

## Predation risk: a potential mechanism for effects of a wind energy facility on Greater Prairie-Chicken survival

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**Citation:** Smith, J. A., M. B. Brown, J. O. Harrison, and L. A. Powell. 2017. Predation risk: a potential mechanism for effects of a wind energy facility on Greater Prairie-Chicken survival. *Ecosphere* 8(6):e01835. 10.1002/ecs2.1835

**Abstract.** Recent expansion of the wind energy industry has raised concerns about the potential effects of wind energy facilities on prairie grouse. For example, efforts have been made to evaluate indirect effects on prairie grouse survival, but it is also critical to investigate the underlying mechanisms to direct conservation strategies. The objective of this study was to investigate the indirect effects of a wind energy facility on the survival of female Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) and on the occupancy of avian and mammalian predators. Between March and July of 2013 and 2014, we investigated spatial variation in predation risk by sampling occupancy of mammalian and avian predators within 10 km of a wind energy facility constructed in 2005 in Brown County, Nebraska, USA. During the same period, we assessed spatial variation in daily survival of radio-marked females within the same area. We found little evidence that probability of site occupancy ( $\Psi$ ) of avian predators was lower near the wind energy facility (within 2 km:  $\Psi = 0.70$ , 95% CI = 0.22–0.95; beyond 2 km:  $\Psi = 0.93$ , 95% CI = 0.02–1.00), suggesting that avian predators did not display local-scale avoidance behavior around wind turbines. Mammalian predators were documented at all of our sample locations, but the capture index for all mammals was lower at sample sites near the wind turbines ( $P = 0.004$ ). Occupancy of coyotes (*Canis latrans*), the likely main mammalian predator of adult prairie-chickens in the area, did not vary significantly throughout our study site (within 0.5 km of wind energy facility:  $\Psi = 0.65$ , 95% CI = 0.07–0.98; beyond 0.5 km:  $\Psi = 0.96$ , 95% CI = 0.04–1.00), although trends were in the direction expected if coyotes were avoiding the wind energy facility. Distance to wind turbine had no effect on daily survival ( $S_D$ ) of female prairie-chickens ( $S_D = 0.9948$ , SE = 0.0015). The potential for predators to avoid wind energy facilities, and thus affect predation risk, underscores the complexity of planning to address potential impacts of wind energy as variation in predation risk may have consequences for the population viability of a wide range of species at risk from wind energy development.

**Key words:** demography; Greater Prairie-Chicken; Nebraska; occupancy; prairie grouse; predator; renewable energy; Sandhills; *Tympanuchus*; *Tympanuchus cupido pinnatus*; wind farm.

**Received** 1 October 2016; revised 2 March 2017; accepted 10 April 2017. Corresponding Editor: Christopher Lepczyk.

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### INTRODUCTION

Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) have faced significant declines in range and population size due to habitat loss, degradation, and fragmentation, and exploitation from hunting (Storch 2007). They historically inhabited

tallgrass prairie across much of the United States and Canada (Svedarsky et al. 2000), but are now found in only 11 of the 20 states that formed their historic range, often in grazing lands planted with native species (Schroeder and Robb 1993, Svedarsky et al. 2000). Thus, Greater Prairie-Chickens are of conservation concern and

considered vulnerable (BirdLife International 2012). Despite continuing population declines across the majority of their range, Greater Prairie-Chicken populations in Nebraska are considered stable (Svedarsky et al. 2000). However, they are increasingly being exposed to wind energy development that is expanding across the region. While prairie grouse may be only minimally affected directly by wind energy facilities (Winder et al. 2014a), the birds may be susceptible to indirect effects. For example, the birds may be sensitive to the presence of tall structures such as wind turbines because they evolved on largely treeless landscapes. Alternatively, sensitivity may be caused by the habitat fragmentation caused by wind energy facilities (Larsen and Madsen 2000).

In the United States, the wind energy industry has expanded rapidly with wind energy capacity increasing 140% over five years from 25,000 megawatts (mw) in 2008 to over 61,000 mw in 2013 (American Wind Energy Association 2014). Further expansion is predicted with wind energy targeted to generate 20% of electricity in the United States by 2030 (U.S. Department of Energy 2008). Future development is expected to center on areas with high wind resources, including the Great Plains region of North America, which provides much of the remaining habitat suitable for prairie-chickens. Therefore, Greater Prairie-Chicken exposure to wind energy development is inevitable.

To date, studies of interactions between wind energy development and Greater Prairie-Chickens have been limited in scope (Smith and Dwyer 2016) and focused mainly on indirect effects on nesting ecology (McNew et al. 2014), female space use (Winder et al. 2014b), and lekking behavior (Smith et al. 2016). Winder et al. (2014a) provided evidence that survival of female Greater Prairie-Chickens increased in a large landscape during the years immediately following the construction of a wind energy facility. However, the effect of turbines could not be separated from roads and other anthropogenic features or temporal effects during the study, and the distance from turbines to females did not explain variation in survival (Winder et al. 2014a). While such studies have raised concerns about the indirect effects of wind energy facilities on Greater Prairie-Chickens, they did not investigate the mechanisms underlying these effects. It

is critical to better understand these mechanisms because they may inform management decisions and direct species conservation strategies.

Given that predation has been cited as a major factor limiting survival of adult Greater Prairie-Chickens (Schroeder and Robb 1993, McNew et al. 2012), changes in predator communities at wind energy facilities may explain changes in survival in response to wind energy development (Winder et al. 2014a). Potential mammalian predators of adult Greater Prairie-Chickens include American badger (*Taxidea taxus*) and coyote (*Canis lastrans*); potential avian predators of adult Greater Prairie-Chickens include Northern Harrier (*Circus cyaneus*), Red-tailed Hawk (*Buteo jamaicensis*), and Rough-legged Hawk (*B. lagopus*; Schroeder and Robb 1993). Changes in predator communities in response to wind energy development may affect survival directly, but also indirectly because female prairie grouse flush from their nests in response to nest predators (Coates et al. 2008), making them more visible, and thus more likely to be depredated by predators targeting adults (Moynahan et al. 2006). Potential mammalian predators of Greater Prairie-Chicken nests that may disrupt nesting activities include northern raccoon (*Procyon lotor*), Virginia opossum (*Didelphis marsupialis*), and striped skunk (*Mephitis mephitis*); potential avian nest predators include American Crow (*Corvus brachyrhynchos*; Schroeder and Robb 1993). Despite the expectation that changes in predator communities at wind energy facilities explain changes in survival in response to wind energy development, the effects of wind energy facilities on predators of Greater Prairie-Chickens remain unstudied, and thus the mechanisms underlying their survival remain largely unknown.

