The Journal of Wildlife Management 81(4):690–711; 2017; DOI: 10.1002/jwmg.21231

Research Article

Greater Sage-Grouse Habitat Selection, Survival, and Wind Energy Infrastructure

CHAD W. LEBEAU,[1] *Western EcoSystems Technology, Inc., 200 South 2nd Street, Laramie, WY 82070, USA*
GREGORY D. JOHNSON, *Western EcoSystems Technology, Inc., 415 W. 17th Street, Suite 200, Cheyenne, WY 82001, USA*
MATTHEW J. HOLLORAN, *Wyoming Wildlife Consultants, LLC, P.O. Box 893, Pinedale, WY 82941, USA*
JEFFREY L. BECK, *Department of Ecosystem Science and Management, University of Wyoming, Dept 3354, 1000 East University Avenue, Laramie, WY 82071, USA*
RYAN M. NIELSON, *Western EcoSystems Technology, Inc., 415 W. 17th Street, Suite 200, Cheyenne, WY 82001, USA*
MANDY E. KAUFFMAN, *Western EcoSystems Technology, Inc., 200 South 2nd Street, Laramie, WY 82070, USA*
ELI J. RODEMAKER, *Wyoming Wildlife Consultants, LLC, P.O. Box 893, Pinedale, WY 82941, USA*
TRENT L. MCDONALD, *Western EcoSystems Technology, Inc., 200 South 2nd Street, Laramie, WY 82070, USA*

ABSTRACT Increasing concern for environmental sustainability, the demand for domestic energy, and an impetus on reducing dependence on fossil fuels have led to substantial investment in renewable energies including wind energy over the last 2 decades. Increases in wind energy development are especially noticeable in prairie habitats with high wind capacity. This has raised concerns over effects on grouse species including greater sage-grouse (*Centrocercus urophasianus*). We monitored 346 female greater sage-grouse via telemetry from 2009 to 2014 in southeastern Wyoming, within a control area and an area influenced by a wind energy development to estimate the potential effects of wind energy infrastructure on greater sage-grouse habitat selection and demography. We developed resource selection functions by comparing habitats used to habitats available relative to the wind energy development during the nesting, brood-rearing, and summer periods. In addition, we used survival models to estimate the variability in nest, brood, and female survival relative to the wind energy development. The relative probability of greater sage-grouse selecting brood-rearing and summer habitats decreased as percentage of surface disturbance associated with the facility infrastructure increased. We did not, however, detect a negative effect of the wind energy facility on nest site selection or on nest, brood-rearing, or female survival during the study. Future wind energy developments should consider the potential effects of wind energy development on sage-grouse habitat selection patterns and survival parameters $\leq$1.20 km from any occupied sage-grouse nesting, brood-rearing, or summer habitats.

KEY WORDS *Centrocercus urophasianus*, energy development, fitness, greater sage-grouse, habitat selection, survival, wind energy, wind turbines.

Wind energy development is occurring across many landscapes, resulting in direct and indirect effects on wildlife (Kuvlesky et al. 2007, Naugle et al. 2011). Direct effects include habitat loss, and bird and bat collisions with wind turbine blades or other infrastructure associated with wind energy development (e.g., guy wires, meteorological towers, power lines, turbine towers; Erickson et al. 2001, Johnson et al. 2004*b*, Beck et al. 2006). Energy development indirectly affects wildlife through behavioral avoidance of areas with infrastructure and habitat fragmentation (Northrup and Wittemyer 2013, Buchanan et al. 2014).

Decreased habitat suitability may lead to behavioral displacement (avoidance) for local populations. Some researchers suggest displacement effects associated with wind energy may have a greater impact than collision mortality (Gill et al. 1996, Pearce-Higgins et al. 2012). Birds displaced by wind energy development may move to lower quality habitat with fewer disturbances, with an overall effect of reducing breeding success (Mahoney and Chalfoun 2016, Shaffer and Buhl 2016). Indirect effects also include habitat fragmentation (e.g., more habitat edges due to roads and smaller areas of contiguous habitat), which could provide more generalized habitats and resistance-free travel lanes for predators and competitors in, for example, large grasslands and forests (Batary and Baldi 2004). This may affect the survivorship and reproductive ability of birds in the vicinity of the wind energy facility (Mahoney and Chalfoun 2016).

Increases in wind energy development are especially noticeable in prairie habitats with high wind capacity. This has raised concerns over impacts to greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) and other prairie

Received: 2 September 2016; Accepted: 30 December 2016

[1] *E-mail: cwlebeau@west-inc.com*

grouse species, including sharp-tailed grouse (*Tympanuchus phasianellus*) and lesser (*T. pallidicinctus*) and greater (*T. cupido*) prairie-chickens (Kuvlesky et al. 2007). The United States Fish and Wildlife Service (USFWS) maintains that because prairie grouse evolved in habitats with little vertical structure, placement of tall man-made structures (e.g., wind turbines) in occupied grouse habitats may result in a decrease in habitat suitability (USFWS 2004). However, most studies on breeding grouse have not isolated structure height from other potentially influencing factors, such as the occurrence of roads, other structures, and cultivation (Walters et al. 2014).

Direct effects on grouse are likely low (Winder et al. 2014*b*), but indirect effects of wind energy infrastructure likely affect movements and habitat selection of these species because of tendencies toward avoiding areas with high human activity (Pruett et al. 2009, Dzialak et al. 2012, Walters et al. 2014), which may affect population viability. In a meta-analysis investigating response of grouse species to energy development in general, Hagen (2010) reported moderate to large displacement effects and small to moderate demographic effects of anthropogenic features on grouse populations. Another meta-analysis assessing the influence of anthropogenic structures on grouse behavior and survival was unable to determine effects of wind turbines because of lack of wind energy and grouse studies (Hovick et al. 2014). The majority of research specific to the response of grouse to wind energy development has been conducted on greater prairie-chickens where the effect of a wind energy development on population viability varied (McNew et al. 2014; Winder et al. 2014*a*,*b*, 2015). Although definitive evidence linking sage-grouse population response to wind energy development is not extensive, LeBeau et al. (2014) reported that within 2 years of the development of a wind energy facility, sage-grouse nest and brood survival were lower as distance to wind turbines decreased but no effect of distance to turbines on adult female survival was documented.

Research suggests that anthropogenic features on the landscape influence sage-grouse populations, with general trends toward decreasing populations as infrastructure densities on the landscape increase. Substantial research has established that oil and gas developments negatively influence the ability of affected landscapes to support sage-grouse (Naugle et al. 2011, Taylor et al. 2013, Gregory and Beck 2014, Smith et al. 2014, Kirol et al. 2015). Sage-grouse are also negatively affected by roads, residential development, and transmission lines and other tall structures (Aldridge et al. 2008, Johnson and Stephens 2011, Copeland et al. 2013, Knick et al. 2013).

We evaluated the response of sage-grouse to wind energy infrastructure in southeastern Wyoming because the potential for effects on sage-grouse in Wyoming from wind energy development is thought to be high (U.S. Department of Energy 2008). Our primary objective was to discern the relationship between sage-grouse nest, brood-rearing, and summer habitat selection patterns and nest, brood, and female survival parameters, and the infrastructure of an existing wind energy facility. We hypothesized that sage-grouse would respond to the presence of a wind energy facility similarly to other forms of anthropogenic disturbances (Dzialak et al. 2011, Smith et al. 2014, Kirol et al. 2015).

STUDY AREA

We conducted this study on Seven Mile Hill (SMH) located north of Interstate 80 and south of the Shirley Basin in Carbon County, Wyoming, USA (latitude 41.91° longitude −106.37°; Fig. 1) from 2009 to 2014. Land ownership included Bureau of Land Management (22.5%), private (69.5%), and State of Wyoming lands (7.8%). The study area was classified as a semiarid, cold desert with a mean annual precipitation of 26.7 cm and average temperatures ranging from −2.33°C to 13.6°C (Western Regional Climate Center 2014). Shrub steppe, dominated primarily by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), was the most common cover type in the study area (U.S. Geological Survey 2011). Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) composed the majority of wild ungulate fauna in the study area. Sage-grouse predators in the study area included raptors, canids, and mustelids. Dominant land uses included wind energy development, an inactive surface coal mine near the southwestern edge of the study area (∼20 km from the nearest turbines), livestock grazing, and hunting. The Seven Mile Hill Wind Energy Facility (SWEF) was situated in the northern portion of the SMH study area.

We included a control and treatment area in the SMH study area. The main sampling unit for our study was occupied lek locations. From these sampling units, we captured female sage-grouse and monitored radio-marked individuals from 2009 to 2014. Leks targeted for captures were located throughout the SMH area. We defined boundaries for the control and treatment areas from the distribution of captured radio-marked female locations. The treatment group consisted of 4 leks that had a mean distance of 1.93 km from the nearest SWEF turbines (range = 0.5–4.1 km). The control group consisted of 6 leks that had an average distance of 11.0 km from the nearest SWEF turbine (range = 7.1–16.2 km). In addition, the average minimum distance between the treatment and control leks was 11.7 km. We considered females captured from treatment area leks to occupy habitats within the treatment study area and females captured from the control area leks to occupy habitats within the control area.

The SWEF consisted of 79 General Electric 1.5-MW wind turbines (77-m rotor diameter and 80-m tower height) and approximately 29 km of access roads (Fig. 1). Construction of this facility began in late summer 2008 and the facility became fully operational in December 2008. The facility was situated north of U.S. Highway 30-287 and south of the Medicine Bow River within the treatment study area (Fig. 1). Elevations in the treatment area ranged from 1,737 m to 2,118 m above sea level. In addition to the wind energy facility, other anthropogenic features present in this portion of the study area included approximately 8 km of paved roads

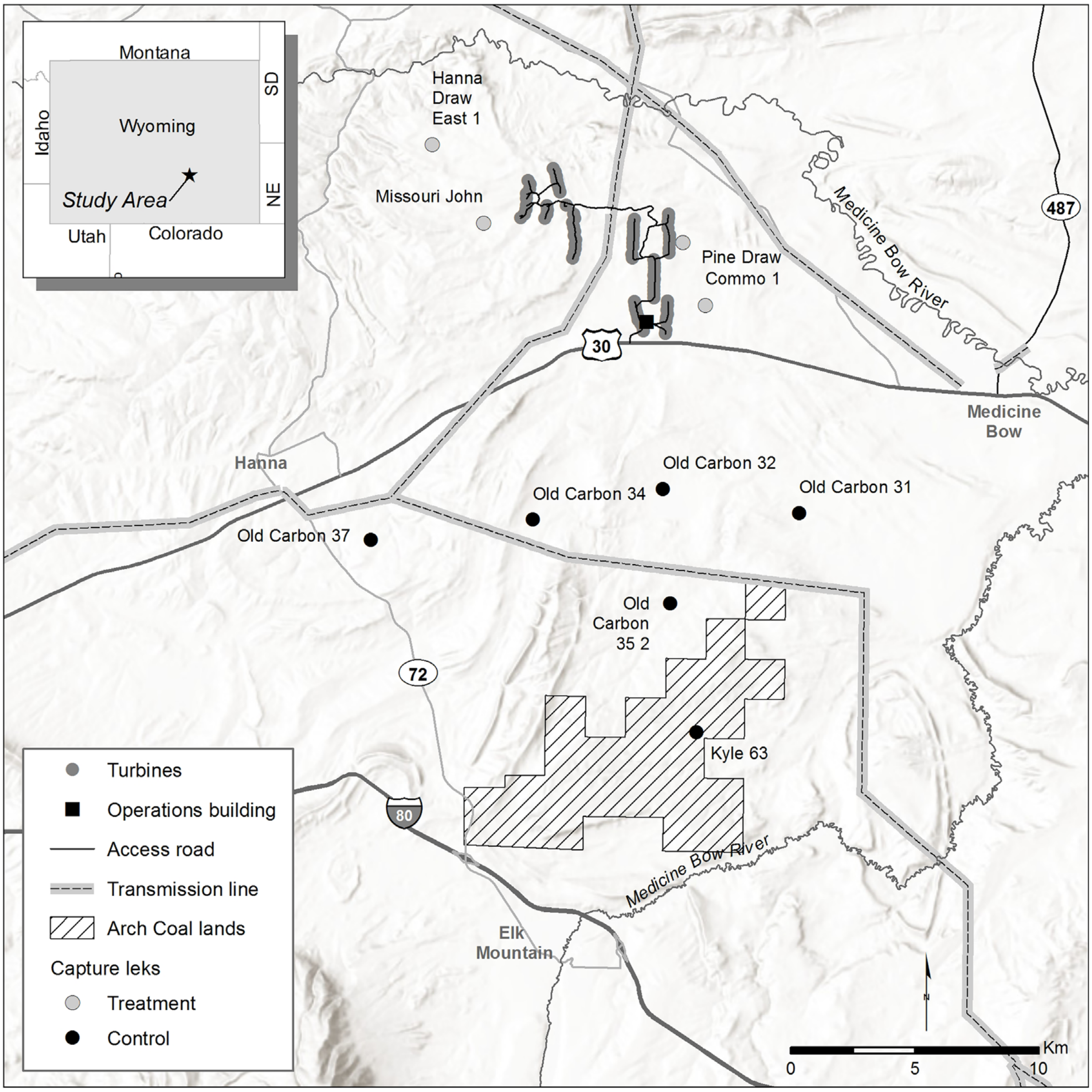

Figure 1. Seven Mile Hill study area and occupied leks targeted for capturing and monitoring female sage-grouse within a treatment and control study area from 2009–2014 in Carbon County, Wyoming, USA. The Seven Mile Hill Wind Energy facility consisted of 79, 1.5-MW wind turbines.

