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Cover Page

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Effects of wind energy development on survival of female greater prairie-chickens

Virginia L. Winder[1], Lance B. McNew[2], Andrew J. Gregory[3], Lyla M. Hunt[1], Samantha M. Wisely[4] and Brett K. Sandercock[1]*

[1]*Division of Biology, Kansas State University, Manhattan, KS 66506, USA;* [2]*United States Geological Survey, Alaska Science Center, Anchorage, AK 99508, USA;* [3]*School of Forestry, Northern Arizona University, Flagstaff, AZ 86002, USA; and* [4]*Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA*

Summary

1. The potential effects of wind energy development on wildlife have received increased attention over the past decade. In Kansas, optimal sites for wind energy development often overlap with preferred habitats of greater prairie-chickens *Tympanuchus cupido*. Our goal was to determine whether wind energy development affected survival of female prairie-chickens in a grassland ecosystem, assessing one potential impact of wind on an upland gamebird of conservation concern. We focused primarily on the response of female prairie-chickens to wind energy development because population dynamics of prairie-chickens are primarily determined by female demography.

2. We monitored prairie-chickens at a wind facility in Kansas during a 2-year pre-construction (2007–2008) and a 3-year post-construction period (2009–2011). We used data from 220 radio-marked females to calculate weekly survival and hazard rates. We used cause of death for 81 mortality events to test for changes in the proportion of mortalities attributed to mammalian predators, avian predators and collisions.

3. We observed an unexpected increase in annual survival during the post-construction period (0·57) compared with the pre-construction period (0·32). Distance from home range centroid to the nearest wind turbine site had no effect on weekly survival of females. Collision mortality events were rare, and most were associated with fences or transmission lines and not turbine blades.

4. Most female mortality was due to predation (*c.* 90%). Differences in annual survival were driven by a higher risk of mortality during lekking activity in March and April during the pre-construction period (weekly hazard rate = 0·050–0·062) compared with the post-construction period (hazard rate = 0·012–0·021). We observed no change in the proportion of mortalities attributed to different causes between the two treatment periods.

5. *Synthesis and applications.* Development of a wind energy facility had no negative effect on survival of female prairie-chickens. The results of our field study indicate that greater prairie-chickens are less sensitive to wind energy development than lesser prairie-chickens *Tympanuchus pallidicinctus* and greater sage-grouse *Centrocercus urophasianus* are to oil and gas development. We have strong evidence that survival increased after wind energy development, and hypothesize that energy development affected the local predator community, resulting in an indirect effect of decreased predation risk during the post-construction period.

Key-words: collisions, grassland bird community, grouse, hazard function, mortality, predation, wind turbine

*Correspondence author. E-mail: bsanderc@k-state.edu

Introduction

Conflicts between energy development and wildlife are widespread, and an estimated 15 million birds are killed each year in the United States due to collisions, displacement and other aspects of energy use (Sovacool 2009). The effects of energy development on lek-mating grouse in grasslands and shrub-steppe habitats are poorly understood but are of growing conservation concern (Manville 2004). Prairie grouse may be particularly sensitive to energy development because they have large home ranges, specific habitat requirements, and use communal display sites where birds are sensitive to disturbance (Connelly *et al.* 2000; Svedarsky *et al.* 2000; Augustine & Sandercock 2011; Hess & Beck 2012). Lek abandonment by greater sage-grouse *Centrocercus urophasianus* has been associated with proximity to oil and gas wells (Hess & Beck 2012). Lesser prairie-chickens *Tympanuchus pallidicinctus* avoid anthropogenic structures related to energy extraction or transmission, such as power lines, roads, or wells (Pitman *et al.* 2005; Pruett, Patten & Wolfe 2009; Hagen *et al.* 2011). Moreover, a higher density of roads, fences, and power lines has been linked to increases in mortality rates of female lesser prairie-chickens (Patten *et al.* 2005; Wolfe *et al.* 2007).

Wind energy is experiencing rapid growth world-wide and is targeted to meet 20% of the U.S. energy demand by 2030 (D.O.E. 2008). Due to rapid expansion over a relatively short period of time, the potential effects of wind energy development on wildlife have received increased attention in the past decade (Drewitt & Langston 2006; Kuvlesky *et al.* 2007; Smallwood & Thelander 2008; Pearce-Higgins *et al.* 2012). Male prairie grouse preferentially select areas of open grasslands at locally high elevations for lek sites, maximizing visibility and auditory detection by females (Aspbury & Gibson 2004; Gregory *et al.* 2011). Lek placement is thought to be driven by predation risk to males and female preference for nearby resources (Schroeder & White 1993). Optimal locations for wind turbines are also open, exposed sites at relatively high elevations to ensure efficiency of wind use (Drewitt & Langston 2006). Thus, habitat requirements of prairie grouse often coincide with preferred locations for wind energy development, increasing the potential for conflict between wind energy development and wildlife.

