999, Hoover and Morrison 2005, Devereux et al. 2008, Pruett et al. 2009, Winder et al. 2013).

The Greater Prairie-Chicken (*Tympanuchus cupido*; hereafter "prairie-chicken") is an indicator species for tallgrass prairie ecosystems (Poiani et al. 2001, Johnson et al. 2011) and is listed as Vulnerable by the International Union for Conservation of Nature because populations have declined by ~70% rangewide over the last three decades (Knopf 1994, Svedarsky et al. 2000, BirdLife International 2012). Prairie-chicken populations are declining in the core of their extant range in Kansas due to low rates of nest, brood, and adult survival, which are related to high rates of predation and intensification of land use for cattle production (McNew et al. 2012, Pitman et al. 2012). Prairie-chickens require a mosaic of habitat types for successful reproduction and survival: open sites at relatively high elevations for display arenas used for lekking, dense vegetative cover for concealment during nesting, and areas of intermediate vegetative structure that are rich in forbs for foraging and rearing of broods (Gregory et al. 2011, Johnson et al. 2011, Matthews et al. 2013). Preferred locations for wind energy development in the Great Plains include high ridges and avoid economically valuable croplands, increasing the potential for conflict between wind energy development and an umbrella species of conservation concern.

Quantitative information on the spatial ecology of prairie-chickens is limited, especially with respect to potential responses to energy development and seasonal differences in habitat use (Niemuth 2011, Patten et al. 2011). Recent field studies have shown that Greater Prairie-Chickens, Lesser Prairie-Chickens (*T. pallidicinctus*) and Greater Sage-Grouse (*Centrocercus urophasianus*) can be negatively affected by energy development. Proximity to extraction wells, roads, towers, or transmission lines has been linked to abandonment of leks, behavioral avoidance, and loss of nesting habitat (Connelly et al. 2000, Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011, Blickley et al. 2012). However, the management implications of the results of past studies cannot be extended to a landscape scale because no study has directly evaluated the role of landscape metrics in spatial interactions between grouse and energy development. Demographic analyses of prairie-chicken populations in Kansas indicate that adult female mortality rates are 3–4 times higher during the 6-month breeding season than the 6-month nonbreeding season (Hagen et al. 2007, Augustine and Sandercock 2011, Winder et al. 2013). However, analyses of demographic rates alone do not allow us to determine whether space use is a driving factor in mortality risk.

Our study is the first application of resource utilization functions (RUFs) to investigate the response of a wildlife population to energy development. RUFs calculate a probabilistic measure of non-uniform space use within an animal's home range, and then use a multiple regression framework to relate space use to resource variables, while accounting for spatial autocorrelation among multiple locations from the same individual. Regression coefficients from the RUF can be used to draw inferences about the direction and magnitude of relationships between intensity of space use and values of selected resources at either an individual or a population level (Marzluff et al. 2004, Kertson et al. 2011). The objectives of our field study were to use resource utilization functions as an improved tool for testing for potential effects of wind energy development on resource use, and for quantifying the breeding and nonbreeding spatial ecology of female prairie-chickens. We collected seasonal movement data on radio-marked females before and after construction of a wind energy facility in the Smoky Hills ecoregion in northcentral Kansas. We developed individual and population level resource utilization functions for four separate periods: the breeding and nonbreeding seasons, both before and after construction of a wind energy facility. We used resource utilization functions to investigate the relationships between prairie-chicken space use and a set of ten landscape metrics describing land cover, patchiness, anthropogenic disturbance, and prairie-chicken social behavior.

We used home range estimates and resource utilization functions to test for three hypothetical effects of wind energy development on space use by prairie-chickens: (1) displacement away from the developed area, (2) expansion of home ranges, or (3) avoidance that leads to changes in space use within home ranges (Fig. 1). If wind energy development decreases habitat quality in developed areas, we predicted that prairie-chickens would shift home ranges or move greater distances to obtain adequate resources for forage, cover, or lek sites (Patten et al. 2011). If wind energy development resulted in behavioral avoidance of impacted areas by female prairie-chickens, we predicted that relative use would have a significant positive relationship with distance to wind turbine. Females require cover for nesting and brood-rearing (McNew et al. 2013), and habitat requirements for foraging and roosting may differ during the nonbreeding season. The results of our field study provide new insights into the quantitative spatial ecology of prairie-chickens in response to energy development, and can be used to improve management and conservation efforts for prairie grouse.

MATERIALS AND METHODS

Study site

Our ~3,000 km^2 study area was located south of Concordia in northcentral Kansas (Fig. 2). Land cover in our study area was primarily native grasslands or pasture (58%) or row crop agriculture (35%; comprised of 52% winter wheat, 18% corn, 14% soybeans, 10% sorghum, and 6% alfalfa), with some lands in the Conservation Reserve Program (5%; mean patch size 0.19 km^2, range = 0.001 to 2.25 km^2) or small woodlands (2%). The landscape was fragmented with a relatively high road density of 1.4 km of road per km^2. Native grasslands were managed for cattle production with prescribed spring fire applied once every three years; and cattle were stocked at densities of ~2–4 ha per head for 90 days (late April through late July). Weekly means of daily weather conditions were similar among years during our 5-year study (Winder et al. 2013).

Horizon Wind Energy started preparations for construction of the 201 MW Meridian Way Wind Power Facility in April 2008, erected towers in October and November 2008, and began commercial operation in December 2008. The completed facility included 67 Vestas V90 3.0 MW turbines; each turbine tower was ~90 m tall with rotating blades ~45 m in length. Mean spacing distance between adjacent turbines was 328 m ± 12 SE (median = 298, range = 257 to 763 m). Major transmission lines were buried underground within the wind energy facility, but a new high capacity transmission line was built to connect the new power substations to the infrastructure of existing transmission lines (~25 km). We collected data for two years pre-construction (2007, 2008) and three years post-construction (2009–2011). We included 2008 in the pre-construction treatment period because road building and erection of turbines occurred after the prairie-chicken breeding season was completed. Construction of the facility did not follow current guidelines for placement of wind turbines (www.fws.gov/windenergy), and 79% of the monitored leks (15 of 19) were located within 8 km of a turbine. No changes in land use or other mitigation for development are known to have occurred during the post-construction period.