(U.S. Highway 30-287) and 26 km of overhead transmission lines.

The control area had no wind turbines and it was adjacent to the SWEF and south of U.S. Highway 30-287 (Fig. 1). This portion of the study area contained numerous ridges interspersed with rolling to hilly plains. Elevations ranged from 2,040 m to 2,390 m above sea level. There were approximately 50 km of paved roads (Interstate-80, U.S. Highway 30-287, and Wyoming State Highway 72) and 17 km of overhead transmission lines in this area. The existing overhead transmission lines and paved roads have existed on the landscape for >10 years. The only anthropogenic features added to the SMH area as a result of constructing the SWEF were wind turbines, associated access roads, and 1 operation building (Fig. 1). A portion of the control area was owned by Arch Coal but lacked any coal mining activity. This area was located south of U.S. Highway 30-287 and we excluded it from consideration because it was not accessible for monitoring (Fig. 1).

METHODS

Field Methods

We captured 346 (160 treatment; 186 control) female sage-grouse on roosts surrounding leks by night-time spotlighting and use of hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) during the 2009 through 2013 breeding seasons. Our yearly targeted sample size for monitoring was 100 females distributed equally between treatment and control study areas each year, but the actual number of sage-grouse captured and monitored varied among years. We attempted to capture sage-grouse at all accessible, occupied, and active lek sites within 16 km of the SWEF wind turbines proportionately to the number of males attending those leks. We aged and fitted each captured grouse with a 22-g necklace-mounted very high frequency (VHF) radio transmitter with a battery life of 666 days (model A4000, Advanced Telemetry Systems, Isanti, MN, USA). Radio-transmitters were equipped with mortality sensors set to trigger when transmitters were stationary for 8 hours. We classified each female as a yearling (first breeding season) or adult (≥second breeding season) based on the shape of the outermost wing primaries (Eng 1955). We gained approval from the Wyoming Game and Fish Department (Chapter 33 permit 572) to capture, handle, and monitor female greater sage-grouse.

We relocated each radio-marked female 3 times each week during the pre-nesting and nesting period (Apr–Jun) and at least once each week for brooding and broodless females from hatch or nest loss through 31 October. We monitored marked sage-grouse primarily from the ground using hand-held receivers and antennas. We determined sage-grouse locations by triangulation or homing until the grouse was visibly observed. We estimated triangulation locations by recording 2 vectors in the direction of the signal from 2 locations.

During the pre-nesting and nesting seasons (1 Apr–15 Jun), we monitored each radio-marked female sage-grouse from long range (>60 m) at least every third day. We assumed females were nesting when movements between locations became small (~equal to telemetry error). Once movements were small, we located nests using a progressively smaller concentric walking circle approach around the radio-signal using the signal strength as an indication of proximity (Holloran and Anderson 2005). We made all future monitoring of the nest from remote locations (>60 m) using long distance triangulation to minimize potential disturbance.

Once we located a nest location, we conducted incubation monitoring on an alternate-day schedule to determine nesting fate. For each first nest and second nesting attempt, we collected data on timing of incubation and nest success. We mapped all nest locations using a hand-held global positioning system (GPS). We considered a nest that successfully hatched (i.e., eggs with detached membranes; Wallestad and Pyrah 1974) ≥1 egg to be a successful nesting attempt (Rotella et al. 2004). We considered nests that failed to hatch successfully ≥1 egg to be failed nesting attempts. We monitored females that were unsuccessful in their first nesting attempt (i.e., broodless) 3 times per week through 15 June to determine possible second nesting attempts.

To evaluate brood survival, we located radio-marked females that successfully hatched ≥1 egg each week through 35–37 days post-hatch (Walker 2008). We categorized the brood-rearing period as early (hatch through 14 days post-hatch; Thompson et al. 2006) or late (15 to 35–37 days post-hatch; Walker 2008). We considered females successful through the early brood-rearing period if ≥1 chick survived to 14 days post-hatch. We established chick presence during this period through visual confirmation of a live chick or the brooding female's response to field observers during flush counts during daylight hours (e.g., chick protective behavior exhibited). The observer performed an additional check in the event chick status could not be determined during the previous check. We determined fledging success (late brood success) for those females who were successful in early brood-rearing by assessing whether a female was brooding chicks through consecutive nighttime spotlight surveys conducted on days 35–37 post-hatch (Walker 2008). Successful females were those we confirmed brooding ≥1 chick determined by flush counts.

Covariates

We developed a suite of anthropogenic, vegetation, and environmental covariates to estimate habitat selection and variability in survival for all marked sage-grouse during the nesting, brood-rearing, and summer periods (Table 1). We included the minimum distance from sage-grouse location to a major road (km), transmission line (km), and wind turbine (km) as metrics for anthropogenic disturbances. In addition, we quantified the percentage of surface disturbance associated with the SWEF infrastructure (e.g., access roads, turbine pads) within multiple spatial scales. For example, we buffered a point on the landscape by 0.80 km and divided the area of access roads and turbine pads included within the buffer by the total area of the 0.80-km buffer. The spatial scales ranged from 0.40 km to 3.2 km and increased by 0.40 km. We collectively referred to distance to wind turbines and percentage of surface disturbance associated with the SWEF infrastructure as SWEF covariates. We included U.S. Highway 30-287, Wyoming State Highway 72, and Interstate 80 as major roads. We digitized major roads, overhead transmission lines, and access roads using aerial satellite imagery and ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, USA). Transmission lines and major roads are anthropogenic features that exist on the landscape and influence habitat selection (Nonne et al. 2013, LeBeau et al. 2014). We obtained turbine locations from PacifiCorp Energy (Salt Lake City, UT, USA), the operators of the SWEF.

Vegetation layers used in the analysis were remote sensed vegetation products developed from 1-m resolution National Agricultural Imagery Program image mosaics acquired in 2009 and 2012. We also used vegetation products developed by Homer et al. (2012). We considered 4 primary continuous field components (% bare ground, % herbaceous cover, % litter, and % shrub cover) and 4 secondary components (% sagebrush [*Artemisia* spp.], % big sagebrush [*A. tridentata* spp.], % Wyoming big sagebrush [*A. t. wyomingensis*], and shrub height) layers (Homer et al. 2009, 2012; Table 1). We obtained percent big sagebrush, litter, and Wyoming big sagebrush cover and shrub height from Homer et al. (2012) and we developed percent bare ground, herbaceous cover, percentage of meadow, and shrub cover covariates for 2009 and 2012. Sage-grouse require different habitat features throughout their annual cycle and we selected vegetation covariates based on sage-grouse habitat preferences during different time periods (Connelly et al. 2011).

The 2009 1-m resolution imagery provided vegetation measures associated with 2009–2011 used and available sage-grouse locations, whereas 2012 imagery provided measures associated with 2012–2014 used and available sage-grouse locations. We employed a proprietary, semi-automated object oriented analysis procedure to generate herbaceous and shrub cover vegetation maps in ERDAS Imagine software (Hexagon Geospatial, Norcross, GA, USA).

Table 1. Explanatory anthropogenic and environmental covariates used in modeling sage-grouse nest, brood, and female habitat selection and survival at the Seven Mile Hill study area, Carbon County Wyoming, USA, 2009–2014. We calculated percent cover at multiple scales specific to each analysis.

Covariates	Variable description
Anthropogenic infrastructure	
Distance to major road	Distance from sage-grouse location to nearest major road (WYO HWY 72, US HWY 287-30, and I-80; km)
Distance to transmission line	Distance from sage-grouse location to nearest overhead transmission line (km)
Distance to turbine	Distance from sage-grouse location to nearest turbine (km)
% disturbance	% of surface disturbed by the SWEF[a] (e.g., turbine pads and access roads) for each spatial scale.
Vegetation	
Bare ground	% bare ground (1-m resolution)
Big sagebrush[b]	% big sagebrush (30-m resolution)
Herbaceous	% herbaceous cover (1-m resolution)
Litter[b]	% litter (30-m resolution)
Sagebrush[b]	% sagebrush (30-m resolution)
Shrub	% shrub cover (1-m resolution)
Shrub height[b]	Shrub height (0–253 cm; 30-m resolution)
Meadow	% meadow (1-m resolution)
Distance to meadow	Distance from sage-grouse location to nearest meadow (km)
Slope	Degrees 0–90 (10-m resolution)
Wyoming big sagebrush[b]	% Wyoming big sagebrush (30-m resolution)
Environmental	
Terrain ruggedness	Variability in slope and aspect (0–1; 1 = complete terrain variation; Sappington et al., 2007; 0-m resolution)
Distance to capture lek	Distance from sage-grouse location to respective lek of capture
Elevation	Altitude above sea level (m; 10-m resolution)
Compound topographic index (CTI)	Water accumulation (large values = high water accumulation; 10-m resolution)
Topographic position index (TPI)	Variability in average elevation within a neighborhood (−1 to 1; Positive values = ridges; negative values = valleys; 10-m resolution)

[a] Seven Mile Hill Wind Energy Facility.
[b] Vegetation covariates obtained from Homer et al. (2012).

We mapped shrub cover at 5% increments from 0–30%. Areas of higher biomass, as evident on the late summer and fall National Agricultural Imagery Program data setting, were ones with perennial surface and subsurface water as compared to drier upland sites. We labeled these types as maximum cover dry and maximum cover wet, and used them to calculate the percentage of meadow. We mapped herbaceous cover at 2.5% increments from 0–35%. Once we plotted shrub and herbaceous cover across the study area, we computed bare ground percentage pixel by pixel. We computed bare ground percentage as the remainder of the combined shrub and herbaceous cover values subtracted from 100%. We included the standard deviation (SD) of shrub and shrub height as a covariate.

We considered landscape features (e.g., elevation, slope, compound topographic index [CTI], topographic positon index [TPI], terrain ruggedness) calculated from a 10-m National Elevation Dataset (DEM; U.S. Geological Survey 2015). We selected these landscape features to complement our vegetation covariates by attempting to explain the variability in the landscape. Terrain ruggedness combined the variability in slope and aspect into a single measure ranging from 0 (no terrain variation) to 1 (complete terrain variation; Sappington et al. 2007; Table 1). The CTI predicted surface water accumulation on the basis of landscape concavity and hydrology and the TPI compared the elevation of each cell in a DEM to the mean elevation of a specified neighborhood around that cell. Positive TPI values represent locations that are higher than the average of their surroundings as defined by the neighborhood (ridges) and negative TPI values represent locations that are lower than their surroundings (valleys; Guisan et al. 1999).

Habitat Selection Analyses

We used a discrete choice habitat selection model (Arthur et al. 1996, Manly et al. 2002, McDonald et al. 2006) to estimate the relative probability of sage-grouse nest site, brood-rearing, and summer habitat selection within the control and treatment areas during the post-development period. We assumed individual sage-grouse selected habitat components from a finite set of discrete habitat units known as choice sets. We chose the discrete choice model over alternative analyses because it allows habitat covariates to vary over choice sets, and hence over time (McDonald et al. 2006). In this case, percent shrub, herbaceous, meadow, and bare ground varied depending on year of the sage-grouse observation. The results of the discrete choice modeling is a resource selection function (RSF), which is defined as any function that provides predictions that are proportional to the probability of use (Manly et al. 1993, 2002). We used the coxph function in the survival package in R (Therneau and Grambsch 2000). We employed a Type I study design where we estimated habitat selection and availability at the population level and over a 6-year time period (Thomas and Taylor 2006).