In 2011, the U.S. Fish and Wildlife Service developed a series of best management practices aimed at reducing negative effects of wind energy development on wildlife (www.fws.gov/windenergy). Recommendations for lek-mating grouse included the following: siting of turbines to avoid disruption to daily activities, minimization of infrastructure and roads that might attract prey and predators to the development site, and establishment of appropriately sized buffer zones. Studies that have examined habitat requirements of grouse in relation to anthropogenic disturbance have recommended an 8-km (5-mile) buffer zone around active leks (Connelly *et al.* 2000; Hagen

et al. 2004; Manville 2004; Patten *et al.* 2005). Formal policies have not yet been established to direct siting of wind turbines relative to grassland bird habitats.

The greater prairie-chicken *Tympanuchus cupido* (hereafter prairie-chicken) is an indicator species for tallgrass prairie ecosystems (Poiani, Merrill & Chapman 2001), and is listed as vulnerable by the International Union for Conservation of Nature because populations have declined over the last three decades (Svedarsky *et al.* 2000; Bird-Life International 2012). Count data from annual lek surveys indicate that Kansas prairie-chicken populations are declining in the core of their extant range (Pitman, Kramer & Michener 2012). Demographic causes of ongoing declines are low rates of nest, brood and adult survival, which are related to high predation rates and intensive land use for cattle production (McNew *et al.* 2012).

The purpose of our 5-year study was to examine the potential effects of wind energy development on seasonal survival, annual survival and causes of mortality for female prairie-chickens in north-central Kansas. Energy development can affect wildlife directly or indirectly (Drewitt & Langston 2006). Direct effects of collision mortality due to wind turbines have been documented in several bird populations (Hunt *et al.* 1998; Drewitt & Langston 2006; Smallwood & Thelander 2008; Slater & Smith 2010), but turbine collision mortalities may be less likely if prairie-chickens fly at heights lower than turbine blades. We predicted that wind energy development might have direct effects through increased rates of collision mortality associated with power lines, fences or other infrastructure (Barrios & Rodriguez 2004; Drewitt & Langston 2006; Wolfe *et al.* 2007; Smallwood & Thelander 2008).

Indirect responses of wildlife to wind energy development are more difficult to measure. Predation is often the primary cause of mortality in prairie grouse populations (Hagen *et al.* 2009; Augustine & Sandercock 2011; McNew *et al.* 2012), and we predicted wind energy development might indirectly affect prairie-chicken populations by altering trophic interactions with predators. Wind energy development might attract predators if development creates novel corridors and edges, providing new foraging opportunities (Tigas, Van Vuren & Sauvajot 2002). Conversely, wind energy development could have a positive effect on prairie-chicken populations if predators show behavioural avoidance or reduced foraging activity in developed areas. For example, greater sage-grouse leks were not affected at intermediate distances from drilling rigs, possibly because predators moved away from sources of disturbance (Holloran 2005).

We collected data on survival of female greater prairie-chickens during a 2-year pre-construction period (2007–2008) and a 3-year post-construction period (2009–2011). Our study design has two potential advantages over previous investigations of the effects of energy development on prairie grouse. First, our project was based on a modified before-after control-impact (BACI) design, which controlled for potentially confounding environmental

variables. Second, we tested for responses to wind energy development with a large sample size of radio-marked individuals in multi-year pre- and post-construction periods. Designation of control and impact sites requires *a priori* determination of a threshold distance below which negative effects may occur. Rather than setting a threshold at the outset, we opted to use distance to eventual or actual turbine site as an index of proximity to disturbance. Thus, the critical tests for negative effects of wind energy development should compare survival rates between treatment periods, as a function of distance to turbine, and the interaction of these two factors. If energy development has negative effects, we predicted the interaction term should be significant, with no relationship between survival and distance to turbine for the pre-construction period but a positive relationship during the post-construction period. We provide some of the first empirical evidence that development of wind energy can have unanticipated positive effects for a sensitive species of grassland bird.

Materials and methods

STUDY AREA

Our study site (*c.* 1300 km²; Fig. 1) was located south of Concordia in the Smoky Hills eco-region of north-central Kansas. Land cover in our study area was native grasslands or pasture (58%), row crop agriculture (35%), restored grasslands in the Conservation Reserve Programme (5%) and small woodlands (2%). The landscape was fragmented with a relatively high road density of 1·4 km of road per km². Native grasslands were managed for cattle production with one prescribed burn every 3 years in spring; cattle were stocked at densities of *c.* 2–4 ha per head for 90 days (*c.* late April to late July). Weekly averages of daily weather con-

ditions during our 5-year study period (1 March 2007–31 December 2011) were similar among years and between treatment periods (Fig. S1, Supporting information).

The Meridian Way Wind Power Facility was constructed 13 km south of Concordia in Cloud County, Kansas. Horizon Wind Energy started preparations for construction in April 2008 and began commercial operation in December 2008. The completed facility comprised 67 Vestas V90 3.0 MW turbines and had a total installed capacity of 201 MW. Turbine towers were *c.* 90 m tall, and rotating blades were *c.* 45 m long. Mean distance between turbines was 328 m ± 12 SE (median = 298 m, range = 257–763 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 (*c.* 25 km). We included 2008 in our 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 the 2004 U.S. Fish and Wildlife Service recommendations with respect to placement of wind turbine sites (Manville 2004); >75% of monitored leks (15 of 19) were located within 8 km of a wind turbine and associated infrastructure. No mitigation or changes in rangeland management were known to have taken place post-construction.