Our goal was to investigate the effects of an existing wind energy facility on the predation risk and survival of female Greater Prairie-Chickens during the breeding season. We predicted that the probability of occupancy of avian predators would be lower closer to the wind energy facility compared to farther away because avian predators are known to avoid wind turbines (Pearce-Higgins et al. 2009). We also predicted that occupancy of mammalian predators would be lower closer to the wind energy facility compared to farther away because mammalian predators of Greater Prairie-Chickens or their nests (hereafter, mammalian predators) tend to

avoid areas associated with human activity (Gese et al. 1989, Gehrt et al. 2009), and coyotes, a main predator of Greater Prairie-Chickens (Schroeder and Robb 1993) are known to avoid wind energy facilities (Tanis 2013). Because the local presence of predators affects the spatial risk of predation, we predicted that female survival would be higher closer, compared to farther from the wind energy facility.

## METHODS

### Study area

Our study was conducted in Brown County in the Nebraska Sandhills, an area of approximately 1345 km<sup>2</sup> of grass-stabilized sand dunes, wetlands, and sub-irrigated meadows in the north-central part of the state. Average elevation was approximately 550 m, and vegetation was dominated by grass species including little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and prairie sandreed (*Calamovilfa longifolia*; Kaul 1998). Land use was primarily cattle ranching (80%), native hay production (10%), and cultivated crop production including corn (*Zea mays*), soy (*Glycine max*), and alfalfa (*Medicago sativa*) that were supported by irrigation (5%; Miller 1998). Average temperatures range from the mid-20°Cs in July to approximately -5°C in January, and precipitation averages 53 cm annually, with 50% falling between May and July (Wilhite and Hubbard 1998). On average, wind speeds exceed 8.5 m/s at 80 m above ground (average height of a wind turbine hub), and Nebraska is ranked fourth in the nation for wind resources (Elliott et al. 1986).

Our study was centered on an existing 1620-ha wind energy facility owned and operated by the Nebraska Public Power District located approximately 10 km south of Ainsworth, Brown County, Nebraska (centered on 42.455 N, 99.915 W; Fig. 1A, B). The facility contains 36 wind turbines and became fully operational in 2005. Each 1.65 mw capacity turbine stands 70 m tall with 40 m long blades, and covers a 0.4-ha footprint. Other infrastructures at the facility include gravel roads, an electrical substation, high tension power 115 kV transmission lines and 7.2 kV distribution lines (collectively “utility lines”), and maintenance buildings. We used a disturbance gradient study design (Ellis and Schneider 1997, Adaramola

2015) to assess the effects of an existing wind energy facility with the assumption that effects, if present near the facility, would ameliorate over distance along the space of the gradient provided by our study design (Fig. 1B).

### Field methods

*Mammalian predator surveys.*—We assessed site occupancy of known mammalian predators of (1) Greater Prairie-Chickens or their nest contents collectively (e.g., coyotes, American badgers, northern raccoons, Virginia opossum; Schroeder and Robb 1993) and (2) coyotes, the likely main mammalian predator of adult Greater Prairie-Chicken in our study area, at 31 locations within 10 km of the wind energy facility (range: 0.03–9.70 km; Fig. 1B) from March to July in both 2013 and 2014. Locations were selected based on (1) the presence of existing continuous fence lines because linear barriers are used by wildlife moving across landscapes (Forman and Alexander 1998, Whittington et al. 2004) and fence posts can be used to mount trail cameras in treeless landscapes, and (2) land access. At each location, we placed a trail camera (Bushnell Trophy Cam Model no. 11963c; Bushnell, Overland Park, Kansas, USA; Reconyx Hyperfire HC600 or Reconyx RapidFire PM75; Reconyx, Holmen, Wisconsin, USA) approximately 50–75 cm above ground on an existing fence post. We randomly placed the three different camera types across the gradient to control for any potential influences of camera type on detection (Wellington et al. 2014). Trail cameras were oriented north or south away from the path of the sun to avoid triggering by bright light and were programmed to take three images in quick succession (two images per second) upon detection of motion, with a period of 5 min between sets of images. We downloaded photos, replaced camera batteries, and baited each trail camera location every two weeks with a mixture of sardines in oil, peanut butter, and rolled oats (55 g of each) placed approximately two meters in front of the trail camera. Because mammalian predators are most active around sunrise and sunset (Andelt and Gipson 1979), trail cameras were checked between 09:00 h and 17:00 h to avoid potential effects of human disturbance (sunrise and sunset times ranged between 05:30–06:50 h and 18:45–20:00 h, respectively). We placed trail cameras at 20 of the 31 locations in both years of