We developed RSFs during 3 biologically meaningful periods: nesting, brood-rearing, and summer. We included all first and second nesting attempts in the nest site habitat selection analysis. We included all early and late brood locations associated with a female that successfully hatched ≥1 egg in the brood-rearing habitat selection analysis. We did not include subsequent locations from females that were not successful during the early brood-rearing period in the brood-rearing analysis because our goal was to model selection patterns of brooding females. We included females that were not successful during the early brood-rearing period and all locations observed after the late brood-rearing period through 31 October of each year in the summer habitat selection analysis.

We defined available habitat by calculating kernel home ranges for all sage-grouse locations observed from 2009–2014 within each time period for both study areas. Yearly kernel home ranges sizes and extents varied slightly during the study; thus, we combined locations and estimated available habitat within a kernel home range that include all data. We selected a 99% kernel home range to capture the extent of all observed sage-grouse locations within the treatment area. Five percent of all sage-grouse captured at control area leks used habitats in the treatment area during the study. We attempted to estimate habitat selection for sage-grouse within the control area that were uninhibited by the presence of the SWEF; thus, we selected a 90% kernel home range to define available habitat within the control study area. Within each study area's available habitat polygon, we generated grid cells with 90-m × 90-m spacing to identify available habitat units. We extracted covariates associated with each available habitat unit to include in the RSF model development. A choice set included all available habitat units associated with a specific nest, brood-rearing, and summer location, and the used nest, brood, or summer habitat unit. Because of the large number of nest, brood, and summer locations, and the resulting large number of available habitat units, estimation of the RSF using the entire dataset was not feasible. Consequently, we randomly sampled 50%, 25%, and 10% of the nest, brood rearing, and summer available habitat units, respectively.

Sage-grouse are a landscape-level species that use multiple habitats throughout their annual cycles and likely select resources at varying scales depending on the seasonal period. We attempted to identify this variation in selection by extracting the average habitat covariate value for each used and available habitat unit at 3 biological meaningful scales. For the nest site selection analysis, we averaged covariates over percentiles (10th, 50th, and 90th) of the distance between annual nest locations among females who nested in consecutive years (0.13 km, 0.46 km, and 2.5 km, respectively). We also included the 0.09-km scale, which was the smallest scale possible. For the brood-rearing and summer analysis, we used percentiles (10th, 50th, and 90th) of distances between consecutive locations from individuals during each seasonal period to define the spatial scales over which we averaged covariate values.

Model development.—Our model development process considered a large number of explanatory covariates measured at multiple scales. We first fit univariate models to identify the most appropriate spatial scale for each covariate. We evaluated the univariate models and all subsequent models by comparing the small sample version Akaike's Information Criterion (ΔAIC_c; Burnham and Anderson 2002). We retained the spatial scale with the lowest ΔAIC_c and considered it further in the model building process.

We used the resulting suite of covariates to develop 10 environmental models to consider all natural processes prior to detecting potential SWEF influences on habitat selection. We included distance to capture lek specific to each choice set into all *a priori* environmental models in an attempt to spatially control habitat selection patterns because the lek at which a female breeds likely influences selection patterns (Holloran and Anderson 2005). Many of the environmental covariates were highly correlated (Pearson's correlation analysis $|r| \geq 0.6$); however, we did not allow 2 highly correlated covariates in the same model. We added distance to existing anthropogenic features (e.g., roads, transmission lines) that have persisted on the landscape for >10 years to the environmental model with the lowest AIC_c in an attempt to control for potential confounding factors associated with habitat selection patterns relative to the SWEF. We determined if the addition of these features considerably improved model fit (i.e., $\Delta AIC_c > 2$; Burnham and Anderson 2002). The resulting best approximating model for each study area explained the variation in habitat selection due to natural processes and existing infrastructure without the influence of the SWEF covariates.

Once the natural variation in habitat selection was controlled to the extent possible, we then added variables representing SWEF infrastructure to explain further the variation in selection patterns within the treatment study area. We did not include covariates associated with the SWEF in the model selection process for observations that were from females captured at the control area leks because we assumed the effect of the SWEF did not extend into the control area. If covariates associated with the SWEF were influencing habitat selection within the treatment area, then we would expect a considerably improved model fit (i.e., $\Delta AIC_c > 2$) with the addition of the SWEF covariates.

We included a covariate in the top model for each habitat selection analysis to explain potential time lags associated with habitat selection. For example, female sage-grouse exhibit strong site fidelity and will select similar habitats in subsequent years (Berry and Eng 1985, Fischer et al. 1993, Holloran and Anderson 2005). Thus, selection patterns may be strongly influenced by fidelity rather than the presence of the SWEF 3 years following development compared to later years as new individuals are recruited into the population. To develop the time lag covariate, for 2012–2014 (i.e., the last 3 years following development of the SWEF) we multiplied the most explanatory SWEF covariate values by 1 and for 2009–2011 (i.e., the first 3 years following development) we multiplied all explanatory SWEF covariate values by 0. If the time lag covariate estimate was statistically significant at the alpha level of 0.10 (i.e., 90% CIs did not include 0), then we considered selection patterns relative to the SWEF to be different the last 3 years compared to the first 3 years following development.

We used 90% confidence intervals to determine if coefficient estimates from the top RSF for each time period and each area were statistically significant (alpha level = 0.10). We calculated confidence intervals for each coefficient using a bootstrapping technique that treated the individual as the primary sampling unit. We randomly sampled with replacement used habitat units and their respective choice sets associated with each individual sage-grouse and refit the top approximating RSF (Manly et al. 2002). We used 200 bootstrap iterations and the percentile method to identify the lower and upper confidence limits for each coefficient. We calculated odds ratios $[(\exp(\beta) - 1) \times 100]$ from coefficients in the final RSF models and used these to interpret the effect and magnitude of each covariate on sage-grouse habitat selection (McDonald et al. 2006).

We evaluated the predictive ability of the top RSF for each time period and each area using a k-fold cross-validation technique (Boyce et al. 2002). We randomly allocated the used habitat units and their respective choice sets into 5 equal-sized groups, maintaining the available habitat units within each choice set. We removed 1 group (testing data) and re-estimated the coefficients in the top RSF models using the used habitat units and their respective choice sets from the 4 groups remaining (training). We then used the coefficients estimated from the training data to make predictions to the testing used habitat units and their respective choice sets. We binned all predictions within each choice set into 20 classes of equal size using percentiles. We compared the number of used habitat units from all the choice sets in each prediction class to the class rank (1 = lowest, 20 = highest predicted odds of selection) using a Spearman's rank correlation coefficient. We repeated this process for each of $K = 5$ groups of used habitat units and their respective choice sets. We averaged the Spearman's rank correlation coefficients (r_s) to test how well the top model performed.

Following model validation, we made nest site, brood rearing, and summer habitat selection predictions for the average sage-grouse that bred on leks within the treatment area. We placed a 90-m × 90-m grid within the 99% kernel home range on the landscape within the SWEF habitat to make predictive maps. There were 3 covariates with values that changed from 2009–2011 to 2012–2014; thus, we generated 2 predictive maps for each period. We used distance to nearest occupied lek in place of distance to capture lek when we made predictions for the average individual sage-grouse. We calculated RSF values and placed them into 5 equal-area bins (low, medium-low, medium, medium-high, and high use) using percentiles to represent progressively selected habitats.

We evaluated the ability of the control and treatment RSFs to predict the relative probability of habitat selection within the treatment area by applying a goodness-of-fit test. We followed model evaluation methods outlined in Johnson et al. (2006) where we compared the expected proportion of use (median predicted RSF value) to the observed proportion of use within 20 equal-area prediction bins. We made predictions to the treatment area using RSFs that were developed at the control and treatment areas. We made predictions for 2 time periods, 2009–2011 and 2012–2014, because habitat characteristics (e.g., shrub and herbaceous cover and bare ground) changed between those periods. For each evaluation, we calculated Spearman's rank correlation between expected and observed use, which provided an assessment of the ability of the RSF to correctly rank the quality of the habitat, and then we fit a normal linear model regressing observed use to expected use for the 20 bins. If the 90% confidence interval for the intercept of the linear model included 0, and the confidence interval for the slope included 1 but excluded 0, then we determined that the RSF produced predictions of habitat use by sage-grouse that were proportional to the observed use (i.e., good predictability). If the confidence intervals did not meet these requirements but had a slope that excluded 0, then we determined that the RSF correctly ranked predictions but did not accurately predict the relative probability of selection (i.e., fair predictability). If the confidence intervals did not meet any of the above requirements, then we determined model fit was lower than expected and the majority of RSF bins were different than expected (i.e., poor predictability). In addition, we calculated the median distance to turbines for each of the 20 prediction bins to help interpret the relationship between expected use and distance to the SWEF turbines. We used these criteria to assess goodness-of-fit for the treatment RSF and the control RSF predicting habitat selection within the treatment area.

Survival Analysis

We estimated Cox models to relate hazard of death to study covariates and estimated survival within the control and treatment study areas using the coxph function in the R survival package (Therneau and Grambsch 2000). Cox models (Cox 1972) estimate the relationship between multiple explanatory variables and the instantaneous probability of death (hazard; Therneau and Grambsch 2000). Cox models provide risk ratios or hazard ratios that can be used to compare the effects of different levels of a particular covariate of interest (e.g., distance to nearest turbine) on the risk of failure (e.g., nest, brood, or female death). In addition, survival can be estimated from Cox models by summing estimated hazard over a time period.

We used the Andersen-Gill (A-G) formulation of the Cox model to estimate brood and female survival (Anderson and Gill 1982). Under the A-G formulation, hazards are assumed proportional within time intervals where covariates are constant, rather than over the entire study period, as assumed by the non-AG formulation. The A-G formulation of the Cox model thus accommodates time-varying covariates by breaking the study period into multiple monitoring intervals (Therneau and Grambsch 2000, Johnson et al. 2004*a*). The ability to use time-varying covariates was important because habitat characteristics changed during the brood and female survival periods.

Survival parameters.—We assessed nest survival for a 28-day incubation period during the 2009 through 2014 nesting seasons (incubation period lasts 25–29 days; Schroeder et al. 1999). We combined nests observed within the SMH study area (treatment and control) into 1 sample to model survival relative to the SWEF. Nests from second attempts following failed nesting (so called re-nests) might not be independent of first nests; therefore, we excluded re-nests from analyses. We considered assumed first nesting attempts that hatched in early July to be re-nests because they were within the hatch date range of other re-nests and we assumed the observer likely missed the first nesting attempt. Failures occurred when a female abandoned its nest or its nest was destroyed by a predator. We did not include in survival analysis abandoned nests thought to be caused by field observers because they were potentially caused by an anthropogenic source other than SWEF. We estimated the nest's date of failure as the mid-point of the final monitoring interval. We evaluated the condition of the nest and eggs to determine type of predator responsible (mammalian or avian). We considered nests that contained ≥ 1 egg at the end of the 28-day incubation period to be successful and were censored (Nur et al. 2004).

We combined early and late brood-rearing locations from all years for survival modeling (Aldridge and Boyce 2007). We used 5 weekly monitoring intervals during the brooding period to assess brood survival. We defined the interval containing the event to be the interval between the last monitoring visit where chick presence was confirmed and the first visit where chicks were absent. Because of our revisit schedule, events could have occurred during weeks 1, 2, and 5 when we assessed survival. The exact week of the event could not be determined if chicks were absent during week 5 (i.e., brood could have failed during weeks 3 or 4). By assigning the event to week 5, we are overestimating the overall magnitude of survival, but the relative difference in survival associated with different covariate values is unbiased because we treated all broods in the same manner. We censored broods that were successful and survived the entire monitoring period to week 5 (Nur et al. 2004). When we located a female twice in a single interval, the covariate value associated with each interval was the average covariate value at the 2 locations.

Lastly, we modeled female sage-grouse survival from time of capture to 31 October during all study years. We monitored female sage-grouse at least once each week during this period. Events or mortalities occurred only when we confirmed mortality via telemetry. We estimated the date of mortality by the condition of the carcass (e.g., fresh or old) and last known monitoring interval. We grouped weeks where we recorded multiple observations and averaged corresponding covariates.