CAPTURE AND MONITORING OF PRAIRIE-CHICKENS

During March and April of each year, we captured prairie-chickens with walk-in traps and drop-nets at lek sites (Table S1, Supporting information). At first capture, we marked all birds with a uniquely numbered metal leg band and three coloured leg bands, and sexed and aged birds by plumage. Each female was outfitted with a 10–11 g radiotransmitter attached with an elastic or wire necklace harness (*c.* 1–1·5% of body weight; Model A3950, ATS, Isanti, Minnesota; Model RI-2B; Holohil, Carp, ON, Canada). Radios had an expected battery life of 12–24 months and were equipped with mortality switches that changed pulse rate when
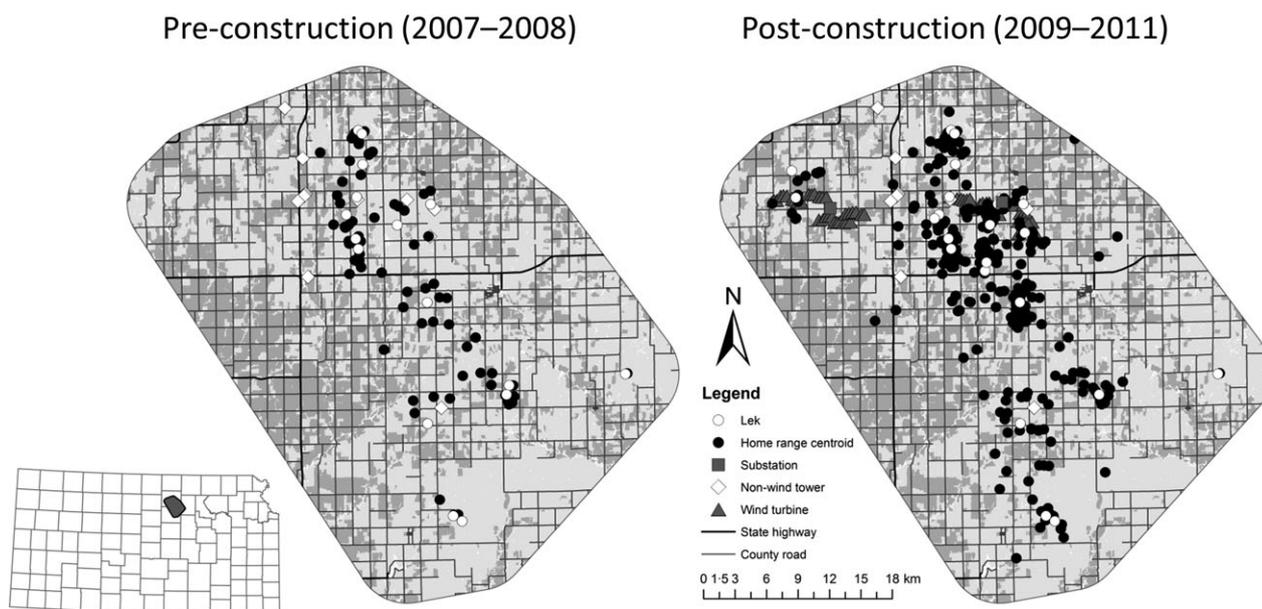
Pre-construction (2007–2008)   ## Post-construction (2009–2011)

Fig. 1. Map of study area for effects of wind energy development on greater prairie-chickens in north-central Kansas, 2007–2011. Light grey shading is native grasslands managed for cattle grazing; dark grey shading is row crop agriculture.

the transmitter was stationary for 6–8 h. Radio-marked females were located by triangulation or homing with portable radio receivers and handheld antennas (Model R2000, ATS, Isanti, MN, USA). We relocated birds 3–4 times per week during the 6-month breeding season (March–August) and weekly during the 6-month non-breeding season (September to February). Coordinates for triangulated locations were estimated using Program Locate III (ver. 3.34, www.locateiii.com, Tatamagouche, Nova Scotia).

If the mortality switch indicated a female had died or a tag had been dropped, observers located the carcass or transmitter within 1–2 days and determined cause of death or transmitter loss from evidence at the site. We considered radios with broken harnesses, no other damage and no bird remains to be *dropped collars*, and we right-censored those birds as survivors. We considered carcasses with tooth marks, chewed feathers or scat to be *mammalian predation* by coyotes *Canis latrans*, American badgers *Taxidea taxus*, or other mesocarnivores. We considered carcasses plucked at a perch site, decapitated, breast muscles removed with no evidence of tooth marks, or presence of white faecal matter to be *avian predation* by raptors or owls. Carcasses with broken necks or wings, long open gashes and no evidence of predator activity that were found within 200 m of a fence line, power line, or turbine were considered to be *collision mortalities*. Most carcasses were recovered within 1–2 days of death; but confounding effects of scavenging could not be completely discounted. If we were unable to determine cause of mortality because a carcass was decomposed at recovery or if conflicting signs of evidence were present, we considered the event to be an *unknown mortality* event.