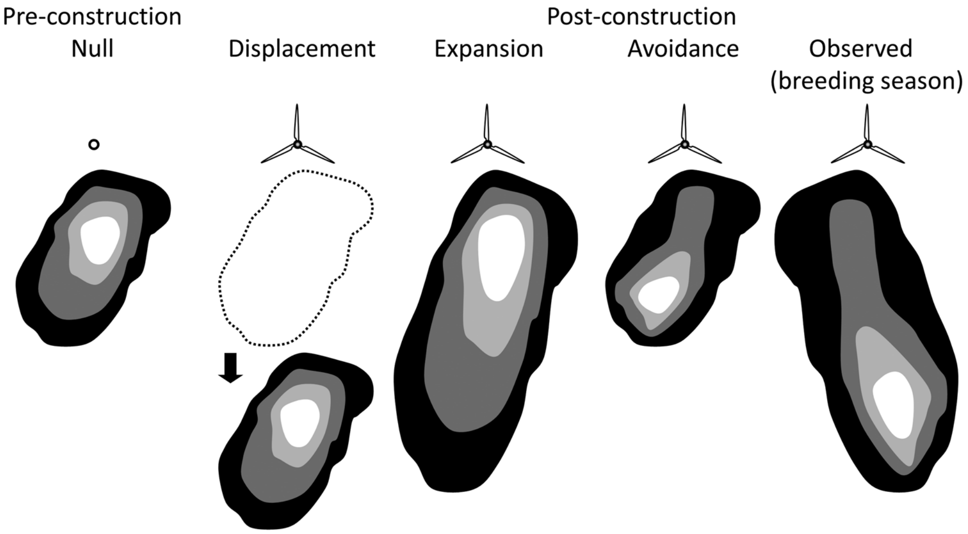

Fig. 1. Hypothetical effects of wind energy development on space use of wildlife. Light colors represent high levels of space use within the home range.

Field methods

During March and April of each year, we captured prairie-chickens with walk-in traps and drop-nets at lek sites. At first capture, we marked all birds with a uniquely numbered metal leg band and three colored leg bands. Each female was outfitted with a 10–11-g radio transmitter attached with an elastic or wire necklace harness (Model A3950, ATS, Isanti, MN; or Model RI-2B, Holohil Systems Ltd., Carp, ON). Radios had an expected battery life of 12–24 months and were equipped with mortality switches that changed pulse rate when the transmitter was stationary for 6–8 hours, indicating the death of the individual or a dropped transmitter. Radio-marked females were located by triangulation or homing with portable radio receivers and handheld antennas (Model R2000, ATS, Isanti, MN). We relocated birds 3–4 times per week during the 6-month breeding season (1 March–31 August) and one or more times per week during the 6-month nonbreeding season (1 September–28 February). Observers altered their routes among monitored females within each week to obtain locations at different times of the day. We double-checked area of triangulated locations in the field to ensure that all sides were <200 m in length, minimizing error in location estimates. Coordinates for locations were estimated using Program Locate III (v. 3.34, Tatamagouche, NS; UTMs projected in NAD 1983, Zone 14N).

Movements and space use

We analyzed location and space use data in a factorial design with two treatment factors: periods of wind energy development (pre- vs. post-construction), and 6-month seasonal period (breeding vs. nonbreeding). If individual prairie-chickens were monitored in multiple seasons or years, we considered each 6-month breeding or nonbreeding season to be independent and accepted limited pseudoreplication to use our complete dataset. For the purposes of our study, we considered the home range to be the amount of space an individual female required to forage, reproduce, and survive. We included females in our RUF analysis if we had ≥30 locations within a 6-month season (Seaman et al. 1999). During the breeding season, we further restricted our analysis to females that had ≥20 locations that were not associated with a nest or a brood. We included multiple locations associated with nest or brood attendance because these activities correspond to the periods of greatest mortality risk for female prairie-chickens in our study population, and resource selection during the breeding season is critical for determining demographic performance. The data requirements for spatial modeling introduce a potential bias because we could only analyze home ranges for

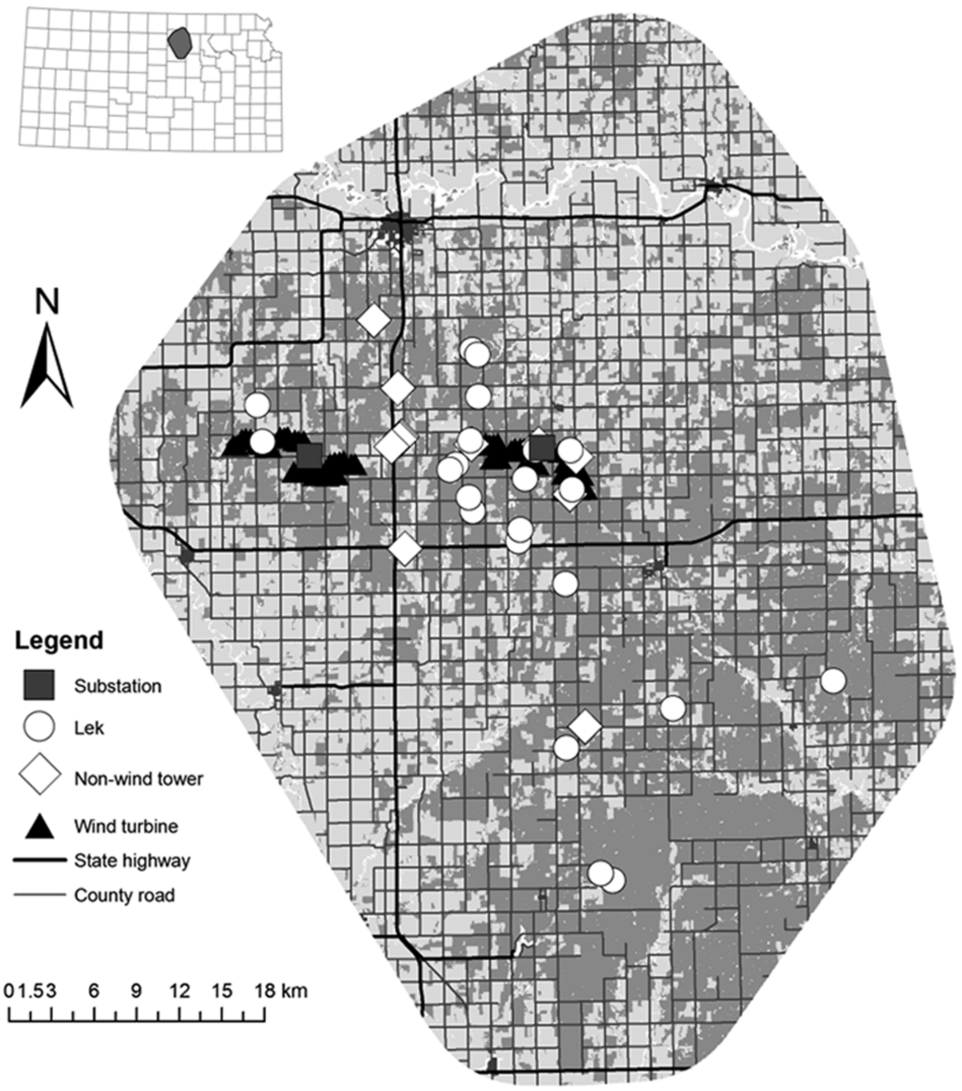

Fig. 2. Map of study area for the effects of wind energy development on female Greater Prairie-Chicken space use in northcentral Kansas, 2007–2011. Dark gray shading represents native grasslands managed for cattle grazing; light gray shading represents row crop agriculture.

individual females which survived long enough to accumulate an adequate number of locations. However, our approach was a balanced effort that included all of the key seasonal events and associated habitat choices in the annual cycle of a female prairie-chicken.