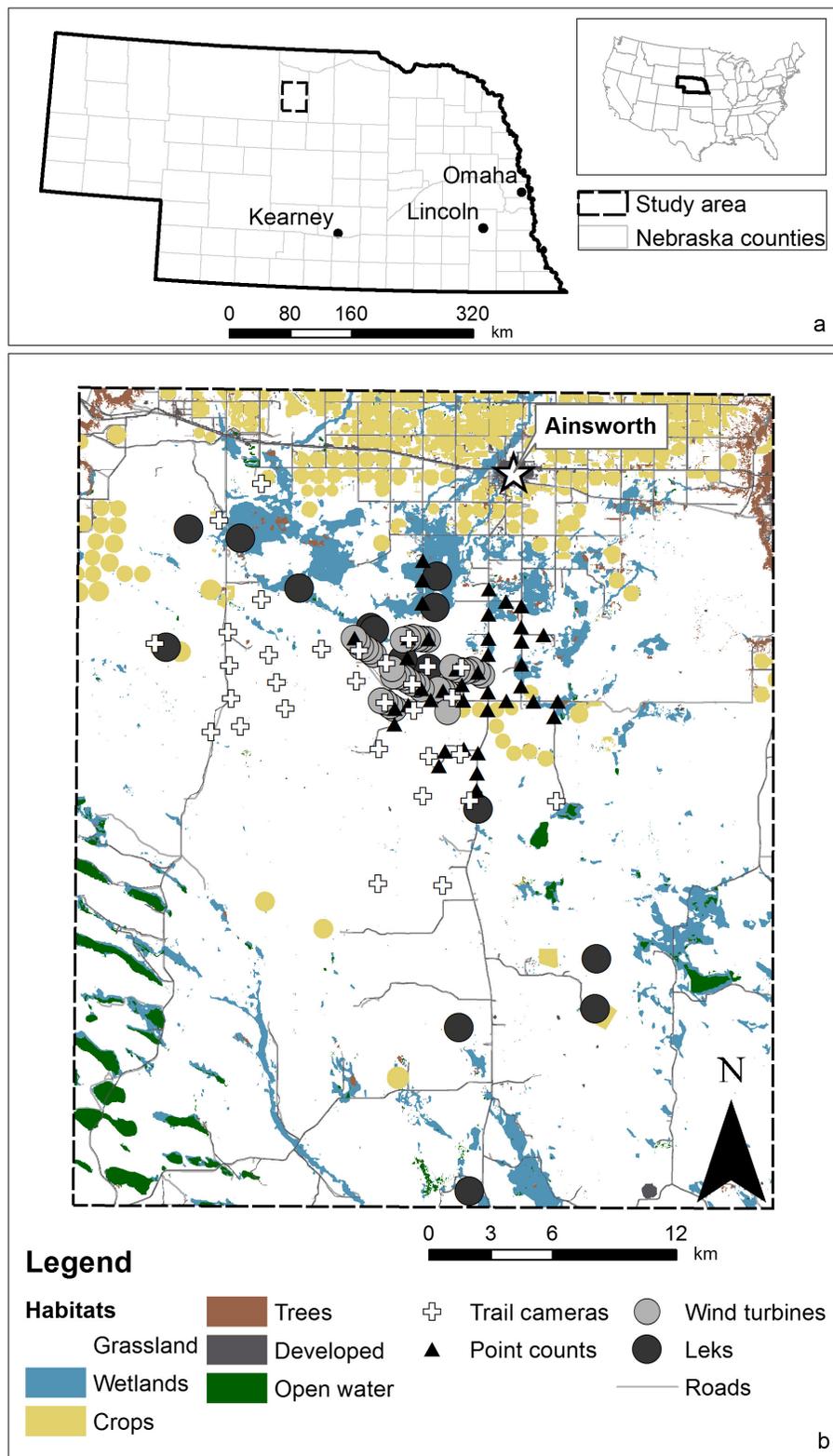


Fig. 1. Location of study area (A) within the USA and Nebraska and (B) in relation to Ainsworth, Brown County,

(Fig. 1. Continued)

Nebraska, USA, with locations of wind turbines, trail cameras, point counts, Greater Prairie-Chicken leks, and roads. The wind turbines collectively formed the wind energy facility upon which our study site was centered.

the study; the remaining 11 locations were sampled either in 2013 or in 2014 (Fig. 1B).

*Avian predator surveys.*—We assessed site occupancy of avian predators of (1) adult Greater Prairie-Chickens or their nest contents collectively (e.g., Red-tailed Hawk and American Crow) and (2) adult Greater Prairie-Chickens (e.g., Northern Harrier and Rough-Legged Hawks; Schroeder and Robb 1993) by conducting 300-m fixed-radius point counts (Ralph et al. 1995) between March and July at 40 locations in 2013, and 38 of the same locations in 2014 (Fig. 1B). All point count locations were located at varying distances away from the wind energy facility within 4 km (range: 0.01–4.1 km; Fig. 1B). All point count locations were road-based to control for potential effects of roads on avian predator activity (Meunier et al. 2000). All point count locations were located so that the landscape did not constrain the field of view within 300 m. We divided the 40 point count locations between four survey routes and numbered each point count within each route from 1 to 10. The four survey routes were completed over a four-day period. On each survey day, we randomly selected a route, and determined the order in which to conduct the surveys within the route (1 to 10 or 10 to 1), using the random number function in Excel. Point counts lasted for 10 min and were conducted between 09:30 h and 13:30 h to account for daily patterns in avian predator activity (Bunn et al. 1995). Within each point count, we identified all potential avian predators of Greater Prairie-Chickens or their nests seen within a 300 m radius using binoculars. We included all avian predators irrespective of flight height due to small sample sizes. Because weather conditions can influence detectability of avian predators (Anderson 2007), we did not conduct point counts during periods of rain, fog, or snow. During surveys, we consciously watched the behavior of avian predators (e.g., flight speed and direction) to avoid double counting in subsequent point count locations, and thus met the closure assumption of occupancy analysis.

*Survival.*—We captured Greater Prairie-Chickens using walk-in traps (Schroeder and Braun 1991)

in both 2013 and 2014 at 15 leks selected in the context of our disturbance gradient study design. Leks were located at varying distances away from the wind energy facility within 23 km (range: 0.38–23.3 km; Fig. 1B). Upon capture, we determined the sex of each bird by plumage and presence/absence of esophageal air sacs (Schroeder and Robb 1993) and marked it with a numbered metal leg band. All females were fitted with a 16-g necklace-style radio transmitter equipped with mortality switches (Model A4050; Advanced Telemetry Solutions, Isanti, Minnesota, USA) and released immediately at the capture location.

We located and confirmed status (i.e., dead or alive) for each radio-collared female five to seven times per week from date of capture to 31 July using a vehicle-mounted null-peak antenna receiver. Once found, birds were tracked within 30 m on foot using a three-element Yagi handheld antenna receiver (Advanced Telemetry Solutions). Locations of birds were recorded within  $\pm$  30 m using a handheld Garmin Etrex Vista GPS device (Garmin International, Olathe, Kansas, USA). We periodically relocated missing birds from an aircraft that was fitted with two externally mounted H-type antennas.

### Statistical analyses

*Landscape covariates.*—We mapped landscape features (major roads [highways], utility lines, trees, and water bodies) and land cover using ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA). We digitized utility lines, tree patches, and water bodies using Google Earth imagery taken on 10 May 2013 and obtained data on road placement from the Nebraska Department of Natural Resources (*public communication*, <http://www.dnr.ne.gov/transportation-data>). We extracted crop cover from land cover datasets obtained from The Rainwater Basin Joint Venture (Bishop et al. 2011). Using these data, we developed a suite of covariates that had potential to influence the distribution of avian or mammalian predators (Dijak and Thompson 2000, Meunier et al. 2000) by calculating the minimum distance between each of our

points of interest (point count, trail camera, or female location) and the associated landscape feature (e.g., major roads, utility lines, trees, water bodies, and crop patches). We did not consider land covers other than crops, trees, water bodies, or roads because habitat availability and configuration was otherwise homogenous across the study area (Fig. 1B).

*Predator occupancy.*— We reviewed images from all trail cameras and identified species, time, and date for all mammalian predators (Schroeder and Robb 1993). We created detection histories using 5 three-week periods for all trail camera locations where each period was assigned a “1” or a “0” to indicate the presence or absence of mammalian predators. We also used species-specific detections to create a coyote-only detection history to assess the occupancy of the species of mammal that was likely the main predator of adult Greater Prairie-Chickens. Similarly, we created detection histories using 6 three-week periods for each point count location to reflect presence or absence of known avian predators of Greater Prairie-Chickens or their nests. We then created a detection history for only avian predators of adult Greater Prairie-Chickens (i.e., *Buteo* spp., Northern Harrier, Cooper’s Hawks (*Accipiter cooperii*), Bald Eagles (*Haliaeetus leucocephalus*), and Prairie Falcons (*Falco mexicanus*)).