Model development.—We estimated daily and weekly Kaplan-Meier survival curves for each year to inspect raw survival during the study period (Kaplan and Meier 1958). If annual variation appeared to exist in the nest, brood, and female survival curves, we added year as a strata to account for underlying factors that may affect nest, brood, and female survival that we could not measure (e.g., cyclical predator-prey interactions, weather).

We included random effects associated with all individuals captured at specific leks to the best approximating model to allow for random fluctuations in the baseline hazard for each individual (Liebezeit et al. 2009). Variation in survival could be related to the habitat associated with the lek at which a female bred (Connelly et al. 2000), and the application of the random effects attempted to capture this variability. Inclusion of the random effects mitigates natural spatial dependencies for individuals breeding on a particular lek if such dependencies exist (Liebezeit et al. 2009). We calculated Cox models containing random effects using R statistical coxme package (Therneau 2015). We assessed the utility of including random effects using an analysis of variance (ANOVA) and a Wald chi-square test (Therneau 2015). We excluded the random effects term from the best approximating survival model if the ANOVA test indicated no significant differences between the random effects model and the proportional hazards model with only fixed effects. We used random effects or frailty estimates associated with each lek of capture from the best approximating survival model to describe the unobserved random proportionality factor that modified the hazard function.

Model development was similar to the habitat selection analysis in that it involved a tiered approach. During the first tier, we identified the best measurement scale (circular buffer size) for each covariate by estimating univariate models and selecting the scale that produced the lowest AIC_c (Table 1). Many of the covariates used to estimate the variability in survival were correlated with one another (Pearson's correlation coefficient $|r| \geq 0.6$); thus, we constructed sets of uncorrelated environmental variables and considered all possible models within each set. We ranked all possible models from each set of uncorrelated environmental variables using AIC_c. We considered the highest-ranking environmental model to have explained the maximum amount of variation in survival due to natural processes within the SMH study area.

Once we identified the best model containing natural covariates, we added covariates representing the SWEF to evaluate the effect of the SWEF on survival. We considered all possible interactions between covariates included in the environmental model and SWEF covariates. If covariates associated with the SWEF were influencing survival, then we would expect model fit to be improved considerably (i.e., $\Delta\mathrm{AIC}_c > 2$) with the addition of SWEF covariates. After identification of the best model, we added age of female (adult = 1, yearling = 0) and the relative probability of habitat selection measured at a nest or observed location to help explain any additional variability in survival within the study area. We investigated whether pooling all nests, broods, and mortalities from females captured at treatment and control area leks may have obscured the influence of the SWEF on survival from females captured at treatment area leks by analyzing survival for sage-grouse captured at treatment study area leks.

We removed year as a strata and estimated survival relative to the most explanatory SWEF covariate to consider the potential differences among years and any potential time lags associated with survival. We added an indicator term for observations within years 2012–2014 and interacted the indicator term with the most explanatory SWEF covariate. If this interaction was significant at the 90% confidence interval level, then the relationship between survival and the SWEF was different among the last 3 years compared to the first 3 years following development.

We considered hazard ratios that included 1 within their 90% confidence interval statistically insignificant (alpha level = 0.10). We estimated confidence intervals for each coefficient in the nest, brood, and female survival models using a bootstrapping technique that treated individuals as the sampling unit because some individuals had >1 nest or brood in multiple years or a female survived multiple summers during the study period. We randomly sampled with replacement individuals and estimated the top approximating survival model from the new sample of nests, broods, and female locations (Manly et al. 2002, Manly 2006). We used 500 bootstrap iterations to identify the lower and upper confidence limits for each coefficient estimate. The value at the 5th percentile of the 500 estimates represented the lower limit of a 90% confidence limit and the value at the 95th percentile represented the upper confidence limit (i.e., the percentile method; Manly 2006).

RESULTS

Habitat Selection

The number of female sage-grouse monitored and number of locations included in the habitat selection analysis were similar between study areas (Table 2). The summer home range was the largest among seasonal home ranges within the treatment area; however, all seasonal home ranges were similar within the control area (Fig. 2). The average distance to nearest turbine for nests from females captured at leks within the treatment area was similar during the study period, ranging from 1.82 (2009) to 3.09 km (2014; Fig. 3). A similar pattern was observed during the brood-rearing period, ranging from 2.37 (2010) to 4.82 km (2014; Fig. 3). The average distance to nearest turbines during the summer for females captured from leks within the treatment area increased from 2.35 (2009) to 5.38 km (2014; Fig. 3).

Nest site selection model fit.—The treatment area environmental model included distance to capture lek, percent bare ground, percent litter, and percent Wyoming big sagebrush, whereas the control area environmental model included distance to capture lek, percent Wyoming big sagebrush, percent bare ground, elevation, and SD percent shrub height (Table 3). The treatment and control environmental models were 9.3 and 11.8 AIC_c values from the next best model, respectively. The control environmental model improved with the addition of distance to transmission lines and the quadratic effect of major roads ($\Delta\mathrm{AIC}_c = 25.2$; Table 3). The treatment environmental model improved with the addition of the quadratic effect of distance to transmission lines ($\Delta\mathrm{AIC}_c = 24.4$; Table 3). Distance to turbine was the most informative SWEF covariate; however, the addition of distance to turbine did not improve model fit and was not significant ($\Delta\mathrm{AIC}_c = 0.34$; $\beta = -0.07$; 90% CI = −0.16–0.02). We did not detect any time lags relative to the SWEF for females selecting nest sites between 2009–2011 and 2012–2014 ($\beta = -0.07$; 90% CI = −0.22 to 0.08). Spatially, we predicted the relative probability of selection to be high around leks (Fig. 4).

The k-fold validation results indicated the RSF model developed at the treatment and control area had good overall predictability ($\bar{x}\, r_s = 0.67$ and $\bar{x}\, r_s = 0.80$, respectively). The RSF developed at the treatment area using habitat data layers from 2009–2011 was good at predicting sage-grouse use based on the goodness-of-fit tests; the RSF using 2012–2014 habitat data was fair (Fig. 5A). The RSFs developed at the control area using habitat data layers from 2009–2011 and 2012–2014 were good at predicting sage-grouse nest site selection within the treatment area (Fig. 5B). Spatially, we estimated a higher proportion of expected use and observed use closer to SWEF turbines using the treatment and control RSFs (Fig. 5A and 5B).

Brood-rearing habitat selection model fit.—>The treatment area environmental model included distance to capture lek, percent Wyoming big sagebrush cover, percent bare ground, elevation, and SD of shrub height (Table 4). The control area environmental model included distance to capture lek, percent herbaceous cover, percent sagebrush cover, TPI, and distance to meadow (Table 4). The treatment and control environmental models were 9.1 and 29.5 AIC_c values from the next best model, respectively. The control environmental model improved with the addition of distance to major road and transmission line ($\Delta\mathrm{AIC}_c = 10.5$; Table 4). The treatment environmental model improved with the addition of the quadratic effect of distance to major road and quadratic effect of distance to transmission line ($\Delta\mathrm{AIC}_c = 86.52$; Table 4). The percentage of disturbance within 1.2 km of SWEF infrastructure was the most informative SWEF covariate and addition of this covariate improved model fit and was significant ($\Delta\mathrm{AIC}_c = 24.31$; $\beta = -0.898$; 90% CI = −2.184 to −0.251; Table 4). Selection decreased by 59.2% for every 1% increase in the percentage of surface disturbance within 1.2 km of SWEF infrastructure (90% CI = 22.2–88.7%; Table 4). The next best fitting model was percentage of surface disturbance within 0.80 km of SWEF infrastructure ($\Delta\mathrm{AIC}_c = 2.32$). In addition, the covariate that estimated the potential time lags associated with brood-rearing selection relative to the percentage of surface disturbance for females with broods between 2009–2011 and 2012–2014 was significant and was at a greater magnitude compared to the coefficient for all years, suggesting selection patterns relative to percentage of surface

Table 2. Number of female sage-grouse monitored and number of locations used to develop seasonal habitat selection models within the treatment and control study areas within the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014

	Treatment		Control	
Season	**Females monitored**	**Locations**	**Females monitored**	**Locations**
Nesting	104	154	118	176
Brood-rearing	42	438	46	543
Summer	125	2,314	153	2,537

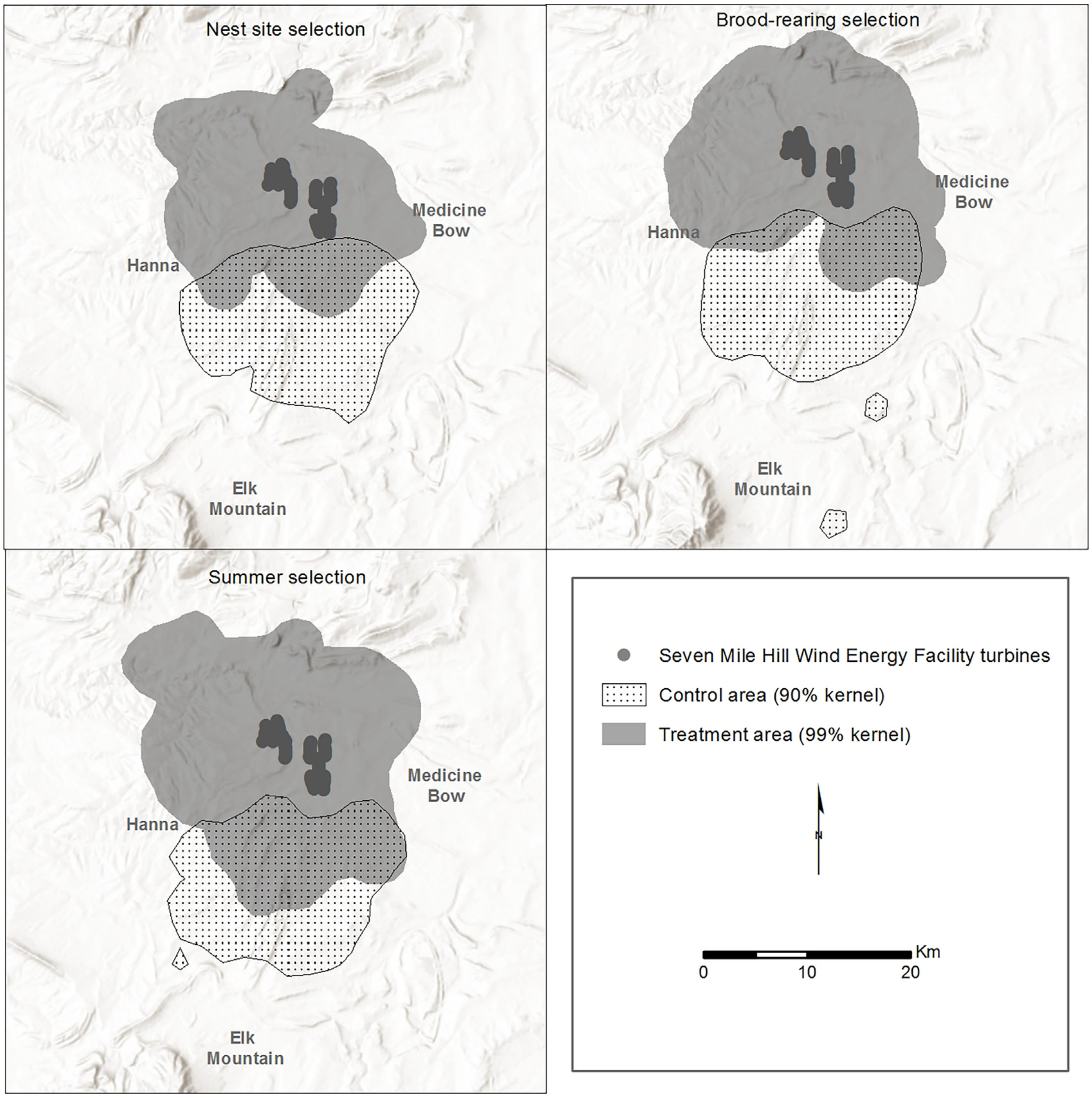

Figure 2. Kernel home ranges (99% for treatment and 90% for control) from greater sage-grouse captured at the treatment and control study area leks during the nesting, brood-rearing, and summer period from 2009–2014 within the Seven Mile Hill study area, Carbon County, Wyoming, USA.

disturbance differed among these time periods ($\beta = -1.49$; 90% CI $= -2.27$ to -0.70). Spatially, we predicted the relative probability of selection to be high around leks (Fig. 4).