DATA ANALYSIS

We tested for effects of wind energy development on prairie-chicken survival using an analysis of covariance design with treatment period as a categorical variable, distance from home range centroid to turbine as a continuous variable, and an interaction term. Treatment period was a fixed effect with two levels (pre- and post-construction). We used all of the locations available within a given bird-year (1 March–28 February) to determine the home range for each female based on fixed kernel-density estimates of 95% volume isopleths with Program Abode (Laver 2005) in ArcGIS (ver. 9.3; ESRI, Redlands, CA, USA). We used least-squares cross-validation to determine smoothing factors, and data were standardized using unit variance. We calculated the centroid of each home range polygon, and measured distance

from centroids to the nearest wind turbine with Hawth's Tools (Beyer 2004). We used eventual turbine sites for the pre-construction period, and actual locations during the post-construction period. Distance to eventual turbine sites during the pre-construction period was a good baseline because it controlled for pre-existing gradients in habitat conditions in a heterogeneous landscape. Distance to the nearest wind turbine was strongly correlated with distance to access roads, transmission lines and other wind energy features ($r \geq 0.8$, $P < 0.001$). Therefore, we used distance to nearest turbine as an index of anthropogenic disturbance, which included the wind turbines but also their associated infrastructure.

Annual survival

We calculated survival rates of radio-marked females with staggered entry Kaplan–Meier models with package survival in Program R (ver. 2.13.11; R Foundation for Statistical Computing, Vienna, Austria). We did not analyse data for individuals who survived <1 week post-capture to account for potential negative effects of handling on survival. We created encounter histories for individual females based on weekly time steps for an annual period from 1 March to 28 February of the following year (i.e. 1–7 March = Week 1). Our data were left-censored with staggered entry of birds into the marked population, and right-censored for radio failure (Table 1). Twenty-eight females were monitored in multiple years (25 in two consecutive years; three in three consecutive years), and we modelled individual identity as a random effect using the cluster function to control for a potential lack of independence among females monitored for more than 1 year.

We used Cox proportional hazards models to test for differences in survival among years within each treatment period (Murray 2006; Sandercock *et al.* 2011). As a first step, we determined if the assumption of proportional hazards was met by our survival data with model diagnostics based on scaled Schoenfeld residuals (cox.zph function, Fox 2002). After testing for annual variation, we pooled data within treatment periods and ran five additional models, testing the additive and interactive effects of treatment and distance to turbine (Table 2). We ranked models using Akaike's information criterion adjusted for small sample sizes (AIC_c). Models with $\Delta AIC_c < 2$ that differed from the minimum AIC_c model by a single parameter were excluded from the set of candidate models if covariates were uninformative parameters (Arnold 2010). We report the effects of treatment as a hazard ratio (e^β) where a hazard ratio is expected to equal one if there is

Table 1. Annual variation and effects of wind energy development on the annual survival of radio-marked female Greater Prairie-Chickens in northcentral Kansas during pre- (2007–2008) and post-construction (2009–2011) periods

Period	Individuals (bird-years)*	Mortalities	Right-censored	Annual survival ± SE (95% CI)
2007	22	13	2	0·27 ± 0·10 (0·13–0·57)
2008	55	25	5	0·35 ± 0·09 (0·22–0·57)
Pre-construction	72 (77)	38	7	0·32 ± 0·07 (0·20–0·50)
2009	64	14	14	0·65 ± 0·08 (0·51–0·83)
2010	67	18	27	0·52 ± 0·10 (0·36–0·75)
2011	62	25	4	0·55 ± 0·07 (0·44–0·70)
Post-construction	167 (193)	57	45	0·57 ± 0·05 (0·48–0·67)

*Count of 'individuals' refers to the number of unique radio-marked females, while the count of bird-years includes multiple years of observations for a subset of females monitored across two or more years.

Table 2. Model selection for Cox proportional hazard models of survival for female greater prairie-chickens in north-central Kansas, 2007–2011

Models for survival*	k	ΔAIC_c	w_i
Treatment	2	0·00	0·658
Treatment + distance to turbine[†]	3	2·04	0·237
Treatment × distance to turbine[†]	4	3·90	0·094
Constant	1	8·80	0·008
Distance to turbine	2	10·82	0·003

*Model notation included two factors: treatment = pre- vs. post-construction of a wind energy facility, distance to turbine = distance from home range centroid to the nearest turbine site, where '+' = main effects models and '×' = factorial model. Model fit was assessed by the following: k = number of parameters, ΔAIC_c = difference in corrected Akaike's Information Criterion value from the minimum AIC_c model (AIC_c = 953·6), and w_i = Akaike's weight.
[†]Models with uninformative parameters that were not competitive with the top model (Arnold 2010).

no difference in the risk of mortality between groups. To examine the effects of treatment and distance to turbine on weekly survival, we fit a binomial model with the nest survival procedure in Program Mark (ver. 7.1; White & Burnham 1999).

Seasonal mortality risk

To examine differences in seasonal patterns of mortality between the two treatment periods, we calculated hazard functions based on weekly survival data using smoothing spline functions in package gss in Program R (DelGiudice *et al.* 2006). Hazard functions assess the instantaneous risk of mortality per week, given that an individual has survived until that point. Hazard functions are rates and not probabilities, and are well suited for calculation of seasonal patterns of mortality risk. We used the default value of 1·2 for the smoothing parameter and did not modify this value to avoid over-fitting splines.