Our initial assessment of our mammalian predator imagery showed that naïve occupancy (proportion of cameras with evidence of a predator) equaled 1.0, which prevented us from continuing with the occupancy analysis. To assess variability in mammalian predators across the landscape, we calculated a capture index as the number of days in which a mammalian predator of any species was captured divided by the number of camera nights at each location. We conducted a regression analysis to evaluate the effect of distance to the wind energy facility on the mammal capture index.

We used the Occupancy Estimation module in program MARK (White and Burnham 1999) to estimate occupancy probability ( $\Psi$ ) for coyotes and avian predators (MacKenzie et al. 2002). We developed occupancy models taking a two-step, step-down model selection approach (Lebreton et al. 1992, Thomas et al. 2010). First, we compared temporal models to describe variation in detection probability ( $p$ ), while keeping occupancy

constant. We then joined the top-ranking detection model with occupancy models that described effects of distance to nearest wind turbine and other landscape features. We evaluated overdispersion by calculating the variance inflation factor ( $\hat{c}$ ) for the global model using program MARK. We used quasi-Akaike’s Information Criterion corrected for overdispersion (i.e., when  $\hat{c} > 1$ ) and for small sample size (QAIC<sub>c</sub>),  $\Delta$ QAIC<sub>c</sub>, and model weights ( $w_i$ ) to evaluate the relative support of candidate models. The model with the lowest QAIC<sub>c</sub> was considered the top-ranking model, and models with  $\Delta$ QAIC<sub>c</sub>  $\leq 2$  were considered to have substantial support from the data (Burnham and Anderson 2002).

To account for potential variability in time-specific detection probabilities for mammalian predators, we constructed a model that featured period-specific detection rates during two periods: (1) early season (13 March–13 June) and (2) late season (14 June–16 July). During the late season period, tall, dense vegetation likely reduced the likelihood of trail cameras detecting mammalian predators, thus reducing detectability. To account for potential variability in time-specific detection probabilities for avian predators, we constructed a model that featured period-specific detection rates during two time periods that accounted for seasonal changes in activity: (1) early season (13 March–12 April) and (2) late season (13 April–29 July). We expected heightened activity at the beginning of the field season due to migrating raptors and birds prospecting for territories and our field observations confirmed this (J. Smith, *unpublished data*). Time period models were then compared with their respective null models with constant detection rates. Despite expecting an increase in avian predator activity during migration, our observations suggest that site occupancy is unlikely to have changed seasonally. We pooled all species of avian predators as one “species” for our analyses (i.e., occupancy inference is to probability of occupancy of any species of avian predator, migratory or resident), which provides further protection against the potential to violate the species-level closure assumptions for occupancy analysis.

To select the best description for the effect of distance to turbine, we created distance categories based on distance to turbine and either distribution of trail cameras for coyotes (trail camera

distance categories: 0.0–0.5, 1.0–2.5, 4.0–5.0, 6.0–7.0, and 8.0–10.0 km) or distribution of point count locations for avian predators (point count distance categories: 0.0–0.5, 0.6–1.0, 1.1–2.0, 2.1–3.5, and 3.6–4.0 km). We then used the naïve probability of occupancy, measured as the proportion of point count locations or trail camera locations within each distance category in which an avian predator or a coyote was observed at some point during the study, to visually identify the closest distance from the wind energy facility at which a pronounced change in the pattern of naïve site occupancy occurred. This threshold distance was then used to create discrete distance categories, “near” and “far,” used in discrete models.

We modeled occupancy as a function of distance to turbine-, year-, and location-specific covariates using the logit link. We first compared the support for linear, quadratic, cubic, and discrete functions of distance to turbine, and selected the model with the most support as the model to represent distance to turbine in the last stage of the analysis. Because distance to major roads, trees, and water bodies can influence distributions of mammalian predators (Dijak and Thompson 2000, Randa and Yunger 2006), we considered them as covariates in the coyote model. We also considered distance to nearest urban center (Ainsworth, Brown County, Nebraska, USA), and crop patch to control for their potential influence on coyote movement (Atwood et al. 2004, Barding and Nelson 2008). Because perch availability can influence the presence of avian predators (Preston 1990), we considered distance to perch as a covariate in the avian predator occupancy model. Distance to perch was calculated as the minimum distance to either a tree or a utility line from each point count location. We also considered distance to urban center (Ainsworth, Brown County, NE) to account for potential effects of urbanization on avian predator abundance (Rodewald et al. 2011) and distance to crop patch to account for potential effects of habitat availability on raptor abundance (Wiggins et al. 2014). We used Spearman’s rank correlation ( $r_s$ ) in SAS (SAS Institute, Cary, North Carolina, USA) to evaluate collinearity between explanatory variables and constructed models using combinations of explanatory variables that were not correlated ( $r_s < 0.5$ ) to reduce the likelihood of making type II errors (Dormann et al. 2013).

*Survival analysis.*—To model survival as a function of distance to turbine, we created six distance categories based on distance to turbine and the trapping locations of all birds considered in the analysis (0.0–1.0, 1.5–3.0, 3.5–5.0, 7.0–10.0, 14.0–16.0, and 23.0–24.0 km). We used the trapping locations of birds (i.e., leks) because female prairie-chickens nest in close proximity to leks (Winder et al. 2015). Thus, using lek location provides an approximation for all other locations used by a female caught at that lek. We then calculated the naïve probability of survival measured as the proportion of tagged females trapped within each distance category that survived during the study. These probabilities were then used to identify visually the closest distance from the wind energy facility at which a pronounced change in survival occurred. We then used the distance identified to create discrete distance categories, “near” and “far.”

We constructed logistic-exposure models to estimate female prairie-chicken daily survival ( $\hat{S}_D$ ; Shaffer 2004) using PROC GENMOD in SAS (SAS Institute, Cary, North Carolina, USA). We considered only the first year of data for birds that survived during both years of the study to avoid pseudoreplication. We developed a set of candidate models that evaluated potential variation in daily survival as functions of year, time period, and average distance from female to nearest wind turbine, major road, and perch during each exposure period (~7 d in length). We also included distance to nearest crop patch to account for potential effects of habitat variation on female survival (McNew et al. 2012). To account for potential variability in time-specific survival rates, we considered three time periods in which we predicted vulnerability to predators would vary. These reflected the times we expected the majority of the birds to be lekking, nesting, or brood rearing (20 March–19 May, 20 May–16 June, and 17 June–31 July, respectively). These dates were based on the median hatch dates for birds in our study population (2013: 18 June, 2014: 16 June). Collinearity between explanatory variables was assessed using Spearman’s rank correlation ( $r_s$ ), and models were constructed using combinations of explanatory variables that were not correlated ( $r_s < 0.5$ ; Dormann et al. 2013).