The k-fold validation results indicated the RSFs developed at the treatment and control area had good overall predictability ($\bar{x}\, r_s = 0.86$ and $\bar{x}\, r_s = 0.82$, respectively). The RSFs developed at the treatment area using habitat data layers from 2009–2011 and 2012–2014 were fair at predicting sage-grouse brood-rearing selection based on the goodness-of-fit tests (Fig. 6A). The RSF developed at the control area using habitat data layers from 2009–2011 was also fair at predicting sage-grouse use within the treatment area; the RSF using 2012–2014 habitat data was good (Fig. 6B). Spatially, we estimated a higher proportion of expected use and observed a higher proportion of use closer to SWEF turbines, although we did detect high correlations for some RSF bins farther from turbines (Fig. 6A and 6B).

Summer habitat selection model fit.—The treatment area environmental model included distance to capture lek, percent herbaceous cover, SD of shrub cover, TPI, and slope (Table 5). The control area environmental model included distance to capture lek, percent meadow, TPI, SD of shrub cover, and slope (Table 5). The treatment and control environmental models were 5.0 and 12.8 AIC$_c$ values from the next best model, respectively. The control environmental model improved with the addition of distance to major road and transmission line (ΔAIC$_c = 108.75$; Table 5). The treatment environmental model improved with the addition of distance to major road (ΔAIC$_c = 59.7$; Table 5). The percentage of surface disturbance within 1.2 km of SWEF infrastructure was the most informative SWEF covariate and addition of this covariate improved model fit and was significant (ΔAIC$_c = 5.24$; $\beta = -0.24$; 90% CI $= -0.46$ to -0.04; Table 5). Selection decreased by 21.0% for every 1% increase in the percentage of surface disturbance within

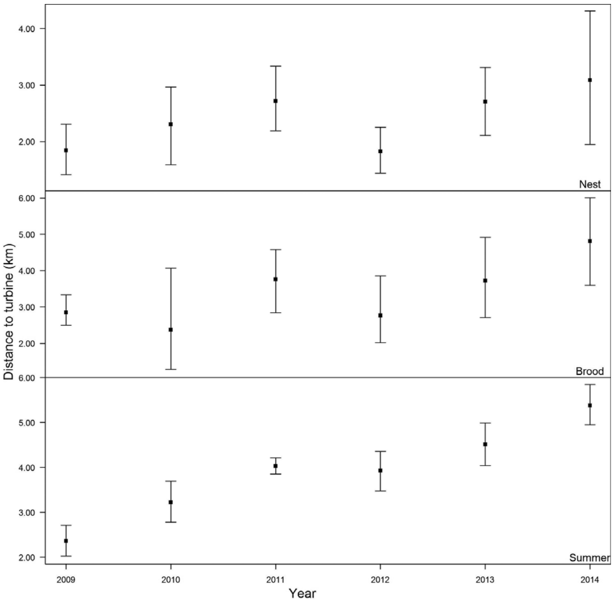

Figure 3. The mean distance to turbines for greater sage-grouse nests, broods, and summer locations observed within the treatment area at the Seven Mile Hill study area from 2009–2014, Carbon County, Wyoming, USA. We estimated 90% confidence intervals (error bars) using a bootstrapping technique that treated the individual as the sampling unit.

1.2 km of the SWEF infrastructure (Table 5). The next best fitting model was percentage of surface disturbance within 1.6 km of SWEF infrastructure ($\Delta\text{AIC}_c = 1.9$). In addition, the covariate that estimated the potential time lags associated with summer site selection relative to the percentage of surface disturbance for female summer habitat selection between 2009–2011 and 2012–2014 was not significant, suggesting selection patterns relative to the percentage of surface disturbance did not differ among these time periods ($\beta = 0.07$; 90% CI = −0.20–0.33). Spatially, we predicted the relative probability of selection to be high around leks (Fig. 4).

The k-fold validation results indicated the RSF model developed at the treatment and control study area had good overall predictability ($\bar{x}\, r_s = 0.95$ and $\bar{x}\, r_s = 0.94$, respectively). The RSF developed at the treatment area using habitat data layers from 2009–2011 was fair at predicting sage-grouse summer use determined by the goodness-of-fit tests; the RSF using habitat data from 2012–2014 was good (Fig. 7A). The RSFs developed at the control study area using habitat data layers from 2009–2011 and 2012–2014 were not adequate and poor at predicting sage-grouse use within the treatment study area (Fig. 7B). Spatially, from the treatment RSFs we estimated a higher proportion of expected use and observed a higher proportion of use closer to SWEF turbines, although we did detect high correlations for some RSF bins farther from turbines (Fig. 7B). Because of the inability of the control RSF to accurately predict use within the treatment study area, we were unable to identify any correlation trends relative to turbines. The control RSF expected high use approximately 9.65 km from turbines but expected use was not proportionate to observed use, suggesting selection patterns differed between study areas possibly because of differences in available summer habitat.

Survival

Nest survival.—Nest hatch dates ranged from 28 April (2014) to 28 June (2010; $\bar{x} = 25$ May) for all assumed first nesting attempts. We observed 35 re-nest attempts within the study area during the study period ranging from 1 in 2012 to 15 in 2011. Eighteen of the 35 (51%) observed re-nests were successful. In addition, we removed 2 nests from the analysis after the female died early in the nest initiation phase. No abandoned nests were thought to be caused by observers. We observed 187 failed nesting attempts and we were able to attribute 105 (56%) and 29 (16%) of those failures to predation by mammalian and avian predators,

Table 3. Odds ratios, slope coefficients, and 90% confidence intervals (CI) for covariates in the sage-grouse nest site selection models for a treatment and control study area within the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014. Odds ratios measure the multiplicative change in relative probability of selection when a covariate changes by one unit, assuming values for all other covariates remain constant. We did not calculate odds ratios for insignificant (alpha level = 0.10) covariates and covariates involved with a quadratic effect because they were dependent on values of other covariates.

			90% CI			90% CI	
Description	**Scale (km)**	**β**	**Lower**	**Upper**	**Odds ratio (%)**	**Lower**	**Upper**
Treatment							
Distance to lek of capture (km)		−0.607	−0.740	−0.496	−45.52	−52.31	−39.10
Bare ground (%)	0.13	−0.041	−0.050	−0.030	−4.04	−4.87	−2.95
Litter (%)	0.46	0.058	0.019	0.106	5.97	1.88	11.16
Wyoming big sagebrush (%)	0.13	0.138	0.017	0.256	14.76	1.76	29.20
Distance to transmission line (km)		0.853	0.439	1.316			
(Distance to transmission line [km])^2		−0.128	−0.184	−0.079			
Control							
Distance to lek of capture (km)		−0.043	−0.084	−0.001	−4.21	−8.01	−0.11
Wyoming big sagebrush (%)	0.46	0.227	0.085	0.357	25.51	8.87	42.87
Elevation (m)	0.09	−0.007	−0.009	−0.004	−0.68	−0.90	−0.44
Bare ground (%)	0.09	−0.018	−0.028	−0.011	−1.81	−2.75	−1.10
SD shrub height (cm)	0.13	0.010	0.005	0.014	0.98	0.52	1.45
Distance to transmission line (km)		−0.142	−0.211	−0.068	−13.27	−19.04	−6.57
Distance to major road (km)		0.381	0.243	0.566			
(Distance to major road [km])^2		−0.026	−0.044	−0.014			

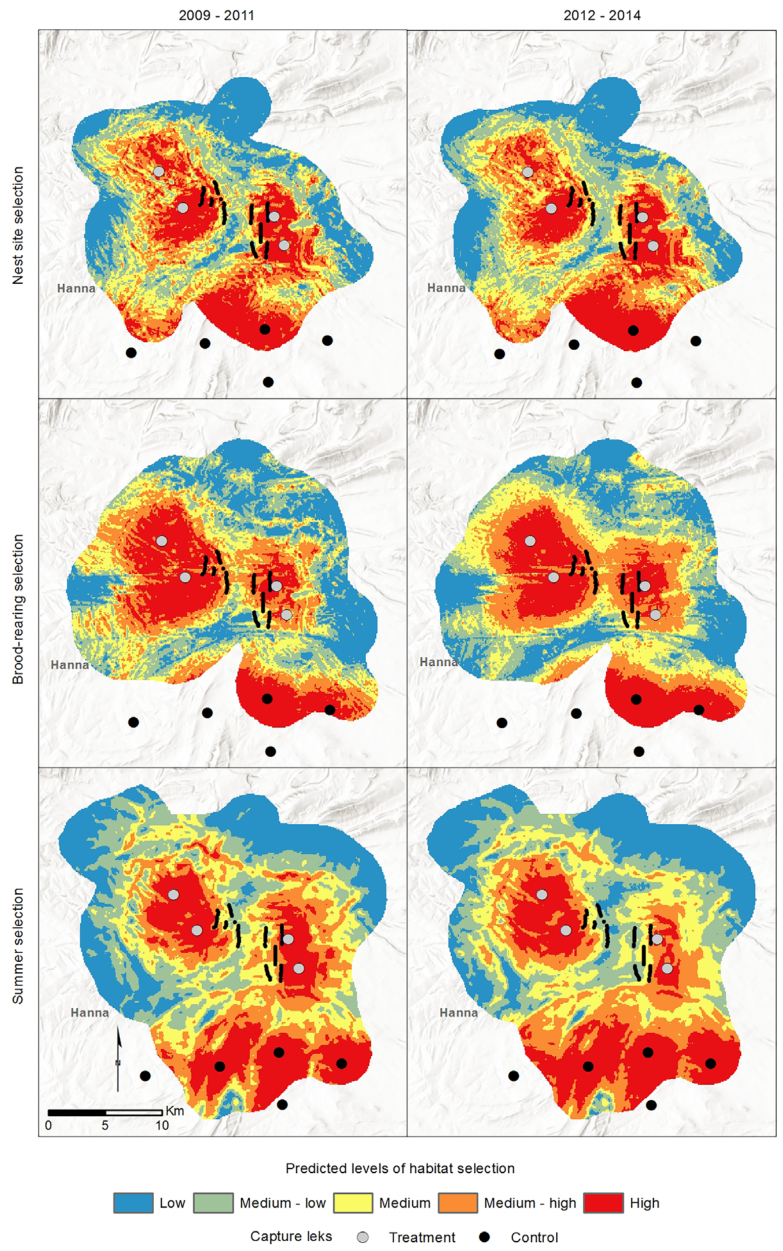

Figure 4. Predicted levels of sage-grouse habitat selection for each seasonal period within the treatment area at the Seven Mile Hill study area, Carbon County, Wyoming, USA. We made predictions for study years 2009–2011 and 2012–2014 using a resource selection function model developed at the treatment study area.

respectively. The median distance to turbines from all successful nests (5.84 km) was similar to all failed nesting attempts (6.29 km). We used 302 first nesting attempts in the Cox proportional hazard modeling. Nest survival did not fluctuate considerably among study areas and years (Fig. 8). The overall nest survival rate estimated from a Cox model that only included year for all sage-grouse nests ranged from 0.23 in 2011 to 0.56 in 2013. To explore yearly variations between study years, we included year and study area in the Cox model and nest survival rate ranged from 0.23 (2011) to 0.68 (2014) for nests from females captured at treatment area leks and from 0.21 (2014) to 0.54 (2013) for nests from females captured at control area leks (Fig. 8).