Resource utilization functions

We used utilization distributions to quantify space use as a continuous, probabilistic variable, and then related space use to landscape metrics using multiple regression in an RUF framework (Marzluff et al. 2004, Hepinstall et al. 2005, Millspaugh et al. 2006, Kertson et al. 2011). Resource utilization functions have several advantages over other commonly used methods for resource selection analysis. RUF methods allow for the quantification of inter-animal variation in resource use, and examine space use as a probabilistic and continuous metric, increasing sensitivity for detection of resource selection. Statistical advantages of RUFs include reduction of the effects of error in location estimation or lack of independence among location points. Individual animals (or populations) are treated as the experimental unit, and utilization distributions incorporate the entire distribution of an individual's movements for a specified time period rather than focusing on individual locations. Last, RUFs use a standardized designation of available habitat, not delineated by the arbitrary boundaries of a study area or other subjective measures (Marzluff et al. 2004).

We followed methods of Kertson and Marzluff (2009) to model animal movements, and build utilization distributions, extract landscape metric values, and develop RUF models using the Ruf.fit package in Program R (ver. 2.13.11, R Foundation for Statistical Computing, Vienna, Austria). The first step in the RUF process was to generate 99% volume contour polygons, defined as the boundary of the area that contains 99% of the volume of the probability density distribution for an individual's movements. For each individual, we determined a unique bandwidth value using least squares cross validation (h, a smoothing parameter; Worton 1989), and then created a 99% volume contour polygon for the seasonal home range with the Fixed Kernel Density Estimator and Percent Volume Contour options in Hawth's Tools for ArcMap 9.3 (ESRI, Redlands, California). In addition to the 99% volume contour home ranges needed for the RUFs, we calculated the 50% volume contour home range for a more restricted area of primary activity (Patten et al. 2011). To facilitate direct comparisons with previous studies, we also calculated the 95% volume contour home range and the 100% minimum convex polygon (MCP) for each individual. We used two-tailed Mann-Whitney U-tests to test whether home range area changed in response to season or wind energy development. For all analyses, we initially tested for year effects within pre- and post-construction periods, but finding none we proceeded with analyses that pooled years within each treatment period ($P > 0.05$; results not shown). We used Hawth's Tools to calculate the 1% volume contour for each home range, and used the geographic center of this contour as the centroid of the home range. We calculated distances from the centroid of the home range to the nearest turbines and lek sites. To estimate irregularity of home range shape, we calculated a ratio between the perimeter of the 99% home range vs. the circumference of a circle of the same area.

The second step in the RUF process was to create a raster of the utilization distribution within the 99% volume contour for each female's home range. We assigned a use value bounded from 1 to 99 for each 30 × 30 m cell within the home range, based on the relative volume (height) of the utilization distribution in that cell (Marzluff et al. 2004, Kertson and Marzluff 2010). The RUF framework combines the products of steps 1 and 2, using the 99% volume contour as the extent of available space, and the utilization distribution as the observed differential space use within the home range.

The third step was to determine landscape conditions at each grid cell within the home range for key resources hypothesized to predict space use. We identified 10 landscape metrics that were hypothesized a priori to be good predictors of prairie-chicken space use. Prairie-chickens have specific habitat requirements, and four metrics described percent cover of different land cover classes (Merrill et al. 1999, Matthews et al. 2013): (1) row crop agriculture, (2) Conservation Reserve Program land, (3) native grassland, and (4) woodland. Prairie-chickens may avoid fragmentation, and two variables described the patchiness of land cover (Patten et al. 2011): (5) distance to land cover patch edge and (6) corrected perimeter area ratio of a land cover patch. Prairie grouse may be sensitive to anthropogenic disturbance, and two variables were indicators of proximity to wind energy development (Manville 2004, Pruett et al. 2009): (7) distance to nearest road and (8) distance to nearest wind turbine. Gregory et al. (2011) showed that leks are often at high points in the landscape, and the last two variables described the landscape in terms of: (9) absolute elevation and (10) distance to nearest monitored lek.

We obtained GIS layers developed in 2005 for land cover classes, roads, and elevation from the Kansas Data Access and Support Center (www.kansasgis.org). Distance to patch edge was estimated using the land cover class grid, the Extract Raster Edge function in Hawth's Tools, and the Spatial Analyst Euclidian distance tool. We estimated patch area and perimeter using the Extract Raster Edge function in Hawth's Tools and estimated corrected perimeter to area ratio values for each patch using the field calculator (Farina 2000). Leks and wind turbine sites were mapped within the study area using a portable GPS unit (±5 m), and we derived raster grids for distance to nearest road, lek, and wind turbine using the Spatial Analyst Euclidian Distance tool. We used separate layers for distance to road for pre- and post-construction periods since ~33 km of additional gravel roads were added during the construction process. New roads contributed little to the existing fragmentation of the overall landscape as an extensive grid of roads was already present at our study site. We used the Spatial Analyst Extraction tool to create spatially explicit data files as input for the Ruf.fit package (Kertson and Marzluff 2010).

The last step in our RUF analyses was to relate the height of the utilization distribution to resource values on a cell-by-cell basis to obtain coefficients of relative resource use. We $\log_e$-transformed space use data to meet the assumptions of linear multiple regression models. We used the Ruf.fit package for Program R to estimate RUFs with standardized and unstandardized β coefficients to investigate the influence of landscape metrics on prairie-chicken space use within home ranges and the potential for interactions with wind energy development (Marzluff et al. 2004, Kertson et al. 2011).

To develop population level inferences, we calculated mean standardized β coefficients ($\bar{\beta}$) for each landscape metric by treatment period and computed a variance that incorporated inter-individual variation (Marzluff et al. 2004). For both individual and population level inferences, standardized coefficients with 95% confidence intervals that did not overlap zero were significant predictors of space use. If a resource coefficient was significantly different from zero, we inferred that resource use was greater (+) or less (−) than expected based on availability of the resource within the home range (Marzluff et al. 2004). We ranked the relative importance of significant landscape metrics using the absolute value of their mean standardized β coefficients. To assess heterogeneity among individuals, we used individual standardized β coefficients and associated 95% confidence intervals to quantify the number of female prairie-chickens with significant positive or negative relationships with each of the ten landscape metrics. To predict space use for each treatment group, we used the field calculator in ArcMap 9.3 to combine mean unstandardized β coefficients and landscape metric values across the study area. We classified predicted relative use into four quartiles following Kertson et al. (2011): 0–25, 26–50, 51–75, and 76–100%.