Cause of death

We conducted *post hoc* analyses of cause of mortality to explore the effects of wind energy development on the relative importance of predation by raptors and mammalian predators. We first tested whether wind energy development affected mortality from avian predators, mammalian predators and collisions between the pre- and post-construction periods by comparing the relative frequencies of mortality causes with a Pearson's chi-square analysis using proc freq in sas (ver. 9.1; SAS Institute, Cary, NC, USA). Next, we tested for changes in the distance from mortality locations to turbines by cause of mortality between pre- and post-construction periods with Mann–Whitney U-tests (chi-square approximation) using proc npar1way in sas.

Results

ANNUAL SURVIVAL

Annual survival did not differ among years within either treatment period (pre-construction $P = 0.27$; post-construc-

tion $P = 0.10$; Table 1, Fig. 2a). A model that pooled annual variation within treatment periods performed better than one that allowed for separate estimates of annual survival. We pooled years within each treatment period and proceeded with further analyses. The assumption of proportional hazards was met for our global Kaplan–Meier model with factorial effects of treatment period and distance to nearest turbine ($P = 0.14$). The minimum AIC_c model included survival as a function of treatment period alone and received *c.* 80 times more support than the next competitive model ($w_i = 0.658$; Table 2). Unexpectedly, annual survival of females was significantly higher during the post-construction period (0.57 ± 0.05 SE) than during the pre-construction period (0.32 ± 0.07 SE; hazard rate = 2·03, 95% CI = 1·35 to 3·07, $z = 3.37$, $P = 0.0008$; Table 1, Fig. 2).

Most radio-marked females had home ranges that were close to the wind turbine sites. Average distance from the centroid of the 95% home range to the nearest turbine was 8·9 km $\pm$ 0·9 SE (ranging from 0·1 to 27·0 km) in
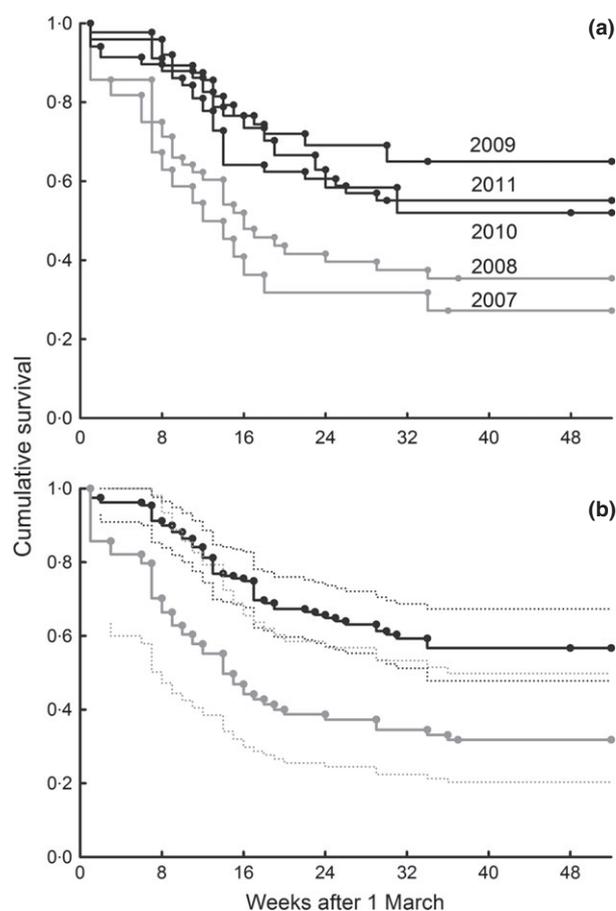
Fig. 2. Kaplan–Meier plots of the cumulative survival of radio-marked female greater prairie-chickens during the pre- (2007–2008; grey lines) and post-construction (2009–2011; black lines) periods of wind energy development in north-central Kansas: (a) annual estimates with confidence intervals omitted for clarity; and (b) estimates for the two treatment periods with 95% confidence intervals.

the pre-construction period and 7·5 km ± 0·5 SE (ranging from 0·03 to 31·0 km) in the post-construction period. Despite the close proximity of prairie-chickens to wind turbines and associated infrastructure, distance to turbine had no effect on female survival either as a main effect ($P = 0.91$) or as part of an interaction term with treatment period in Kaplan–Meier models ($P = 0.94$). Similarly, a binomial model using the nest survival procedure in Program Mark indicated that the interactive effect of treatment and distance to turbine was non-significant ($\beta = -0.009$, 95% CI = -0.065 to 0·046), and that weekly survival differed between treatment periods ($\beta = -0.547$, 95% CI = -0.960 to -0.133), but was not related to distance to turbine ($\beta = 0.003$, 95% CI = -0.025 to 0·30; Fig. S2, Supporting information).