Model selection revealed that 24 environmental models were within 2 AIC_c values of the top model. We added the SWEF covariates to the 24 competing environmental models and none of the SWEF covariates improved model fit. The top model that explained the environmental variation in daily nest survival included SD of shrub cover, TPI, quadratic effect of distance to major road, and distance to transmission line (Table 6). The addition of female age or RSF values did not improve the environmental model (age $\Delta AIC_c = 0.37$; RSF values $\Delta AIC_c = 0.68$). The percentage of surface disturbance within 0.40 km of SWEF infrastructure was the most informative SWEF covariate and addition of this covariate to the top environmental model did not improve

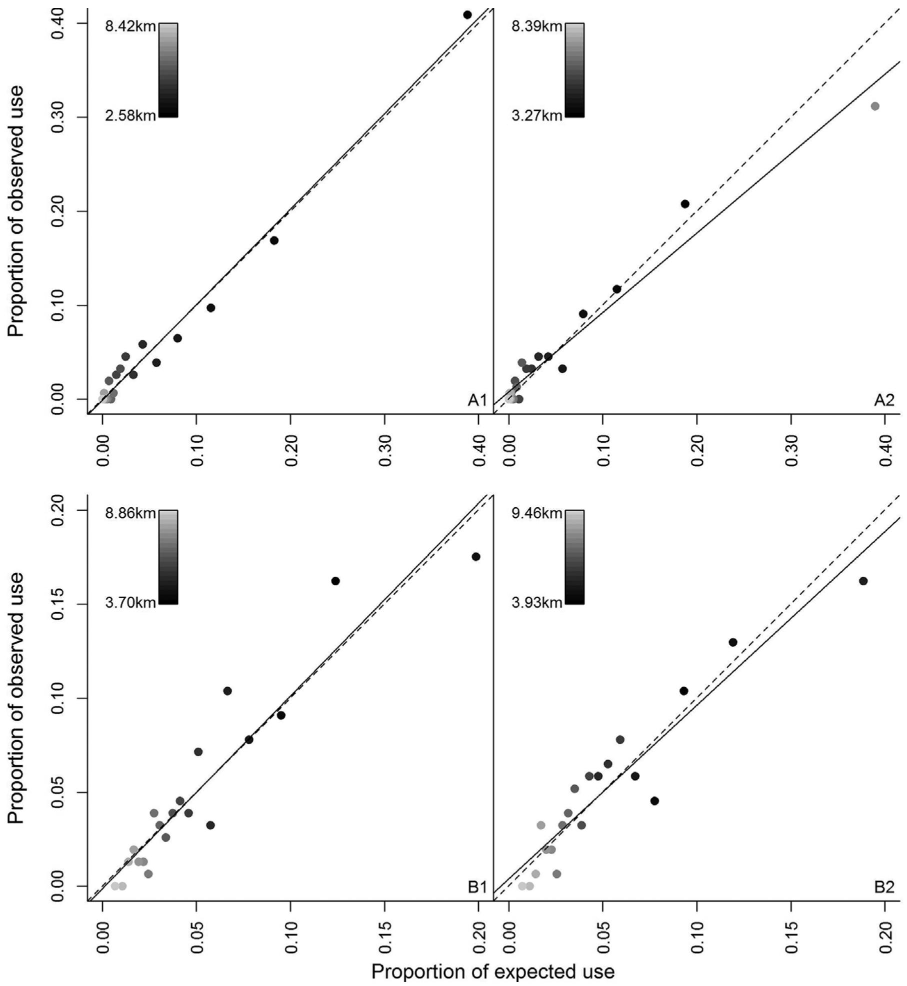

Figure 5. Proportion of expected use compared to the proportion of observed use for sage-grouse nest locations within the treatment area at the Seven Mile Hill study area, Carbon County, Wyoming, USA. We calculated expected use using resource selection functions developed at the treatment (A) and control (B) area for covariate values observed during 2009–2011 (1) and 2012–2014 (2). The dashed line represents observed use equals expected use and the dark line represents the fitted regression line. Darker points represent smaller median distances to wind turbines for each bin value.

model fit and was not significant ($\Delta\text{AIC}_c = 1.31$; $\beta = 0.15$; 90% CI = −0.12–0.43). The environmental model with lek of capture included as a random intercept term was not significantly different ($P = 0.21$) from the top environmental model that did not include the random term. In addition, the model that estimated the potential differences between study periods associated with nest survival relative to the turbines for nests between 2009–2011 and 2012–2014 was not significant, suggesting survival relative to percentage of surface disturbance within 0.40 km did not differ among these time periods ($\beta = -0.003$; 90% CI = −0.009–0.002). We did not detect a significant negative turbine effect when we pooled all nests from females captured at treatment area leks, which suggests the SWEF did not negatively influence survival for sage-grouse captured at treatment study area leks.

Brood survival.—We monitored 123 females with broods (502 locations) during the brood-rearing period from 2009–2014 (treatment $n = 59$; control $n = 64$). Brood survival fluctuated among study areas and years (Fig. 8). Brood survival during the brood-rearing period was relatively high at both study areas, ranging from 0.46 (2009) to 0.68 (2015) for broods from females captured at treatment study area leks and from 0.54 (2010) to 1.00 (2014) for broods from females captured at control study area leks (Fig. 8). The overall, brood survival rate estimated from an A-G model that only included year for all sage-grouse broods ranged from 0.48 in 2010 to 0.75 in 2015.

Model selection revealed that 26 environmental models were within 2 AIC_c values of the top model. We added the SWEF covariates to the 26 competing environmental models and none of the SWEF covariates improved model fit. The top model that explained the environmental variation in weekly brood survival included terrain ruggedness, TPI, distance to capture lek, distance to major road, and a quadratic effect of distance to transmission line (Table 7). The addition of female age or RSF values did not improve the environmental model (age $\Delta\text{AIC}_c = 1.26$; RSF values $\Delta\text{AIC}_c = 1.66$). Distance to turbine was the most informative SWEF covariate and addition of this covariate to the top environmental model did not improve model fit and was not significant ($\Delta\text{AIC}_c = 0.234$; $\beta = -0.069$; 90% CI = −0.107–0.048). In addition, the model that estimated the potential differences between study periods in brood survival relative to the turbines for broods between 2009–2011 and 2012–

Table 4. Odds ratios, slope coefficients, and 90% confidence intervals (CI) for covariates in the sage-grouse brood-rearing habitat selection models for a treatment and control study area within the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by one unit, assuming all other covariates remain constant. We did not calculate odds ratios for insignificant (alpha level = 0.10) covariates and covariates involved with a quadratic effect because they were dependent on values of other covariates.

			90% CI			90% CI (%)	
Description	**Scale (km)**	**β**	**Lower**	**Upper**	**Odds ratio (%)**	**Lower**	**Upper**
Treatment							
Distance to lek of capture (km)		−0.547	−0.705	−0.463	−42.11	−50.57	−37.04
Wyoming big sagebrush (%)	0.18	0.188	0.104	0.288	20.66	10.98	33.33
Elevation (m)	0.89	0.012	0.004	0.018	1.17	0.36	1.86
Bare ground (%)	0.18	−0.058	−0.079	−0.033	−5.64	−7.57	−3.27
SD shrub height (cm)	0.18	−0.003	−0.018	0.010	−0.29	−1.76	0.97
Distance to transmission line (km)		0.368	−0.030	0.915			
(Distance to transmission line [km])^2		−0.064	−0.150	−0.007			
Distance to major road (km)		0.454	0.198	0.788			
(Distance to major road [km])^2		−0.020	−0.045	−0.005			
SWEF[a] surface disturbance (%)	1.20	−0.898	−2.184	−0.251	−59.25	−88.75	−22.16
Control							
Distance to lek of capture (km)		−0.288	−0.375	−0.211	−24.99	−31.30	−19.06
Herbaceous (%)	0.89	0.151	−0.051	0.336	16.34	−4.98	39.93
Sagebrush (%)	0.18	0.030	−0.004	0.067	3.00	−0.40	6.91
Topographic Position Index (−1 to 1)	0.89	−0.006	−0.014	0.002	−0.65	−1.42	0.17
Distance to meadow (km)		−0.893	−1.255	−0.543	−59.05	−71.48	−41.88
Distance to transmission line (km)		0.105	−0.022	0.230	11.08	−2.19	25.80
Distance to major road (km)		0.037	−0.061	0.128	3.77	−5.91	13.68

[a] Seven Mile Hill Wind Energy Facility.

2014 was not significant, suggesting survival relative to distance to turbines did not differ among these time periods ($\beta = -0.92$; 90% CI = −0.23–0.07).

The model with lek of capture included as a random intercept term improved model fit ($P = 0.039$); however, the addition of turbines to the random lek intercept model did not improve model fit ($P = 0.12$). Two leks had significant frailty effects estimates: Old Carbon 31 ($\beta = 0.893$; 90% CI = 0.231–2.681) and Old Carbon 35 2 ($\beta = -0.972$; 90% CI = −2.621 to −0.448) located within the control study area (Fig. 1 and Table 8). Females with broods captured at the Old Carbon 31 lek had 2 times the risk of failing compared to females with broods captured at other leks. The risk of failing decreased by 62.2% for females with broods captured at Old Carbon 35 2 (Table 8). We did not detect a significant negative turbine effect when we pooled all broods from females captured at treatment area leks, which suggests the SWEF did not negatively influence survival for sage-grouse captured at treatment study area leks.

Female survival.—We monitored 340 females from 2009 to 2014 (treatment $n = 156$; control $n = 184$). We observed 189 mortalities (treatment = 85; control = 99). There were 14 instances where the radio-transmitter possibly fell off the female and we censored those individuals at the time and location of their last known location. In addition, we removed 5 mortalities from the analysis that could have been related to the stress of capture and handling because these mortalities occurred within 10 days of capture. We recorded the majority of mortalities (56.1%) during the first 10 weeks of the survival period (1 Apr–10 Jun). The cause of mortality for the majority of females was unknown ($n = 101$; 55%). We attributed 24 (13%) and 57 (31%) mortalities to avian and mammalian predators, respectively. The control study area appeared to incur more avian predator mortalities (17) than the treatment study area (7). Carcasses from 2 mortalities tested positive for West Nile virus. To explore yearly variations between study years, we included year and study area in the A-G model and female summer (1 Apr–31 Oct) survival fluctuated at both study areas during the study period, ranging from 0.16 (2011) to 0.64 (2010) for females captured at treatment area leks and from 0.28 (2010) to 0.63 (2012) for females captured at control area leks (Fig. 8). Overall, summer survival rate estimated from an A-G model that only included year for all female sage-grouse during the summer ranged from 0.34 in 2009 to 0.52 in 2012.

We used 6,378 locations, 31 monitoring intervals, and 511 females (340 individuals monitored across multiple study years) to model female survival relative to the SWEF. We included year as a strata in the A-G model to allow different baseline hazards each year. Model selection revealed that 74 environmental models were within 2 AIC$_c$ values of the top model. We added the SWEF covariates to the 74 environmental models and the percentage of disturbance within 0.81 km of SWEF infrastructure was the most informative SWEF covariate. The addition of this covariate improved model fit when comparing to the environmental model with the lowest AIC$_c$ (ΔAIC$_c$ = 2.03) and was significant ($\beta = -0.71$; 90% CI = −1.95 to −0.18; Table 9). The top model that explained the highest amount of variation in female survival included CTI, herbaceous cover, terrain ruggedness, TPI, shrub cover, distance to capture lek, and percentage of surface disturbance (Table 9). The addition of female age and RSF values covariates did not improve the top model (age ΔAIC$_c$ = 0.01; RSF values ΔAIC$_c$ = 1.91). The risk of mortality decreased by 49.2% for every 1% increase in percentage of disturbance within 0.81 km of a location (90%

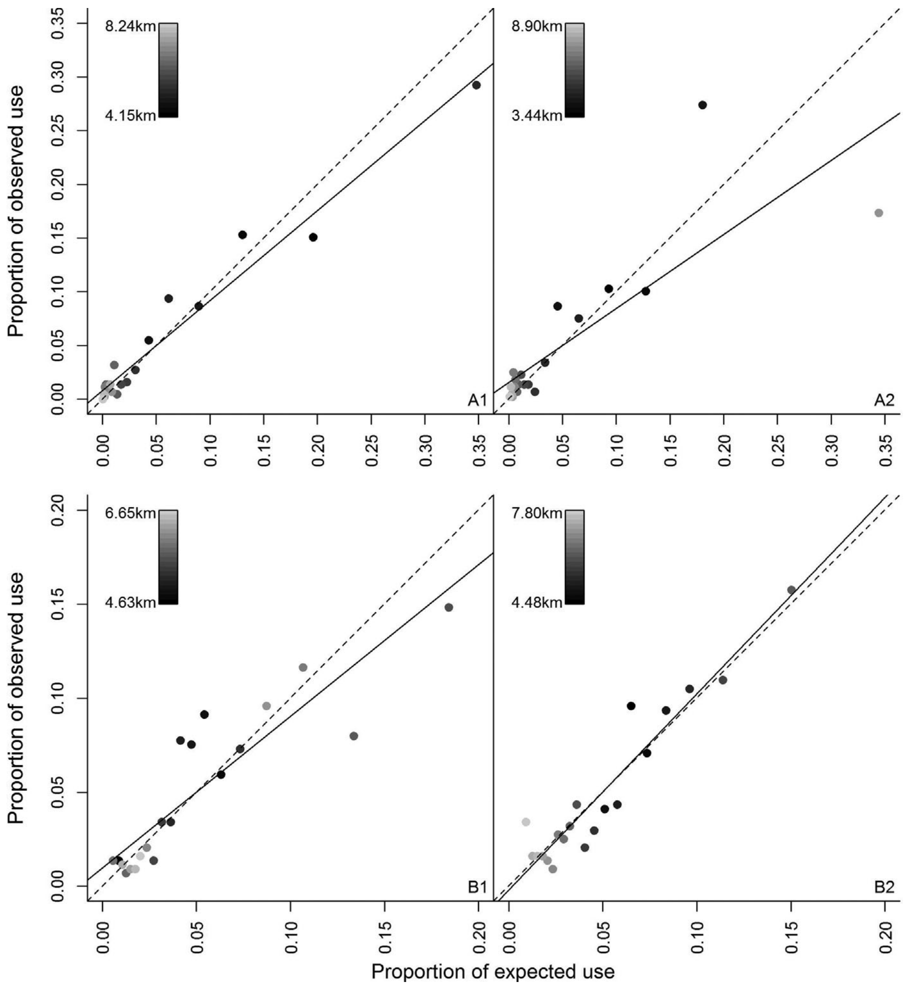

Figure 6. Proportion of expected use compared to the proportion of observed use for sage-grouse brood-rearing locations within the treatment area at the Seven Mile Hill Wind Energy Facility (SWEF) study area, Wyoming, USA. We calculated expected use using resource selection functions developed at the treatment (A) and control (B) area for covariate values observed during 2009–2011 (1) and 2012–2014 (2). The dashed line represents observed use equals expected use and the dark line represents the fitted regression line. Darker points represent smaller median distances to wind turbines for each bin value.