RESULTS

Home range estimation

We estimated home ranges and population-level RUFs for female Greater Prairie-Chickens during four periods: breeding/nonbreeding and pre-/post-construction, with an average of 48–65 locations per individual for each 6-month season, 14 to 102 birds per group, and a total of 181 bird-seasons (Table 1). A subset of birds was monitored in both years during the pre- ($n = 2$ females) or post construction periods ($n = 14$) or during both the pre- and post-construction periods ($n = 12$). Home range size was estimated without bias with respect to sampling effort because the 99% volume contour home range area was not related to the number of individual locations (ANCOVA; $F_{1,174} = 0.41$, $P = 0.53$), treatment period ($F_{3,174} = 0.52$, $P = 0.67$), or the interaction between these factors ($F_{3,174} = 0.27$, $P = 0.85$; Appendix A). Home range size and shape varied considerably among individuals (Appendix B). Estimates of the area of 99% volume contour home ranges during the breeding season in the pre-construction period were ~45% lower (54.0 ± 13.1 km^2) than space use in the post-construction period (96.8 ± 24.5 SE km^2; Table 1). Comparative estimates of 50% volume contour home ranges during the breeding season were also ~49% lower during pre-construction (7.2 ± 1.9 km^2) than the post-construction period (14.0 ± 3.9 SE km^2; Table 2). In both cases, interindividual variability was high, and these differences were nonsignificant ($P > 0.30$). Home ranges were larger in the post-construction period, but overall displacement was negligible because the mean distance from the centroid of a female's 99% volume contour home range to the nearest wind turbine did not differ among treatment periods (7.2 to 9.2 km, $P > 0.34$; Table 1).

Table 1. Home range size (99% volume contour), shape, and proximity to wind energy development [mean ± SE (range)] for radio-marked female Greater Prairie-Chickens at a wind energy development site in northcentral Kansas, 2007–2011.

Study period	No. bird-years	No. relocations	Area (km^2)	Perimeter (km)	P:A	P:C	Distance to lek (km)	Distance to turbine (km)
Pre-construction (2007–2008)								
Breeding	28	48.5 ± 2.0 (30, 71)	54.0 ± 13.1 (3.5, 282.75)	28.4 ± 3.3 (6.8, 81.4)	0.9 ± 0.1 (0.2, 2.0)	1.2 ± 0.03 (1.0, 1.7)	1.4 ± 0.2 (0.2, 4.7)	8.2 ± 1.2 (0.9, 26.4)
Nonbreeding	14	54.1 ± 0.9 (44, 58)	51.1 ± 14.7 (7.3, 220.8)	26.4 ± 3.4 (12.1, 62.1)	0.7 ± 0.1 (0.3, 1.7)	1.1 ± 0.04 (1.0, 1.5)	2.2 ± 0.5 (0.5, 7.0)	9.2 ± 1.8 (0.2, 24.2)
Post-construction (2009–2011)								
Breeding	102	65.4 ± 1.7 (32, 110)	96.8 ± 24.5 (2.7, 1937.7)	29.8 ± 2.9 (6.4, 169.9)	1.1 ± 0.1 (0.1, 3.4)	1.20± 0.02 (1.0, 1.7)	1.8 ± 0.2 (0.1, 9.7)	7.9 ± 0.8 (0.03, 32.2)
Nonbreeding	37	47.9 ± 2.5 (34, 93)	45.9 ± 10.3 (4.9, 252.6)	22.9 ± 2.5 (10.6, 64.7)	0.9 ± 0.1 (0.3, 2.3)	1.1 ± 0.02 (1.0 1.5)	1.8 ± 0.3 (0.2, 7.8)	7.2 ± 1.1 (0.3, 30.7)

Note: Abbreviations are: P = home range perimeter, A = home range area; C = circumference of a circle with the same area as the home range.

Drivers of space use

The strongest significant predictor of space use by female prairie-chickens was distance to lek, with highest use of areas within home ranges at short distances from leks for all treatment groups ($\bar{\beta}$ ranging from −0.89 to −0.52; Fig. 3, Appendix C). Space use was negatively related to distance to lek in 79% (143 of 181) of home ranges across all treatment periods (Appendix C). Mean distance from the centroid of a female's 99% volume contour home range to the nearest lek ranged from 1.4 to 2.2 km and did not change across treatments ($P > 0.08$; Table 1).

Distance to turbine was not a significant predictor of space use during the pre-construction period (Fig. 3). However, we found evidence of behavioral avoidance during the post-construction period because space use by female prairie-chickens was positively related to distance to wind turbine ($\bar{\beta} = 0.32 \pm 0.11$ SE, 95% CI = 0.11, 0.53; Fig. 3). We observed a coefficient of similar magnitude during the nonbreeding season in the post-construction period, but the 95% confidence intervals overlapped zero ($\bar{\beta} = 0.41 \pm 0.25$ SE, 95% CI = −0.072, 0.891; Fig. 3). An 8-km buffer zone has been suggested for energy development near prairie grouse leks, but we found that centroids of home ranges were <8 km from the nearest wind turbine for a majority of females during both the pre-construction (~65%) and post-construction periods (~70%).

Low use coefficients from the RUFs indicated that land cover had less influence on space use than distance to lek or turbine. Individual RUFs showed that drivers of space use were highly variable among female prairie-chickens. Non-

Table 2. Home range size (50% volume contour), shape, and proximity to wind energy development [mean ± SE (range)] for radio-marked female Greater Prairie-Chickens at a wind energy development site in northcentral Kansas, 2007–2011.

Study period	Bandwidth (km)	Area (km^2)	Perimeter (km)	P:A
Pre-construction (2007–2008)				
Breeding	1.1 ± 0.1 (0.3, 3.3)	7.2 ± 1.9 (0.6, 48.2)	10.2 ± 1.3 (3.3, 34.5)	2.5 ± 0.3 (0.7, 6.6)
Nonbreeding	1.1 ± 0.2 (0.4, 2.8)	7.8 ± 2.1 (0.9, 30.3)	11.2 ± 1.6 (3.5, 24.3)	2.0 ± 0.2 (0.8, 4.0)
Post-construction (2009–2011)				
Breeding	1.2 ± 0.1 (0.2, 8.8)	14.0 ± 3.9 (0.3, 330.1)	6.0 ± 0.5 (1.9, 13.5)	2.8 ± 0.2 (0.3, 7.8)
Nonbreeding	1.0 ± 0.1 (0.3, 2.8)	7.1 ± 1.6 (0.4, 39.6)	9.2 ± 1.2 (2.4, 25.2)	2.4 ± 0.2 (0.7, 5.4)

Note: Abbreviations are: P = home range perimeter, A = home range area.