SEASONAL MORTALITY RISK

To investigate seasonal patterns of mortality risk, we calculated hazard functions for the instantaneous risk of mortality for each treatment period. During the pre-construction period, the highest instantaneous risk of mortality coincided with the period of lek activity in weeks 1–9 (March–April). During lekking, the instantaneous risk of mortality was *c.* 3–4 times higher during the pre- compared with post-construction period (hazard rate = 0·050–0·062 vs. 0·012–0·021, respectively; Fig. 3). During the post-construction period, the highest instantaneous risk of mortality coincided with nesting and brood rearing periods when females were attending eggs or young (Weeks 7–20 in mid-April–July; Fig. 3). For both treatment periods, if a female survived the 6-month breeding season, natural mortality was low during the 6-month non-breeding season from September to February (hazard rate <0·015 per week; Weeks 30–52; Fig. 3).
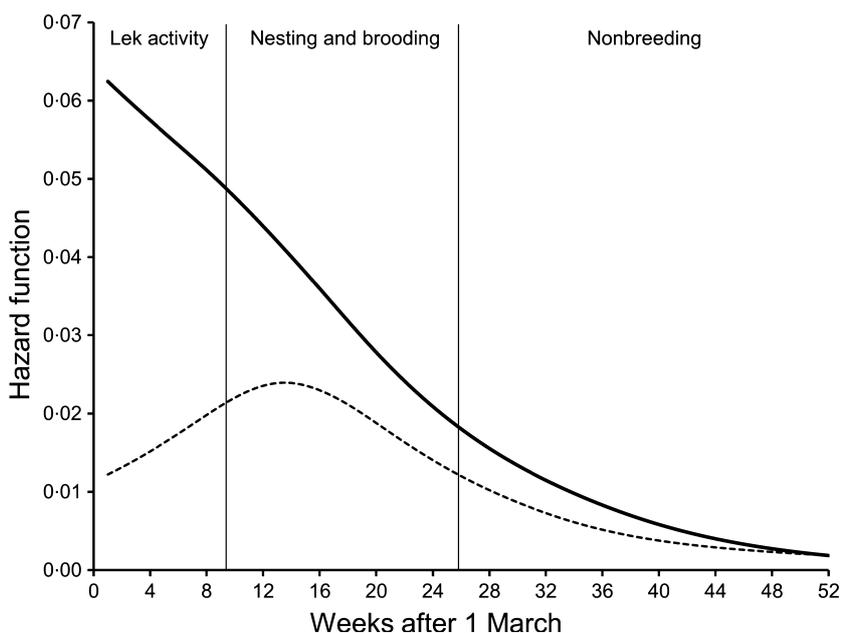
CAUSE OF DEATH

Ninety radio-tagged females were found dead during our 5-year study. Cause of death was successfully determined by inspection of carcass or recovered transmitter for 81 birds (85%). The main cause of death was predation by mammals during both the pre- (72%) and post-construction periods (54%), followed by losses to avian predation and collision (Table 3). No radio-marked females were harvested by hunters during our field study. The proportion of mortalities attributed to mammalian predators, avian predators or collisions did not differ between the pre- and post-construction periods ($\chi^2 = 4.38$, d.f. = 2, $P = 0.11$). Similarly, the distance from mortality locations to nearest turbine did not differ for female prairie-chickens killed by mammalian predators (pre vs. post: median = 7·8 vs. 3·7 km, range = 0·07 to 27·0 vs. 0·13 to 28·2 km, $n = 18$ and 30; chi-square approximation to Mann–Whitney U-test, $\chi^2 = 3.12$, d.f. = 1, $P = 0.08$), or by avian predators (pre vs. post: median = 2·9 vs. 5·9 km, range = 2·6–14·7 vs. 0·7–28·8 km, $n = 4$ and 22; $\chi^2 = 0.02$, d.f. = 1, $P = 0.90$). Moreover, distance to turbines for collision mortalities was similar for the small sample of mortality events during pre-construction (median = 4·2 km, ranging from 0·8 to 4·3 km, $n = 3$) and post-construction periods (median = 2·9 km, ranging from 0·2 to 28·4 km, $n = 4$).

Discussion

ANNUAL SURVIVAL

Investigations of the effects of energy development on lek-mating grouse have generally reported negative effects, including reduced rates of lek attendance (Walker, Naugle & Doherty 2007; Harju *et al.* 2010; Blickley, Blackwood

Fig. 3. Hazard functions for radio-marked female greater prairie-chickens during the pre- (2007–2008; solid line) and post-construction (2009–2011; dashed line) periods of wind energy development in north-central Kansas.

Table 3. Cause of mortality for radio-marked female greater prairie-chickens found dead (percentage, *n*) at a wind energy facility site in north-central Kansas, 2007–2011

	Mammalian predation	Avian predation	Collision mortality
Pre-construction (2007–2008)	72 (18)	16 (4)	12 (3)
Post-construction (2009–2011)	54 (30)	39 (22)	7 (4)
Total	59 (48)	32 (26)	9 (7)

& Patricelli 2012; Hess & Beck 2012), behavioural avoidance of anthropogenic structures (Pitman *et al.* 2005; Doherty *et al.* 2008; Pruett, Patten & Wolfe 2009; Hagen *et al.* 2011; Johnson & Stephens 2011) and reduced survival rates (Holloran, Kaiser & Hubert 2010). We observed an effect of treatment period before and after wind energy development, but no effect of distance to turbine or evidence of an interaction. Overall, wind energy development did not negatively affect survival in our 5-year study of female prairie-chickens even though the recommended 8-km buffer zone around active leks was not maintained during construction of the Meridian Way Wind Power Facility. However, we cannot discount the potential importance of such a buffer to other sensitive species in grassland ecosystems.