We first tested for an effect of year on survival independently from other explanatory variables

and pooled data when year had no effect. Next, we selected the most appropriate model to describe our main effect of interest: distance to nearest turbine. We compared the support for linear, quadratic, cubic, and discrete functions of distance to turbine, and used the model with the most support to represent the main effect in the last stage of the analysis. We assessed goodness of fit of the global model using Pearson's  $\chi^2/df$  and included an overdispersion parameter in all models when the Pearson chi-square statistic divided by the degrees of freedom was greater than 1. We used  $AIC_c$ ,  $\Delta AIC_c$ , and model weights ( $w_i$ ) to compare models in our candidate set. The model with the lowest  $AIC_c$  was considered the top-ranking model, and models with  $\Delta AIC_c \leq 2$  were considered to have substantial support from the data (Burnham and Anderson 2002).

## RESULTS

### *Mammalian predator occupancy*

Between 2013 and 2014, we captured 1417 images of mammalian predators (2013: 582, 2014: 835) over 4715 camera trap nights (2013: 2029, 2014: 2686). We identified two species known to depredate adult birds (American badger and

coyote), and an additional three known to depredate nest contents (northern raccoon, striped skunk, and Virginia opossum; Schroeder and Robb 1993). Coyotes were identified in 723 (51.0%) of the images, American badgers in 135 (9.5%), northern raccoons in 374 (26.4%), striped skunks in 150 (10.6%), Virginia opossums in 30 (2.1%), and unidentified mammalian predators in 5 (0.4%). The only spatial variables to exhibit correlation were distance to turbine and distance to urban center ( $r_s = 0.78$ ,  $P < 0.0001$ ), so we omitted distance to urban center.

*All mammalian predators.*—Mammalian predators were documented at all of our camera locations (naïve occupancy = 1.0). However, the capture index increased as distance from turbine increased (slope = 0.008, SE = 0.003;  $P = 0.004$ ; Fig. 2).

*Coyotes.*—The model in which probability of detection of coyotes varied as a function of year ( $p_{\text{year}}\Psi$ ) received less support from the data ( $\Delta QAIC_c = 2.18$ ) compared with the null model ( $p, \Psi$ ); thus, we pooled data across years for subsequent analyses. Probability of detection for coyotes was best explained by the model in which detection probability was constant across time ( $p, \Psi$ ), therefore, in subsequent models we used ( $p$ ).

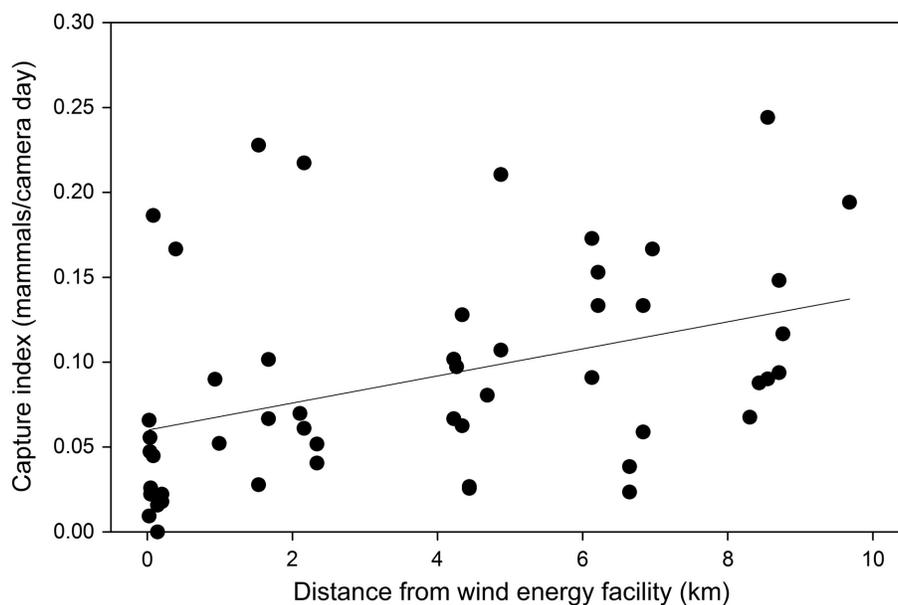


Fig. 2. Relationship between capture index of all mammalian predators (number of images containing a mammalian predator per camera day) and distance from sample site to the wind energy facility during 2013–2014 near Ainsworth, Nebraska, USA.

The estimates for naïve probability of observation for coyotes suggested that the closest distance from the wind energy facility at which a pronounced change in site occupancy occurred was 0.5 km. Therefore, we used 0.5 km to delineate the discrete distance categories, “near” and “far.” Of the models that we constructed to describe site occupancy of coyotes as different functions of distance to turbine, the discrete distance model received the most support. Although the second-ranked model, the linear distance model ( $\Delta\text{QAIC}_c \leq 2$ ), received some support, we used the top-ranked model, the discrete distance model, to represent potential variation in occupancy as a function of distance to turbine in the next stage of model comparisons.

Of the models that we constructed to model variation in occupancy for coyotes as a function of distance category- and location-specific covariates, the null model received most support from the data (Table 1). The second-ranked model, the discrete distance model ( $p, \Psi$  [distance category]), received some support ( $\Delta\text{QAIC}_c \leq 2$ ; Table 1), but assessment of the model structure ( $k$ ), model coefficients, and values of  $\Delta\text{QAIC}_c$  suggested that distance to turbine was an uninformative parameter (Arnold 2010). Further, estimates from the second-ranked model suggested that the probability of occupancy by coyotes was similar throughout our study site (within 0.5 km of wind energy facility:  $\Psi = 0.65$ , 95% CI = 0.07–0.98; beyond 0.5 km:  $\Psi = 0.96$ , 95% CI = 0.04–1.00).