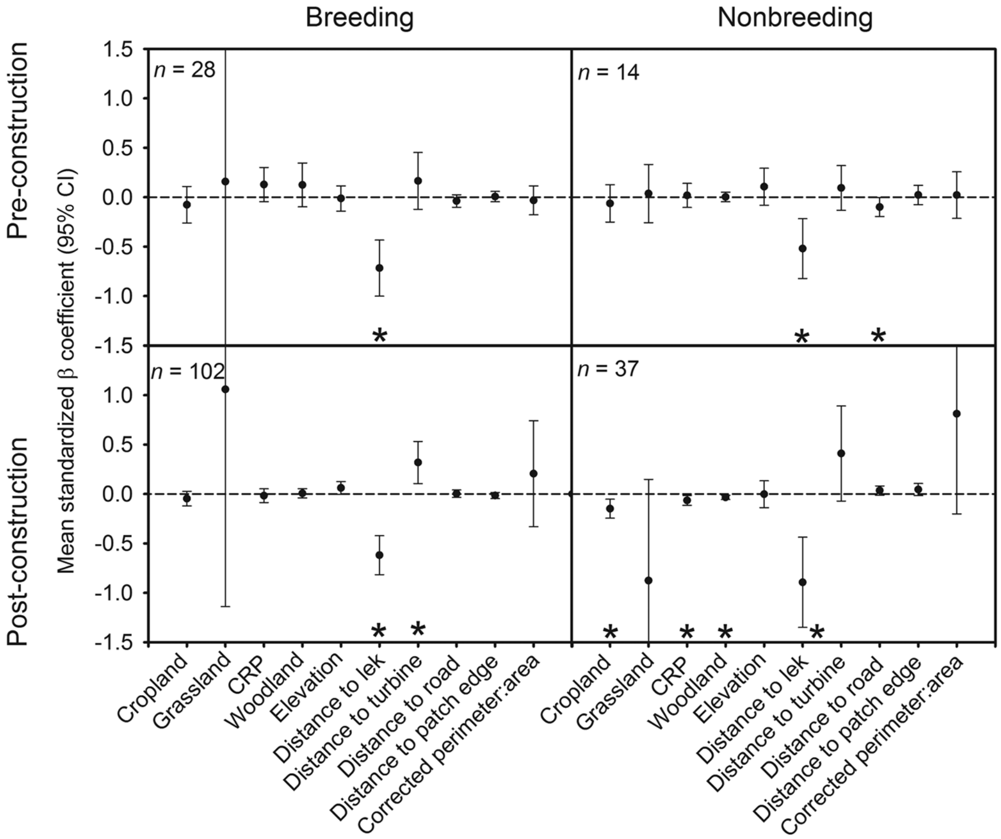

Fig. 3. Mean standardized β coefficients (95% CI) for female Greater Prairie-Chicken resource utilization functions. We examined space use in a factorial design with two treatment factors: wind energy period (pre- [2007–2008] vs. post-construction [2009–2011]) and 6-month seasons of year (breeding [1 March through 31 August] vs. nonbreeding [1 September through 28 February]). Asterisks denote significant responses at the population level; 95% confidence intervals of β do not overlap zero. CRP = land enrolled in the Conservation Reserve Program.

breeding female prairie-chickens exhibited avoidance of roads before construction, and then avoidance of cropland, woodland, and Conservation Reserve Program lands after construction (Fig. 3, Appendix C). Elevation and distance to patch edge were significant predictors of space use for a majority of radio-marked females (62–92%), but the direction of the relationship between space use and these landscape metrics was not consistent among individuals, and 95% confidence intervals for the population means included zero (Appendix C). A high degree of inter-individual heterogeneity was reflected in the population-level RUF, as inter-individual variation accounted for 98–100% of the total variation in covariate estimates. Space use for most female prairie-chickens was not related to the grassland cover or corrected perimeter to area ratio for land cover patches, and these landscape metrics were not significant predictors of space use at a population level. A lack of predictive ability for these landscape metrics implies female prairie-chickens used these resources in direct proportion to their availability within their home ranges.

Predicted space use

We used unstandardized $\bar{\beta}$ coefficients to predict patterns of relative space use for female prairie-chickens across the study site (Fig. 4, Appendix D). Predictive surfaces showed avoidance of wind turbines during the post-construction period and preference for areas near leks during all treatment periods. In the pre-construc-