Table 5. Odds ratios, slope coefficients, and 90% confidence intervals (CI) for covariates in the sage-grouse summer habitat selection models for a treatment and control study area within the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014. Odds ratios measure the multiplicative change in odds of selection when a covariate changes by one unit, assuming all other covariates remain constant. We did not calculate odds ratios for insignificant (alpha level = 0.10) covariates and covariates involved with a quadratic effect because they were dependent on values of other covariates.

			90% CI			90% CI (%)	
Description	**Scale (km)**	**β**	**Lower**	**Upper**	**Odds ratio (%)**	**Lower**	**Upper**
Treatment							
Distance to lek of capture (km)		−0.181	−0.210	−0.163	−16.55	−18.92	−15.04
Herbaceous (%)	1.80	−0.059	−0.112	0.013	−5.76	−10.59	1.32
Topographic Position Index (−1 to 1)	0.81	−0.005	−0.008	−0.001	−0.45	−0.82	−0.12
Shrub SD (%)	0.37	0.136	0.080	0.198	14.56	8.36	21.91
Slope (degrees)	0.37	−0.054	−0.079	−0.026	−5.25	−7.60	−2.60
Distance to major road (km)		0.027	0.006	0.054	2.79	0.59	5.52
SWEF[a] disturbance (%)	1.20	−0.236	−0.459	−0.039	−21.00	−36.81	−3.83
Control							
Distance to lek of capture (km)		−0.019	−0.032	−0.006	−1.84	−3.11	−0.64
Meadow (%)	1.80	0.335	0.276	0.399	39.80	31.82	49.08
Topographic Position Index (−1 to 1)	0.81	−0.012	−0.016	−0.008	−1.19	−1.61	−0.75
Shrub SD (%)	0.37	0.153	0.107	0.202	16.57	11.25	22.38
Slope (degree)	1.80	−0.116	−0.139	−0.091	−10.99	−12.97	−8.70
Distance to transmission line (km)		0.045	0.021	0.074	4.64	2.16	7.73
Distance to major road (km)		0.090	0.074	0.107	9.45	7.65	11.32

[a] Seven Mile Hill Wind Energy Facility.

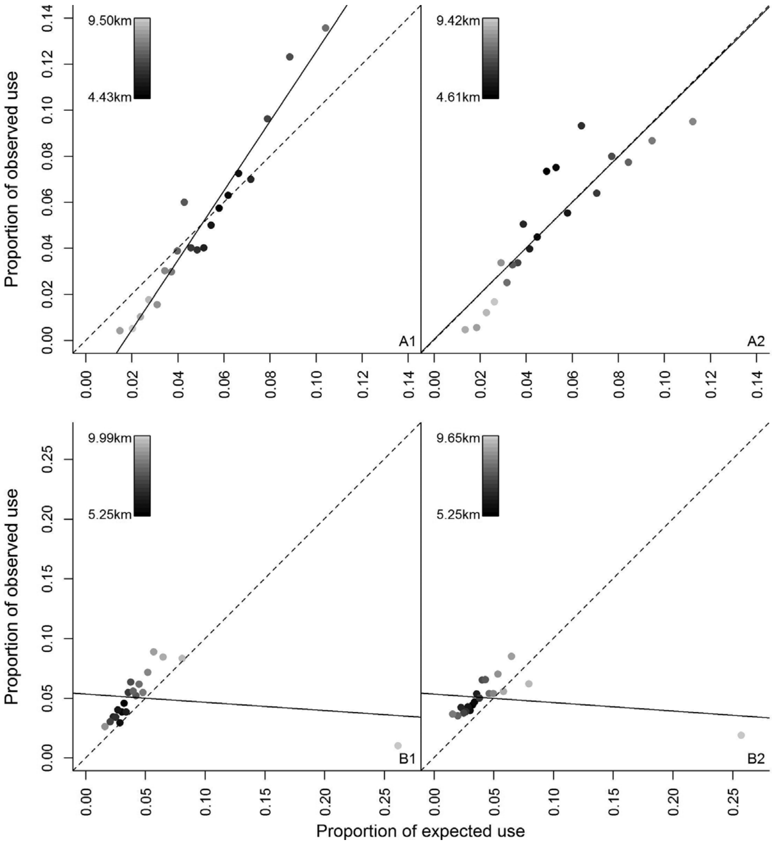

Figure 7. Proportion of expected use compared to the proportion of observed use for sage-grouse summer locations within the treatment area at the Seven Mile Hill Wind Energy Facility (SWEF) study area, Wyoming, USA. We calculated expected use using resource selection functions developed at the treatment (A) and control (B) area for covariate values observed during 2009–2011 (1) and 2012–2014 (2). The dashed line represents observed use equals expected use and the dark line represents the fitted regression line. Darker points represent smaller median distances to wind turbines for each bin value.

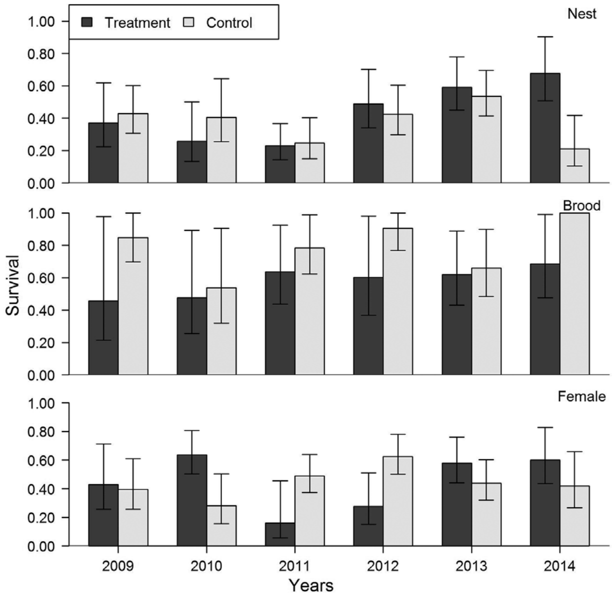

Figure 8. Mean nest, brood, and summer female sage-grouse survivorship and 90% confidence intervals at each study area and year, calculated from the terminus of respective Kaplan–Meier curves within the Seven Mile Hill study area, Carbon County, Wyoming, 2009–2014.

CI = 14.2–83.6%; Table 9 and Fig. 9). This implies higher survival in areas with higher surface disturbance, at least up to the maximum disturbance percentage observed in this study at the 0.81-km scale (3%).

The addition of lek of capture included as a random intercept term in the top model was not significantly different from the model that excluded the random intercept term ($P = 0.50$). In addition, the covariate that estimated the potential differences between study periods associated with female survival relative to the percentage of surface disturbance for females between 2009–2011 and 2012–2014 was not significant, suggesting survival relative to percentage of surface disturbance did not differ among these time periods ($\beta = -0.13$; 90% CI = -1.52–1.27). We did not detect a significant negative SWEF effect analyzing the restricted data set, which suggests the SWEF did not negatively influence survival for sage-grouse captured at treatment study area leks.

DISCUSSION

Habitat Selection

We found good predictability for all of our RSFs developed at the treatment and control areas during each time period. We observed little changes in the predictions using treatment and control RSF predictions at the treatment area during the

Table 6. Relative risks of sage-grouse nests for each covariate or risk factor included in the top model at the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014.

				Hazard ratio 90% CI	
Covariate	**Scale (km)**	**Estimate**	**Hazard ratio [exp(estimate)]**	**Lower**	**Upper**
Shrub SD (%)	90	−1.466	0.231	0.072	0.712
Topographic Position Index (−1 to 1)	90	−0.133	0.875	0.784	0.985
Distance to major road (km)		0.145	1.156	0.997	1.385
(Distance to major road [km])^2		−0.016	0.984	0.969	0.997
Distance to transmission line (km)		−0.074	0.928	0.859	0.994

nesting period, further suggesting no influence of the SWEF on nesting habitat selection. The ability of the control RSF to adequately predict brood-rearing and summer selection at the treatment area diminished during these periods, suggesting different habitat selection patterns among individuals between the 2 study areas and a possible SWEF affect.

Nest site selection was not influenced by the SWEF 6 years following development but was influenced by proximity to lek of capture, vegetation variables including a positive effect of Wyoming big sagebrush cover, negative effect of bare ground, and anthropogenic effects of distance to transmission lines and major roads. At the treatment study area, the average distance of nest locations from SWEF turbines did not show a consistent trend from 2009 through 2014, suggesting little change in nest locations in response to wind turbines. In addition, the time lag covariate we considered at the treatment area that compared short-term (2009–2011) and long-term (2012–2014) nest site selection relative to SWEF covariates was not significant, providing further evidence that sage-grouse were not avoiding the SWEF during the study period.

As females with successful nests began to raise their broods, we observed a shift in selection away from areas with higher percentage of surface disturbance. Although avoidance was consistent across the years of our study, avoidance of habitats with higher percentage of surface disturbance was more pronounced in 2012–2014 compared to 2009–2011, suggesting a lag period in the ultimate population-level response to the development of the SWEF. The lag in the reaction to SWEF is similar to reactions documented for nesting females in a natural gas development (Holloran et al. 2010), and may be related to adult philopatry of seasonal habitats dictating that eventual reactions to SWEF are determined by individuals born after the infrastructure has been constructed.

Similar to the brood-rearing period, females shifted their selection patterns away from areas with higher percentage of surface disturbance following the nesting and brood-rearing period. Unlike brood-rearing, avoidance of percentage of disturbance during summer during the first 3 years (2009–2011) was not significantly different from the last 3 years (2012–2014), suggesting this avoidance effect did not become stronger over time. However, the average distance from summer locations to nearest turbine increased from 2.21 km to 5.26 km between 2009 and 2014, indicating a possible lag effect of turbines on summer habitat selection and the full impact of the SWEF facility on summer habitat selection may not be fully realized 6 years following development. The RSFs developed from data in the control area did not adequately predict the relative probability of sage-grouse summer habitat selection in the treatment area. Even though sage-grouse from both study areas use habitats that are relatively close to each other, we did detect substantial differences between habitat selection patterns of the 2 groups during summer. The different selection patterns between the 2 groups could be influenced by the facility; however, we do not suspect this to be the case because the treatment RSF indicated a small avoidance of the facility and estimated areas of low predicted levels of use far from the SWEF. It was more likely related to variability in available habitat among the 2 areas.

Our results suggest that female sage-grouse selected nest sites regardless of distance to wind energy infrastructure, which differs from nest site selection in oil and gas fields. For instance, Lyon and Anderson (2003) reported 91% of female sage-grouse from undisturbed leks nested within 3 km of lek of capture compared to only 26% of females captured on leks disturbed by oil and gas development in southwestern Wyoming. If nesting females had responded to the SWEF similarly to oil and gas, we would have expected increasing

Table 7. Relative risks of sage-grouse broods for each covariate or risk factor included in the top model at the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014.