#### Avian predator occupancy

Between 2013 and 2014, we conducted a total of 1156 point counts (2013: eight replicate surveys per point count, 2014: 22 replicate

surveys per point count). We recorded 194 observations from nine species known to be predators of Greater Prairie-Chickens or their nest contents; American Crows were identified in 61 (5.3%) point counts, Red-tailed Hawks in 31 (2.8%), Swainson’s Hawks (*Buteo swainsoni*) in 11 (1.0%), Northern Harriers in 11 (1.0%), unidentified *Buteos* spp. in 6 (0.5%), Rough-legged Hawks in 5 (0.4%), Cooper’s Hawks in 5 (0.4%), Bald Eagles in 3 (0.3%), Sharp-shinned Hawks (*Accipiter striatus*) in 2 (0.2%), and Prairie Falcons in 1 (0.1%). Avian predators were absent in 88.2% of point counts. The only spatial variables to exhibit correlation were distance to turbine and distance to perch ( $r_s = -0.50$ ,  $P < 0.0001$ ); therefore, we omitted distance to perch.

*All avian predators.*—The model in which probability of detection varied as a function of year ( $p_{\text{year}}, \Psi$ ) was ranked lower ( $\Delta\text{QAIC}_c = 0.47$ ) than the null model ( $p, \Psi$ ). Thus, we pooled data across years for subsequent analyses. Probability of detection for avian predators was best explained by the model in which detection probability varied by time period ( $p$  [time period],  $\Psi$ ). Detection probability was higher during time period one than during time period two (time period one [13 March–12 April]:  $p = 0.60$ , 95% CI = 0.25–0.87; time period two [13 April–29 July]:  $p = 0.20$ , 95% CI = 0.10–0.35). Therefore, in the assessment of occupancy models, we used ( $p$  [time period]) to represent variation in detection.

The estimates for naïve probability of observation for avian predators suggested that the closest distance from the wind energy facility at which a pronounced change in site occupancy occurred was 2 km. Therefore, we used 2 km to delineate the discrete distance categories, “near”

Table 1. Models describing site occupancy ( $\Psi$ ) and detection probability ( $p$ ) for coyotes in the vicinity of a wind energy facility, Brown County, Nebraska, USA, between April and July 2013 and 2014.

| Models  | $k^\dagger$ | $\text{QAIC}_c^\ddagger$ | $\Delta\text{QAIC}_c^\S$ | $w_i^\P$ |
|---|-------------|--------------------------|--------------------------|----------|
| $p(\cdot), \Psi(\cdot)$   | 2           | 49.13                    | 0.00                     | 0.45     |
| $p(\cdot), \Psi(\text{distance category})$                            | 3           | 50.49                    | 1.36                     | 0.23     |
| $p(\cdot), \Psi(\text{distance category} + \text{distance to crops})$ | 4           | 52.09                    | 2.95                     | 0.10     |
| $p(\cdot), \Psi(\text{distance category} + \text{distance to water})$ | 4           | 52.75                    | 3.62                     | 0.07     |
| $p(\cdot), \Psi(\text{distance category} + \text{distance to trees})$ | 4           | 52.82                    | 3.69                     | 0.07     |
| $p(\cdot), \Psi(\text{distance category} + \text{distance to road})$  | 4           | 52.83                    | 3.69                     | 0.07     |

$^\dagger$  Number of parameters.

$^\ddagger$  Quasi-Akaike’s Information Criterion corrected for sample size.

$^\S$  Difference in  $\text{QAIC}_c$  score relative to top-ranking model.

$^\P$  Quasi-Akaike weight indicating the relative support of the model.

(0–2 km) and “far” (>2 km). Of the models that we constructed to describe site occupancy of avian predators as different functions of distance to turbine, the discrete distance model received the most support ( $\Delta\text{QAIC}_c \leq 2$ ,  $w_i = 0.22$ ,  $k = 4$ ). Although the second-ranked model, the linear distance model ( $\Delta\text{QAIC}_c \leq 2$ ,  $w_i = 0.21$ ,  $k = 4$ ), received some support, we used the top-ranked model, the discrete distance model, to represent potential variation in occupancy as a function of distance to turbine in the next stage of model comparisons.

The null model received the most support from the data, which suggested less support for any variables we used to model variation in site occupancy for avian predators (Table 2). The second model, the discrete distance model ( $p$  [time period],  $\Psi$ [distance category]), received some support ( $\Delta\text{QAIC}_c \leq 2$ ; Table 2), but assessment of the model structure ( $k$ ), model coefficients, and values of  $\Delta\text{QAIC}_c$  suggested that distance to turbine was an uninformative parameter (Arnold 2010). The estimates from the second-ranked model suggested that the probability of occupancy by avian predators was lower within, compared to beyond 2 km of, the wind energy facility (within 2 km:  $\Psi = 0.70$ , 95% CI = 0.22–0.95; beyond 2 km:  $\Psi = 0.93$ , 95% CI = 0.02–1.00). However, wide overlapping 95% CIs suggested that any effects of distance to turbine on predator occupancy were weak.

*Avian predators of adult Greater Prairie-Chickens.*—The model in which probability of detection varied as a function of year ( $p_{\text{year}}$ ,  $\Psi$ .) received equivalent support from the data compared with the null model ( $\Delta\text{QAIC}_c = 1.63$ ). Thus, we pooled

data across years for subsequent analyses. Probability of detection for avian predators of adult Greater Prairie-Chickens was best explained by the model in which detection probability varied by time period ( $p$  [time period],  $\Psi$ ). Detection probability was higher during time period one than during time period two (time period one [13 March–12 April]:  $p = 0.47$ , 95% CI = 0.16–0.80; time period two [13 April–29 July]:  $p = 0.11$ , 95% CI = 0.04–0.25). Therefore, in the assessment of occupancy models, we used ( $p$  [time period]) to represent variation in detection.

The estimates for naïve probability of observation for avian predators suggested that the closest distance from the wind energy facility at which a pronounced change in site occupancy occurred was 2 km. Therefore, we used 2 km to delineate the discrete distance categories, “near” (0–2 km) and “far” (>2 km). All of the models that we constructed to describe site occupancy of avian predators as different functions of distance to turbine were ranked lower than the null model (null model;  $\Delta\text{QAIC}_c = 0.00$ ,  $w_i = 0.48$ ,  $k = 3$ ). Both the second-ranked model, the discrete distance model ( $\Delta\text{QAIC}_c \leq 2$ ,  $w_i = 0.21$ ,  $k = 4$ ), and the third-ranked model, the linear distance model ( $\Delta\text{QAIC}_c \leq 2$ ,  $w_i = 0.18$ ,  $k = 4$ ), received some support. Therefore, we used the discrete distance model to represent potential variation in occupancy as a function of distance to turbine in the next stage of model comparisons.