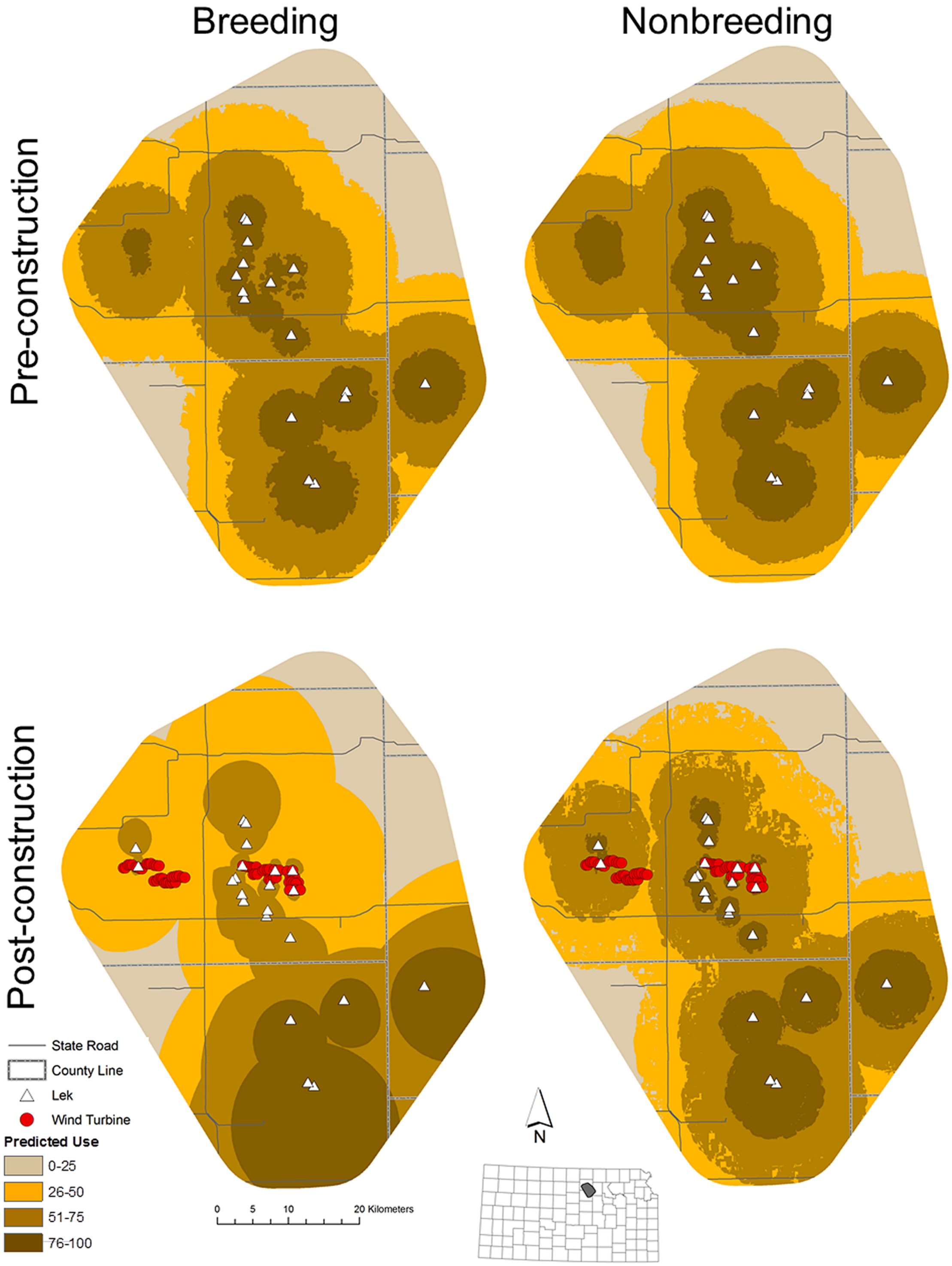

Fig. 4. Predictive relative use values for female Greater Prairie-Chickens based on mean unstandardized resource utilization function β coefficients. We examined space use in a factorial design with two treatment factors: wind energy period (pre- [2007–2008] vs. post-construction [2009–2011]) and 6-month seasons of year (breeding [1 March through 31 August] vs. nonbreeding [1 September through 28 February]).

tion period, the area predicted as the relative upper 50% of use encompassed 100% of the wind turbine sites. During the breeding season post-construction, the area predicted as the relative upper 50% of use included only 29% of wind turbine sites (18 of 67; Fig. 4).

Discussion

Responses to wind energy development

We used resource utilization functions to quantify the breeding and nonbreeding spatial ecology of female prairie-chickens and to test for potential effects of wind energy development in northcentral Kansas. We found no evidence of displacement because the mean distance between home range centroids and the nearest wind turbine did not change between pre- and post-construction periods. Nevertheless, we observed two changes in space use by female prairie-chickens during the breeding season as a response to wind energy development (Fig. 1). First, home range area increased nearly two-fold during the post-construction period. Patten et al. (2011) found a strong relationship between extent of habitat fragmentation and prairie-chicken home range size. Habitat fragmentation can potentially negatively affect demographic rates via increased risk of predation or energy use. Space use decisions during the breeding season may be tightly linked to demographic rates, as female prairie-chicken mortality rates are often higher during the breeding season (Hagen et al. 2007, Augustine and Sandercock 2011). However, additional analyses from our project found no negative effects of wind energy development on either fecundity or female survival, highlighting the importance of studying spatial ecology together with demography (McNew et al. 2013, Winder et al. 2013; McNew et al., *unpublished manuscript*).

Second, female prairie-chickens avoided wind turbines during the breeding season after construction of the wind energy facility. Distance to turbine was the second most important factor after distance to lek in explaining space use patterns of female prairie-chickens. Predictive surfaces based on unstandardized use coefficients illustrate one possible scenario for the future of prairie-chicken populations at our study site. If habituation to disturbance does not occur, and the mean population level response continues to be behavioral avoidance of wind turbines, wind energy development will result in habitat loss in managed grasslands. Winder et al. (2013) found that annual survival of female prairie-chickens increased from 0.32 in the pre-construction period to 0.57 in the post-construction period. Behavioral avoidance of wind turbines combined with improved female survival is consistent with the concept of a perceptual trap, which may occur if habitats with potential for high fitness are avoided because habitat cues do not accurately reflect habitat quality (Gilroy and Sutherland 2007, Patten and Kelly 2010). Nevertheless, we also observed considerable heterogeneity in individual responses to wind energy development. Female prairie-chickens that exhibited significant relationships between space use and distance to turbine were nearly equally divided between positive and negative responses. Our results are consistent with analyses of heterogeneity in the space use patterns of Steller's Jays (*Cyanocitta stelleri*), Common Ravens (*Corvus corax*), and cougars (*Puma concolor*), indicating that inter-individual variability is a common and perhaps unappreciated feature of wildlife populations (Marzluff et al. 2004, Roth et al. 2004, Kertson et al. 2011).

Potential for wildlife impacts was high in our study because the Meridian Way Wind Power Facility was constructed in grassland habitats preferred by prairie-chickens. We found behavioral avoidance of wind energy development during the breeding season but no evidence of negative impacts on demographic performance. Thus, Greater Prairie-Chickens may be less sensitive to wind energy development than Lesser Prairie-Chickens and Greater Sage-Grouse are to oil and gas development.

Spatial ecology

Analyses of movements and space use provided new insights into the annual cycle and spatial ecology of female prairie-chickens. The strongest predictor of female prairie-chicken space use within home ranges was distance to lek. Our findings are consistent with the hotspot hypothesis of lek evolution that posits leks have evolved because males cluster along routes used by females to travel among resources (Beehler and

Table 3. Estimates of home range size for female Greater Prairie-Chickens.

Method	Years of field study	Season	Months of monitoring	Minimum no. points	*n* (females)	Mean home range area estimate (km^2)	Source
100% MCP							
Kansas	1964–1968	B	1	15	28	1.9	Robel et al. 1970
Kansas	2003–2006	B	6	10	9	4.0	Augustine and Sandercock 2011
Missouri	2010–2011	B	5	30	32	7.7–9.6	Kemink and Kesler 2013
Kansas	2007–2011	B or N	6	30	14–102	9.4–17.2	This study
Oklahoma	1997–2000	A	12	20	29	20.7	Patten et al. 2011
50% KDE							
Kansas	2003–2006	B	6	15	5	1.0	Augustine and Sandercock 2011
Oklahoma	1997–2000	A	12	20	29	5.2	Patten et al. 2011
Kansas	2007–2011	B or N	6	30	14–102	7.1–14.0	This study
95% KDE							
Kansas	2003–2006	B	6	15	5	5.8	Augustine and Sandercock 2011
Oklahoma	1997–2000	A	12	20	29	22.9	Patten et al. 2011
Kansas	2007–2011	B or N	6	30	14–102	31.6–64.8	This study
99% KDE							
Kansas	2007–2011	B or N	6	30	14–102	45.9–96.8	This study

Note: Abbreviations are: MCP = minimum convex polygon; KDE = kernel density estimation; B = 6-month breeding season: March–August; N = 6-month nonbreeding season: September–February; A = annual.