Annual survival of females was nearly twice as high during the post-construction period (0·57) compared with the pre-construction period (0·32). We have only circumstantial evidence that wind energy development was a driver of the difference in demography because survival was unaffected by proximity to development. No other environmental covariate is known to have changed between the two treatment periods: livestock management practices and precipitation and temperature patterns did not vary, and no radio-tagged individuals were harvested during the 5 years of our study. Our study improves upon previous assessments of effects of energy development on prairie grouse because our BACI design explicitly controlled for potential confounding environmental variables. Our analyses were based on a large sample size of radio-marked prairie-chickens close to the wind power facility, multiple years of monitoring during the pre- and post-construction periods, and similar patterns of survival within each treatment period.

Annual survival during the pre-construction period (0·32) was low compared to published estimates for greater prairie-chickens (0·23–0·68; Johnson, Schroeder & Robb 2011) and lesser prairie-chickens (0·31–0·60; Hagen *et al.* 2007; Lyons *et al.* 2009), whereas survival during the post-construction period (0·57) was near the upper end of the range of published estimates. Annual survival of grouse has been viewed as a constant demographic parameter and not a target for management action (Schroeder & Baydack 2001). Recent demographic analy-

ses have shown that rates of population change in prairie grouse can be sensitive to adult survival, particularly in declining populations (Lyons *et al.* 2009; McNew *et al.* 2012). McNew *et al.* (2012) observed regional differences in female prairie-chicken survival between the Smoky Hills (0·32) and managed rangelands in the Flint Hills of Kansas (0·47 and 0·68) and attributed differences in survival to variation in predation pressure and habitat quality. Lyons *et al.* (2009) also found habitat-specific annual survival rates for lesser prairie-chickens occupying in shinnery oak *Quercus havardii* (0·31) and sagebrush habitats (0·52). Variation in population dynamics across different habitats can be a fundamental driver of resource-use patterns; generally habitat use reflects the quality and abundance of required resources in an area (Boyce & McDonald 1999). Perceptual traps – the opposite of ecological traps – can occur when habitat with potential for high fitness is avoided because habitat cues do not accurately reflect habitat quality (Gilroy & Sutherland 2007; Patten & Kelly 2010). Our study was not designed to test these alternative hypotheses, but our observations of improvements in female survival during the post-construction period are consistent with the concept of a perceptual trap (Patten & Kelly 2010).

SEASONAL MORTALITY RISK

A majority of the demographic losses in our study were due to predation, and hazard rates indicated that lower annual survival pre-construction was due to higher rates of mortality during the period of lek attendance. Prairie-chickens are vulnerable to attacks by predators at lek sites, and predation risk is a key factor affecting lek site selection and persistence (Gregory *et al.* 2011; Alonso, Alvarez Martinez & Palacin 2012; Behney *et al.* 2012). One possible explanation for the decreased instantaneous risk of mortality during the post-construction period of lek activity is that wind energy affected predator activity, leading to changes in trophic interactions with prairie-chickens. We did not record predator numbers during our field study, but elsewhere raptor populations have been reduced where energy-related structures caused direct mortality via collisions (Hunt *et al.* 1998; Kuvlesky *et al.* 2007; de Lucas *et al.* 2008, 2012; Smallwood, Rugge & Morrison 2009), or where raptors avoided foraging near wind turbines (Osborn *et al.* 1998, 2000; Holloran 2005; Garvin *et al.* 2011). Mammalian predators have also been documented to avoid wind energy development sites. Occupancy modelling has shown that coyotes *C. latrans* were detected less often at the Central Plains Wind Farm east of Marienthal, Kansas than a nearby reference site with similar habitat characteristics (B. Tanis and E. Finck, unpublished data). Indirect effects of wind energy development, such as changes in trophic interactions, remain poorly understood but could have important implications for population responses to energy development and might be more pervasive than direct effects of

collision mortality (Gill, Sutherland & Watkinson 1996; Leddy, Higgins & Naugle 1999; Hoover & Morrison 2005; Devereux, Denny & Whittingham 2008; Pruett, Patten & Wolfe 2009).

During the post-construction period, hazard functions indicated that the highest instantaneous risk of mortality coincided with the nesting and brood rearing stages of breeding. Estimates of seasonal survival for grouse are rare, but high mortality rates during nesting and brood rearing are common in greater and lesser prairie-chickens (Hagen *et al.* 2007; Lyons *et al.* 2009; Augustine & Sandercock 2011). We found higher survival among female prairie-chickens during the non-breeding period compared with the breeding period (ratio = 1·4–2·1), similar to previous reports from sites in the northern Flint Hills (ratio = 1·6–2·0, Augustine & Sandercock 2011). Similarly, Hagen *et al.* (2007) found that female lesser prairie-chickens caring for a nest or brood had lower daily survival rates than females not attending young. Females may be vulnerable to predators during breeding because they rely on cryptic coloration for concealment and are less likely to flush if attending eggs or young. Our results indicate that management for habitat conditions that increase female survival during the breeding season have the potential to greatly improve population dynamics.