Of the models that we constructed to model variation in site occupancy for avian predators as a function of distance category and site-specific covariates, the null model received most support from the data (Table 3). The second-ranked model,

Table 2. Models describing site occupancy ( $\Psi$ ) for all avian predators in the vicinity of a wind energy facility, Brown County, Nebraska, USA, between April and July 2013 and 2014.

| Models   | $k$ † | $\text{QAIC}_c$ ‡ | $\Delta\text{QAIC}_c$ § | $w_i$ ¶ |
|--|-------|-------------------|-------------------------|---------|
| $p(\text{time period})$ , $\Psi(\cdot)$  | 3     | 80.51             | 0.00                    | 0.52    |
| $p(\text{time period})$ , $\Psi(\text{distance category})$                                   | 4     | 82.09             | 1.58                    | 0.24    |
| $p(\text{time period})$ , $\Psi(\text{distance category} + \text{distance to urban center})$ | 5     | 83.73             | 3.21                    | 0.10    |
| $p(\text{time period})$ , $\Psi(\text{distance category} + \text{distance to crops})$        | 5     | 84.36             | 3.84                    | 0.08    |
| $p(\cdot)$ , $\Psi(\cdot)$   | 2     | 84.71             | 4.20                    | 0.06    |

Note: All models, apart from the null model, contain a time-specific detection probability ( $p$ ) to account for higher detection probabilities between 13 March and 12 April compared to between 13 April and 29 July.

† Number of parameters.

‡ Quasi-Akaike's Information Criterion corrected for sample size.

§ Difference in  $\text{AIC}_c$  score relative to top-ranking model.

¶ Quasi-Akaike weight indicating the relative support of the model.

Table 3. Models describing site occupancy ( $\Psi$ ) for avian predators of adult Greater Prairie-Chickens in the vicinity of a wind energy facility, Brown County, Nebraska, USA, between April and July 2013 and 2014.

| Models  | $k$ † | QAIC <sub>c</sub> ‡ | $\Delta$ QAIC <sub>c</sub> § | $w_i$ ¶ |
|---|-------|---------------------|------------------------------|---------|
| p(time period), $\Psi(\cdot)$   | 3     | 80.02               | 0.00                         | 0.53    |
| p(time period), $\Psi$ (distance category)                            | 4     | 81.63               | 1.60                         | 0.24    |
| p(time period), $\Psi$ (distance category + distance to crops)        | 5     | 83.14               | 3.11                         | 0.11    |
| p(time period), $\Psi$ (distance category + distance to urban center) | 5     | 83.32               | 3.30                         | 0.10    |
| p( $\cdot$ ), $\Psi(\cdot)$   | 2     | 86.39               | 6.36                         | 0.02    |

Note: All models, apart from the null model, contain a time-specific detection probability (p) to account for higher detection probabilities between 13 March and 12 April compared to between 13 April and 29 July.

† Number of parameters.

‡ Quasi-Akaike's Information Criterion corrected for sample size.

§ Difference in AIC<sub>c</sub> score relative to top-ranking model.

¶ Quasi-Akaike weight indicating the relative support of the model.

the discrete distance model (p [time period],  $\Psi$  [distance category]), received some support ( $\Delta$ QAIC<sub>c</sub>  $\leq$  2; Table 3), but assessment of the model structure ( $k$ ), model coefficients, and values of  $\Delta$ QAIC<sub>c</sub> suggested that distance to turbine was an uninformative parameter (Arnold 2010). Estimates from the second-ranked model provided weak evidence that the probability of occupancy by avian predators of adult Greater Prairie-Chickens was lower within, compared to beyond 2 km of, the wind energy facility (within 2 km:  $\Psi = 0.70$ , 95% CI = 0.14–0.97; beyond 2 km:  $\Psi = 0.96$ , 95% CI = 0.0000003–1.00).

### Survival

We trapped, radio-collared, and monitored 62 female Greater Prairie-Chickens (2013: 32, 2014: 30). Of the 62 hens monitored, 22 died during the study period (2013: 11, 2014: 11), and our daily survival probability from the null model was 0.9948 (SE = 0.0015; 30-d survival = 0.8550, SE = 0.0382). The model in which survival varied as a function of year ( $\hat{S}_D$  [year]) received less support ( $\Delta$ AIC<sub>c</sub> = 1.61) from the data compared with the null model ( $\hat{S}_D(\cdot)$ ), suggesting that year had no effect on survival. Therefore, we pooled data across years for subsequent analyses. The only spatial variables to exhibit correlation were distance to perch and distance to major road ( $r_s = 0.66$ ,  $P < 0.0001$ ); therefore, we omitted distance to perch in our analyses.

The estimates for naïve probability of daily survival suggested that the closest distance from the wind energy facility at which a pronounced change in survival occurred was 1 km. Therefore, we used 1 km to delineate discrete distance

categories, “near” and “far.” Of the models that we constructed to model daily survival as different functions of distance to turbine, all were ranked higher than the null model ( $\hat{S}_D(\cdot)$ ;  $\Delta$ AIC<sub>c</sub> = 14.07,  $w_i = 0.001$ ). The top-ranked model was the quadratic model ( $\hat{S}_D$  [distance category<sup>2</sup>]; AIC<sub>c</sub> = 94.81,  $w_i = 0.66$ ). Although the second-ranked model ( $\hat{S}_D$  [distance category<sup>3</sup>]) received similar support from the data ( $\Delta$ AIC<sub>c</sub> = 1.88,  $w_i = 0.26$ ), we used the simpler quadratic model to represent the distance to turbine effect in future model comparisons.

Of the models used to model variation in daily survival of female Greater Prairie-Chickens, three models received essentially equivalent support from the data ( $\Delta$ AIC<sub>c</sub>  $\leq$  2; Table 4). The top-ranked model contained distance to turbine<sup>2</sup> ( $\hat{S}_D$  [distance category<sup>2</sup>]) and received most support from the data (Table 4). The second model ( $\hat{S}_D$  [distance category<sup>2</sup> + distance to crops]) and the third model ( $\hat{S}_D$  [distance category<sup>2</sup> + distance to roads]) received some support ( $\Delta$ AIC<sub>c</sub>  $\leq$  2; Table 4), but assessment of the model structure ( $k$ ), model coefficients, and values of  $\Delta$ AIC<sub>c</sub> suggested that distance to crops and distance to roads were uninformative parameters (Arnold 2010). Estimates from the top-ranked model provided little evidence of an effect of distance to turbine on survival ( $\beta$  [distance to turbine] = 0.16, 95% CI = –0.08–0.40;  $\beta$  [distance to turbine<sup>2</sup>] = –0.004, 95% CI = –0.01–0.01).