Foster 1988, Schroeder and White 1993, Westcott 1994). Lek count surveys are often used as an index of population trends, but may be problematic if used to estimate population numbers or density (Applegate 2000). To estimate density, it is necessary to have information on home range size and proximity to leks. In this study, mean distance from the centroid of a female's home range to the nearest lek ranged from 1.4 to 2.2 km, and mean home range size ranged from 46 to 97 km^2 across our four treatment periods (99% volume contour). Comparable estimates of space use across the species' range could be combined with lek survey data to estimate prairie-chicken population size and density or to quantify the necessary amount of habitat to preserve around a lek of a given size.

Preferred prairie-chicken lek habitats are rare even within the region containing some of the largest remaining tracts of native prairie in North America (Gregory et al. 2011). Based on the strong ecological link between female prairie-chicken space use and lek sites, we infer that habitats preferred by female prairie-chickens are also rare in remaining native prairie. Given a critical need for conservation of key grassland habitats, our results indicate that lek surveys could serve as a reliable index of female prairie-chicken habitat use when intensive demographic monitoring is not feasible.

Female prairie-chickens exhibited weak avoidance of several landscape features during the nonbreeding season: roads during the pre-construction period, and cropland, woodland, and Conservation Reserve Program lands during the post-construction period. Avoidance of these landscape features may be related to patterns of habitat fragmentation. Fragmentation of native prairie by cropland and anthropogenic features such as roads, power lines, fences, and towers has been linked to elevated mortality rates and shifts in life-history strategies in Greater and Lesser Prairie-Chickens, leaving these populations more vulnerable to local extinction (Ryan et al. 1998, Patten et al. 2005, McNew et al. 2012).

Our estimates of seasonal home range size for female prairie-chickens were substantially larger than estimates from previous studies (Table 3). Published estimates were taken from populations in different ecoregions with varying levels of habitat fragmentation and anthropogenic disturbance, and differences in habitat quality, monitoring intensity, and estimation techniques among studies make it difficult to draw comparisons. Nevertheless, female prairie-chickens in fragmented landscapes at our study site had larger home ranges than any other population of this species studied thus far. Our home range estimation methods were similar to Patten et al. (2011), but future comparisons would be facilitated by standardized methods. We recommend use of 95–100% volume contour kernel density estimation methods with standardized bandwidth selection, and restriction of analyses to individuals with at least 30 relocations (Kernohan et al. 2001).

Conclusions

Our project is the first quantitative examination of the spatial ecology of a wildlife population in response to energy development. We found that the mean home range size of female prairie-chickens nearly doubled, and females preferentially used space at greater distances from wind turbines during the breeding season after wind energy development. We observed a high level of inter-individual variability in space use, and studies that focus only on population-level patterns may overlook important variation in individual behavior and ecology. We recommend management actions that maintain large tracts of heterogeneous grasslands surrounding existing lek sites. Our new estimates of female home range size and proximity to leks could be used to set management areas around active leks of various sizes. The resource utilization function approach was designed to allow researchers to investigate why animals use resources and space disproportionately within their home ranges (Marzluff et al. 2001). By adopting this new approach, we have provided a quantitative link between prairie-chicken spatial ecology and a set of landscape metrics that can be targeted in management actions (Boyce et al. 2002, Millspaugh et al. 2006, Niemuth 2011).

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SUPPLEMENTAL MATERIAL

APPENDIX A

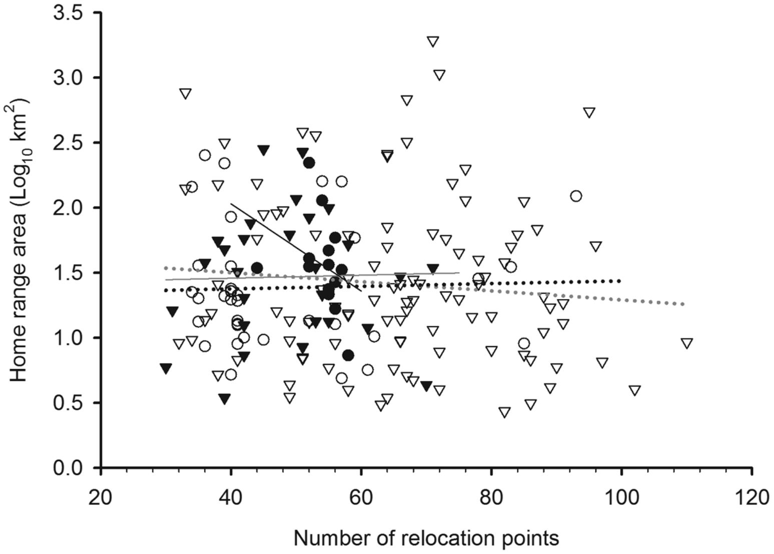

Fig. A1. Home range size (99% percent volume contour) of female prairie-chickens vs. number of individual relocation points. Data were collected during a study of seasonal space use in response to wind energy development in northcentral Kansas. Filled triangles and solid gray line = breeding season pre-construction (2007–2008); filled circles and solid black line = nonbreeding season pre-construction; open triangles and dotted gray line = breeding season post-construction (2009–2011); open circles and dotted black line = nonbreeding season post-construction.