Low rates of natural mortality have been reported during the non-breeding season for prairie-chicken populations in Kansas (0·11–0·18 in the current study; 0·06–0·28 in Augustine & Sandercock 2011). A large-scale experiment on willow ptarmigan *Lagopus lagopus* provided evidence that harvest mortality can be partially compensatory at harvest rates <15% (Sandercock *et al.* 2011). At our study site, prairie-chicken harvest occurs during a 1-month early season from 15 September to 15 October and a 2·5-month regular season from mid-November to January with a daily limit of two birds per hunter (kdwpt.state.ks.us). Total prairie-chicken harvest in Kansas ranged from *c.* 3600 to 19 300 individuals per year since 2000 and typically does not approach legal limits (Dahlgren, Kramer & Mitchener 2011). Based on low natural rates of mortality during the non-breeding season, partial compensation is possible but would support only low levels of harvest mortality in prairie-chickens.

CAUSE OF DEATH

We observed no change in the proportion of total mortalities attributed to mammalian predators, avian predators or collisions during the pre- and post-construction periods. However, our analyses of mortality are a relatively weak test for changes in cause-specific mortality rates because scavenging precludes unambiguous determination of cause of death (Bumann & Stauffer 2002; Larsen, Bentley & Flinders 2008). We are unable to discount the possibility that some prairie-chickens were killed by raptors, but scavenged by mammals before we located and inspected the carcasses.

A majority of our study area was located on private lands open to hunting by landowner permission (>95%), but we recorded no hunting mortality of females. Unlike patterns of mortality in lesser prairie-chickens (Wolfe *et al.* 2007), collision mortalities were rare during our field study, and distances from carcasses to turbines indicated that most collision mortalities were due to fence lines or power lines rather than turbine blades or towers. Distance to turbine did not affect female survival, and wind turbines did not pose a direct threat to female prairie-chickens. Instead, predators were the main cause of demographic losses and determined variation in seasonal and annual survival rates (Schroeder & Baydack 2001; Augustine & Sandercock 2011; McNew *et al.* 2012). Our field study provides good evidence for an increase in survival of female prairie-chickens after wind energy development; however, the potential benefits could have resulted from changes in avian predation, mammalian predation or both.

IMPORTANCE OF FEMALE SURVIVAL

Wind energy development has the potential to affect behaviour, survival and reproductive success of male and female prairie-chickens. However, the response of female prairie-chickens to wind energy development is the most important driver of overall population dynamics for three reasons. First, female prairie-chickens are likely to be more susceptible to negative effects of habitat fragmentation and anthropogenic disturbance because they have larger home ranges and greater overall movement rates than males, increasing the likelihood that their activities will intersect with energy development infrastructure (Patten, Pruett & Wolfe 2011). Second, individual female reproductive success drives overall population dynamics because all female prairie-chickens make at least one nest attempt each year, and parental care is female-only, whereas male reproductive success is highly skewed (Nooker & Sandercock 2008; McNew *et al.* 2011). Third, one hypothesis for lek evolution is that lek placement is driven by female habitat preference (Westcott 1994; Alonso, Alvarez Martinez & Palacin 2012). Female movements provide strong support for this hypothesis in our study system. Here, we focused primarily on female survival vs. anthropogenic disturbance because our demographic models indicate that female survival drives population dynamics and our movement data indicate that female space use influences male behaviour (McNew *et al.* 2012; Winder *et al.*, in press).

CONCLUSIONS

In summary, we found no evidence for a negative effect of wind energy development on the survival of female prairie-chickens during our 5-year field study. Increases in annual and seasonal survival rates during the post-construction period were consistent with the concept of a per-

ceptual trap. The ecological mechanisms driving changes in survival were unclear but could have been related to an indirect effect of wind energy development on predation risk. Our results highlight the potential need for ecosystem level study of the impacts of energy development; future studies should investigate changes in habitat selection and predator–prey interactions. Female survival increased for the 3-year period following wind energy construction, but the effects might be transitory if benefits do not persist (Harju *et al.* 2010). We are currently testing for potential effects of wind energy development on lek persistence, reproductive performance and space use in our study population. Our study addressed the effects of wind energy development on a single species of grassland bird. An overall reduction in predation pressure could potentially benefit other ground-nesting species of grassland birds as well. The wind energy facility at our study site was constructed in tallgrass prairie habitats optimal for prairie-chickens. Greater prairie-chickens appear to be less sensitive to energy development than previously studied species of prairie grouse (Pitman *et al.* 2005; Hagen *et al.* 2011; Blickley, Blackwood & Patricelli 2012; Hess & Beck 2012). Thus, management actions should be based on species-specific objectives and responses. Extrapolation of our results to other sites and species may depend on local habitat conditions and species-specific requirements during the annual cycle. Nevertheless, future predictions and mitigation of wind energy effects on wildlife populations should consider the possibility that changes in trophic interactions may benefit wildlife populations in unexpected ways.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Lek of capture for radio-collared female greater prairie-chickens monitored during pre- (2007–2008) and post-construction (2009–2011) of a wind energy facility in north-central Kansas.

Figure S1. Weekly climatic conditions during our 5-year field study in north-central Kansas.

Figure S2. Weekly survival (95% CI) of female greater prairie-chickens in relation to distance to turbine site for the pre-construction (2007–2008: grey line) and post-construction (2009–2011: black line) periods.