### DISCUSSION

Our study appears to be the first to assess the effects of an existing wind energy facility on the

Table 4. Log-exposure models describing daily survival ( $\hat{S}_D$ ) of female Greater Prairie-Chickens breeding in the vicinity of a wind energy facility, Brown County, Nebraska, USA, between March and July 2013 and 2014.

| Models  | $k^\dagger$ | $AIC_c^\ddagger$ | $\Delta AIC_c^\S$ | $w_i^\P$ |
|---|-------------|------------------|-------------------|----------|
| $\hat{S}_D(\text{distance to turbine} + \text{distance to turbine}^2)$                            | 3           | 94.81            | 0.00              | 0.34     |
| $\hat{S}_D(\text{distance to turbine} + \text{distance to turbine}^2 + \text{distance to crops})$ | 4           | 94.83            | 0.01              | 0.34     |
| $\hat{S}_D(\text{distance to turbine} + \text{distance to turbine}^2 + \text{distance to roads})$ | 4           | 94.98            | 0.16              | 0.32     |
| $\hat{S}_D(.)$  | 1           | 108.88           | 14.07             | 0.00     |
| $\hat{S}_D(\text{distance to turbine} + \text{distance to turbine}^2 + \text{time period})$       | 5           | 113.80           | 18.99             | 0.00     |

$^\dagger$  Number of parameters.

$^\ddagger$  Akaike's Information Criterion corrected for sample size.

$^\S$  Difference in  $AIC_c$  score relative to top-ranking model.

$^\P$  Akaike weight indicating the relative support of the model.

survival of birds in the context of information on two possible mechanisms underlying survival, mammalian and avian predation risk. We found little evidence that site occupancy of avian predators was lower within than beyond 2 km of the wind energy facility, suggesting that avian predators did not display local-scale avoidance behavior around wind turbines. Previous studies have either demonstrated avoidance of wind turbines by avian predators (Pearce-Higgins et al. 2009), or found no effect (corvid spp., Devereux et al. 2008). These results suggest that avoidance in response to wind energy development by avian predators may be species and site specific.

Similarly, distance to turbine appeared to have little effect on site occupancy of coyotes within 0.5 km of the wind energy facility. In contrast, Tanis (2013) found that occupancy of coyotes was higher at control locations compared to at locations at a wind energy facility in Kansas. Activity within the Ainsworth facility (e.g., construction, vehicle traffic) during our study may have been lower than at the Kansas wind energy facility. However, the Ainsworth facility and the Kansas facility used by Tanis (2013) were equivalent in size (36 vs. 33 turbines, respectively), and Tanis (2013) reported lower levels of human activity at the wind energy facility compared to at control locations. Thus, we suggest that the inconsistent results between the studies likely result from differences in the timing of the studies; the Ainsworth wind energy facility became fully operational in 2005, eight years before the start of our study. In comparison, the time period between the wind energy facility becoming fully operational and data collection in the Kansas study was only two years (Tanis 2013). Effects of wind energy facilities on wildlife can subside over time

(Madsen and Boertmann 2008), so these results suggest that coyotes may have become habituated to the Ainsworth wind energy facility between construction and the start of our study.

Contrary to our avian predator analysis, our analyses of mammalian predators did suggest an effect of the wind energy facility. Mammalian predators were present near the facility, although they encountered our cameras less frequently (Fig. 2). This effect seemed most pronounced at camera sites immediately adjacent to the wind energy facility, which suggests that predation risk from mammals may be lower at sites close to the wind energy facility. We note that the catch-per-unit-effort statistic assumes detection does not vary with time or space, and our more rigorous analysis of detection probability for coyotes suggested no temporal trends in detection.

Given the apparent absence of an effect of distance to turbine on site occupancy of most types of predators, it is not surprising that an effect of distance to turbine on the daily survival of female Greater Prairie-Chickens was not detected. Similarly, although Winder et al. (2014a) showed an increase in survival of female Greater Prairie-Chickens after construction of a wind energy facility in the Flint Hills of Kansas, they found no effect of distance to wind turbine on survival. LeBeau et al. (2014) also found no effect of distance to wind turbine on the survival of female Greater Sage-Grouse (*Centrocercus urophasianus*) at a wind energy facility in south-central Wyoming. Collectively, these results suggest that wind energy facilities may not affect the survival of prairie grouse as much as other anthropogenic disturbances (e.g., oil and gas development; Hovick et al. 2014). However, we emphasize the context of our analyses: a relatively small facility,

eight years post-construction in a largely unfragmented landscape.

Mammalian predators showed the expected response to the wind energy facility. Although we found no evidence for a strong effect of distance to turbine on predation risk from coyotes or avian predators, the trends in those data are in the direction expected if predators were avoiding the wind energy facility. Thus, our results provide insight into a potential ecological mechanism (i.e., predation risk) that may have consequences for population viability of a wide range of species occupying landscapes near wind energy development. We suggest that future research should consider predation risk in assessments of wind energy development and wildlife interactions. We also encourage researchers to consider alternative mechanisms such as changes in food and habitat availability along disturbance gradients in addition to disturbance due to turbine noise that could influence the behavior and demographics of species occupying landscapes near wind energy development (Whalen 2015, Zwart et al. 2016). We urge future studies to adopt a disturbance gradient design, or if possible a before-after-gradient design (Ellis and Schneider 1997, McNew et al. 2014), and to further explore the effects of installation and construction, as well as effects of larger facilities on predation risk and survival of prairie grouse.

#### ACKNOWLEDGMENTS

This project was funded with U.S. Fish and Wildlife Service Wildlife Restoration dollars administered by the Nebraska Game and Parks Commission. Larkin A. Powell was supported by Hatch Act funds through the University of Nebraska Agricultural Research Division, Lincoln, Nebraska. Mary Bomberger Brown was supported by the Nebraska Environmental Trust and the Nebraska Game and Parks Commission. Jocelyn O. Harrison was supported by a Graduate Research Fellowship Program from the National Science Foundation. All authors conceived the idea and design of the study and wrote the manuscript, Jocelyn O. Harrison and Jennifer A. Smith collected the data, and Larkin A. Powell and Jennifer A. Smith analyzed the data. Animal capture and handling protocols were approved by the University of Nebraska-Lincoln Institutional Animal Care Use and Committee (Protocol no. 650). We thank the Nebraska Department of Roads and Scott Hyngstrom (University of Nebraska-Lincoln) who

provided trail cameras. For assistance, we thank Nate Bieber, Candice Doyle, Michelle Dvoracek, Matthew Gonnerman, Emily Kermath, Jeff Lusk, Rocky Plettner, Jackie Mather, Lindsey Sanders, Elsie Shogren, Tyler Trump, Nate Turner, Bill Vodehnal, Chris Walnofer, and Cara Whalen. We thank numerous private land owners and the Nebraska Public Power District who allowed us access to their property. We thank Lance McNew, Virginia Winder, and an anonymous reviewer for insightful comments that helped improve this manuscript.

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