APPENDIX B

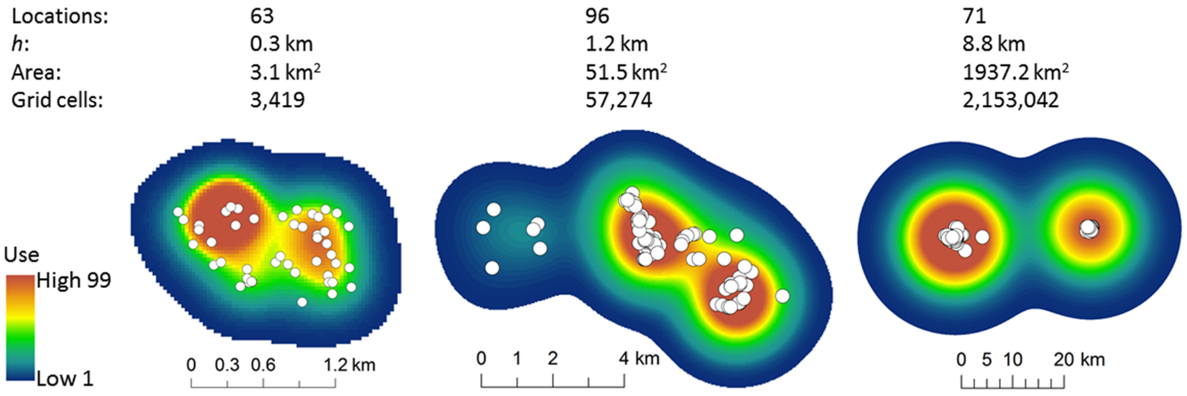

Fig. B1. Home range area and shape (99% volume contour) for three representative radio-marked female Greater Prairie-Chickens. Grid cells indicate the number of 30 × 30 m cells in the utilization distribution, and white dots represent bird locations.

APPENDIX C

Table C1. Mean standardized resource utilization function coefficients ($\bar{\beta}$) and percentage of birds with significant positive (+), negative (–), or non-significant (ns) space use associated with each landscape metric. Resource utilization functions were calculated for 99% volume contour home ranges of radio-marked female Greater Prairie-Chickens during the pre- (2007–2008) and post-construction (2009–2001) periods of development for a wind energy facility in northcentral Kansas.

	Breeding season					Nonbreeding season				
Landscape metric	$\bar{\beta}$	95% CI	+	−	ns	$\bar{\beta}$	95% CI	+	−	ns
Pre-construction										
Cropland	−0.077	−0.262, 0.108	14	18	68	−0.063	−0.252, 0.125	21	14	64
Grassland	0.157	−4.185, 4.499	21	4	75	0.036	−0.258, 0.331	29	14	57
Conservation Reserve Program land	0.127	−0.046, 0.300	11	11	79	0.018	−0.104, 0.139	21	7	71
Woodland	0.124	−0.098, 0.345	18	0	82	0.002	−0.046, 0.050	14	0	86
Elevation	−0.013	−0.141, 0.114	39	39	21	0.106	−0.081, 0.293	57	29	14
Distance to lek	**−0.717**	**−1.001, −0.434**	7	93	0	**−0.520**	**−0.823, −0.217**	14	79	7
Distance to turbine	0.165	−0.123, 0.452	50	36	14	0.093	−0.133, 0.319	50	36	14
Distance to road	−0.038	−0.101, 0.025	25	39	36	**−0.101**	**−0.196, −0.005**	14	64	21
Distance to patch edge	0.006	−0.046, 0.058	36	43	21	0.022	−0.076, 0.120	36	36	29
Corrected perimeter to area ratio for land cover patches	−0.033	−0.179, 0.113	7	29	64	0.021	−0.215, 0.257	29	36	36
Post-construction										
Cropland	−0.047	−0.121, 0.027	6	13	81	**−0.149**	**−0.245, −0.053**	8	14	78
Grassland	1.058	−1.139, 3.255	10	15	75	−0.877	−1.900, 0.147	5	19	76
Conservation Reserve Program land	−0.017	−0.0871, 0.053	7	18	75	**−0.065**	**−0.115, −0.015**	5	19	76
Woodland	0.007	−0.040, 0.054	3	10	87	**−0.035**	**−0.056, −0.013**	3	14	84
Elevation	0.061	−0.004, 0.126	47	29	24	−0.002	−0.138, 0.133	54	38	8
Distance to lek	**−0.619**	**−0.817, −0.422**	18	76	6	**−0.894**	**−1.350, −0.438**	16	76	8
Distance to turbine	**0.318**	**0.105, 0.532**	42	43	15	0.409	−0.072, 0.891	51	38	11
Distance to road	0.003	−0.035, 0.040	33	32	34	0.034	−0.013, 0.082	43	22	35
Distance to patch edge	−0.016	−0.046, 0.015	26	38	35	0.045	−0.017, 0.106	38	32	30
Corrected perimeter to area ratio for land cover patches	0.205	−0.332, 0.742	22	13	66	0.811	−0.201, 1.823	24	5	70

Notes: The 6-month breeding season was designated as 1 March through 31 August with the 6-month nonbreeding season from 1 September through 28 February. Boldface indicates a significant result (95% CI not overlapping zero). Confidence intervals (95% CI) are based on conservative standard errors include inter-animal variation (Marzluff et al. 2004: eqn. 3 – eqn. 2). For breeding season pre-construction, $n = 28$; for nonbreeding season pre-construction, $n = 14$; for breeding season post-construction, $n = 102$; for nonbreeding season post-construction, $n = 37$.

APPENDIX D

Table D1. Mean unstandardized coefficients ($\bar{\beta} \pm$ SE) for resource utilization functions calculated for home ranges of radio-marked female Greater Prairie-Chickens during the pre- (2007–2008) and post-construction (2009–2001) periods of development for a wind energy facility in northcentral Kansas.

	Pre-construction		Post-construction	
Landscape metric	Breeding ($n = 28$)	Nonbreeding ($n = 14$)	Breeding ($n = 102$)	Nonbreeding ($n = 37$)
Intercept	6.375 (3.044)	−0.985 (3.608)	0.880 (1.479)	0.813 (3.317)
Cropland	−0.157 (0.109)	−0.515 (0.200)	−0.096 (0.059)	−0.438 (0.099)
Grassland	−0.303 (2.421)	−0.222 (0.238)	−0.090 (0.468)	−2.425 (1.564)
Conservation Reserve Program land	−0.107 (0.103)	−0.167 (0.213)	−0.090 (0.070)	−0.371 (0.089)
Woodland	−0.112 (0.098)	−0.141 (0.153)	−0.157 (0.058)	−0.382 (0.095)
Elevation	0.008 (0.024)	0.009 (0.008)	0.007 (0.014)	0.001 (0.006)
Distance to lek	−0.012 (0.044)	−0.001 (0.0002)	−0.146 (0.047)	−0.001 (0.0002)
Distance to turbine	0.019 (0.023)	0.0001 (0.0001)	0.075 (0.041)	0.0002 (0.0002)
Distance to road	0.001 (0.003)	−0.0003 (0.0001)	−0.004 (0.009)	0.0002 (0.0001)
Distance to patch edge	−0.020 (0.012)	0.0003 (0.0004)	−0.004 (0.007)	0.0003 (0.0002)
Corrected perimeter to area ratio for land cover patches	−0.013 (0.058)	0.0006 (0.005)	0.055 (0.050)	0.053 (0.036)

Note: Conservative standard errors include inter-animal variation (Marzluff et al. 2004: eqn. 3 − eqn. 2).