				Hazard ratio 90% CI	
Covariate	**Scale (km)**	**Estimate**	**Hazard ratio [exp(estimate)]**	**Lower**	**Upper**
Terrain ruggedness (0–1)	130	−1.350	0.259	0.038	0.685
Topographic Position Index (−1 to 1)	90	−0.575	0.563	0.28	1.043
Distance to capture lek (km)		0.121	1.129	1.006	1.316
Distance to major road (km)		0.191	1.21	1.096	1.51
Distance to transmission line (km)		0.766			
(Distance to transmission line [km])^2		−0.105			

Table 8. Frailty estimates associated with each lek of capture included in the best approximating brood survival model at the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014. We considered frailty estimates with confidence intervals not containing 1 to be statically significant (alpha = 0.10).

Lek of capture	Frailty estimate (exp(β))	90% Lower	90% Upper
Treatment			
Commo 1	0.639	0.194	1.308
Hanna Draw East 1	0.862	0.302	1.573
Missouri John	1.143	0.552	2.211
Pine Draw	0.755	0.174	2.243
Control			
Kyle 63	1.675	0.814	9.506
Old Carbon 31	2.442	1.26	14.606
Old Carbon 32	0.922	0.389	1.721
Old Carbon 34	1.113	0.422	2.709
Old Carbon 35 2	0.378	0.073	0.639
Old Carbon 37	1.324	0.527	6.510

numbers of female sage-grouse from the treatment study area to nest farther away from leks and away from the SWEF (e.g., south of Highway 30-287) over time. However, there was little evidence of that response, suggesting nesting females responded to habitat conditions nearest to leks instead of avoiding wind energy infrastructure. Greater prairie-chicken nest site selection was not reported to be influenced by a commercial wind energy facility in Kansas but was reported to be influenced by environmental conditions, which is consistent with our findings (McNew et al. 2014).

Our results suggest that sage-grouse during the brood-rearing and summer period were responding to the infrastructure associated with a wind energy development similarly to that found in a natural gas field. Results from studies of sage-grouse response to natural gas development suggest that birds were avoiding human activity rather than the infrastructure itself (Dzialak et al. 2012, Holloran et al. 2015). Although vehicle activity levels at a wind turbine are markedly less than a natural gas well (LeBeau et al. 2014), responses suggest similar mechanisms. The movement of turbines themselves may be adding to the perception by sage-grouse of high levels of human activity. Conversely, the threshold of human activity levels at which sage-grouse respond by avoiding sites may be below the levels found in a wind energy development (Lyon and Anderson 2003, Dinkins et al. 2014, Holloran et al. 2015). Regardless, our results suggest that management approaches established for oil and gas development may be pertinent to managing sage-grouse during the brood-rearing and summer period for wind energy developments (Doherty et al. 2011, Naugle et al. 2011). In addition, these results are similar to those documented for greater prairie-chickens at a wind energy facility in Kansas, where habitat selection during the 6-month breeding period (1 Mar–31 Aug) increased with increasing distance to turbine, suggesting behavioral avoidance of turbines (Winder et al. 2014*a*).

The percentage of surface disturbance was more influential than proximity of turbines, suggesting that use continued to occur around the edges of the facility and in less densely developed areas (e.g., single turbine string) but was lower within the facility. The percentage of surface disturbance within 1.2 km of SWEF ranged from 0% to 2.7%; thus, a 1% increase in percentage of disturbance resulted in large changes in the relative probability of brood-rearing and summer habitat selection. To put this in perspective, given that a turbine pad is approximately 0.07 ha (e.g., 30-m diameter circle), turbines are spaced 150 m apart, and access roads are 10 m wide, approximately 10 turbines and associated access roads within 1.2 km of a point on the landscape would result in 2% disturbance and reduce the average relative probability of habitat selection during the brood-rearing and summer period by 60%. The scale of the relationship between the percentage of disturbance, as estimated as the disturbance footprint within 1.2 km, and brood-rearing habitat selection was similar to studies investigating brood response to the infrastructure of a natural gas development. Aldridge and Boyce (2007) reported a negative association between visible well densities within 0.5 km and brood occurrence, Kirol et al. (2015) reported a negative relationship with the number of visible wells within 1.26 km and the density of disturbance with brood occurrence. In addition, Dinkins et al. (2014) reported a negative relationship between brood occurrence and well densities within 3 km. The distribution of brood locations (Fig. 3) corroborated that the scale of avoidance of wind energy development infrastructure during brood-rearing was relatively small. Our approach to establishing window size over which to calculate percentage of surface disturbance associated with the SWEF was not designed to identify distance thresholds but to establish the window size where the

Table 9. Relative risk of female sage-grouse summer mortality for each covariate or risk factor included in the top model at the Seven Mile Hill study area in Carbon County, Wyoming, USA, 2009–2014.

Covariate	Scale (km)	Estimate	Hazard ratio [exp(estimate)]	Hazard ratio 90% CI Lower	Hazard ratio 90% CI Upper
Compound topographic index	0.37	0.016	1.016	0.718	0.979
Herbaceous (%)	0.37	−0.157	0.855	0.994	1.233
Terrain ruggedness (0–1)	0.13	0.104	1.110	1.046	1.603
Topographic Position Index (−1 to 1)	0.37	0.235	1.265	0.933	0.983
Shrub (%)	1.80	−0.040	0.961	0.590	0.971
Distance to capture lek (%)		0.081	1.084	1.043	1.124
SWEF[a] disturbance (%)	0.81	−0.709	0.492	0.142	0.836

[a] Seven Mile Hill Wind Energy Facility.

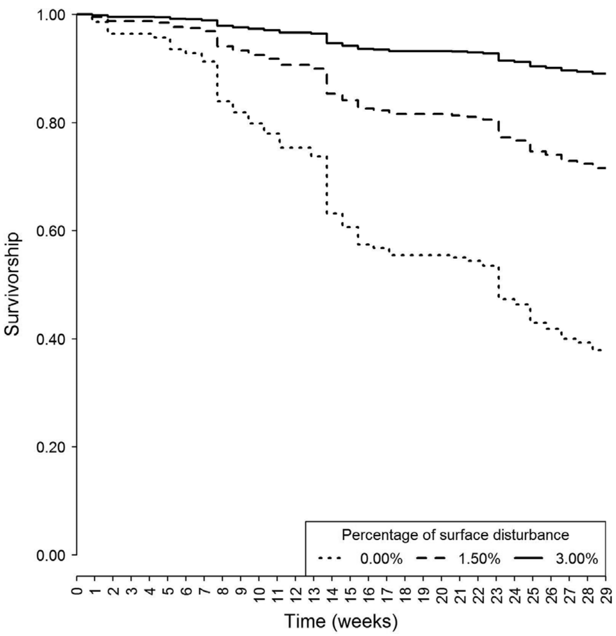

Figure 9. Sage-grouse female summer survivorship predicted from the top proportional hazards model containing, bare ground, compound topographic index, herbaceous cover, terrain ruggedness, topographic position index, distance to capture lek, and percentage of surface disturbance in 2012 within the Seven Mile Hill study area, Carbon County, Wyoming, 2009–2014. All covariates where held at their median values except percentage of surface disturbance.

relationship between selection and survival and sage-grouse response was strongest; therefore, the distances reported do not establish that impacts could not occur at greater distances.

Although we controlled for confounding factors during the model-building process by first identifying the best environmental model before considering wind and anthropogenic model variables, there was a chance we did not consider a particular covariate that would have better elucidated habitat selection (e.g., forb availability). However, we feel confident in our modeling approach and in the set of variables we considered, which are supported in the literature (Connelly et al. 2011). Our results could have been strengthened with pre-construction data allowing for a before-after control-impact (BACI) analytical approach, and the results should be interpreted given the limitations in the design of the study. However, we benefited from a long-term dataset that should have allowed us to detect a large magnitude of avoidance of the SWEF within the treatment study over the 6-year study if such avoidance existed.

Survival

The SWEF did not have a negative effect on sage-grouse nest, brood, and summer female survival within the study area over the 6-year period. LeBeau et al. (2014) estimated a negative effect of SWEF turbines on sage-grouse nest and brood survival; however, this study occurred over a 2-year time period and did not account for temporal variability in the survival models. The addition of multiple study years allowed us to investigate the effect of temporal variability on survival relative to the SWEF. We concluded that the variability in survival was related more to natural temporal variability and habitat features than the SWEF. Survival did not differ between nests, broods, and females captured at treatment and control area leks over the study period. Survival was lower for broods from females captured at the treatment area in 2009 and 2012 but small sample sizes within both study areas made it difficult to detect any significant differences in annual survival. As with most sage-grouse demographic studies (Connelly et al. 2011), we did not detect any influence of female age on nest, brood, or female survival. The presence of the SWEF could act as an ecological trap to nesting and brooding females and female sage-grouse during the summer period where habitats close to the facility appear to be of high quality but in fact fitness associated with these habitats are low. We attempted to identify these source-sink habitats (Aldridge and Boyce 2007, Kirol et al. 2015) by including the RSF value associated with each nest, brood, and summer location as an explanatory variable in the survival models but were unable to identify such habitats.

Variation in survival could be related to the habitat associated with the lek at which a female breeds (Connelly et al. 2000). Adding capture lek as a random effect did not improve model fit for the nest or female survival model but did improve the brood survival model, suggesting that the lek at which an individual breeds affects brood survival. None of the leks within the treatment area had significant frailty effects; however, 2 leks within the control area did have significant effects. Broods from females captured at the Old Carbon 35 2 lek had approximately half the risk of failing compared to broods from females captured at other leks. Conversely, the risk of failing for broods from females captured at the Old Carbon 31 lek was twice that of broods from females captured at other leks. We attempted to account for the unobserved frailty and not underestimate the true hazard function associated with broods from females captured at different leks within the study area. However, there was a possibility that we did not include all possible covariates to explain the variability in brood survival and the effect of turbines on survival could be confounded by an unknown covariate. The lek at which a female breeds is highly influential as to which habitats they will likely use to nest and raise their broods (Holloran and Anderson 2005). Our brood survival model indicated that survival was higher closer to the lek of capture and there may be some features associated with these leks that we were unable to detect or include in our analysis. By including the frailty effects, we were able to determine if leks located within the treatment area had a higher frailty effect, suggesting the effect of the SWEF on survival was masked by some unknown habitat feature that was not measured; however, we did not detect such an effect. Identifying the reasons why Old Carbon 35 2 had lower frailty effects and Old Carbon 31 had higher frailty effects compared to other leks is difficult because we captured the additional risk that cannot be identified by the model covariates.

Transmission lines are tall structures similar to wind turbines, and survival relative to each feature could be confounded, especially for females located close to both features. We removed transmission lines from the nest and brood survival model and added turbines to identify any potential confounding issues, but this *post hoc* analysis suggested that our results were not influenced by confounding effects between turbines and transmission lines. We detected a negative effect of transmission lines on nest and brood survival, but we suggest expanding the survival analysis specific to transmission lines to limit potential confounding factors because our modeling procedure focused on isolating the effect of the SWEF on survival and not transmission lines.

Female survival was related to habitat features and the percentage of disturbance within the SWEF. Female survival was highest for females that used habitats characteristic of less bare ground, more ridges, more wet areas, closer to their lek of capture, and greater percentage of disturbance. Avian predation is the primary cause of female mortality (Hagen 2011) and, similar to brood survival, females that used habitats with flat topography appeared to be at higher risk of predation than females that used more rugged habitats. In addition, females that used habitats with more bare ground may be more susceptible to avian predators because of reduced cover in these areas. After controlling for annual and natural variability, we observed a positive effect of the SWEF on female survival when the percentage of disturbance within 0.81 km of the bird increased from 0% to 3%. A similar relationship was observed in a study of greater prairie-chickens in Kansas (Winder et al. 2014*b*). In that study, females had higher survival near the wind energy facility post-development compared to pre-development (Winder et al. 2014*b*). The effect of the SWEF is large relative to the natural variability within the SMH study area, but this effect does not exist beyond 0.81 km of the SWEF, suggesting the effect is small relative to the larger SMH study area. Regardless, we did not detect a negative effect of the SWEF on female survival. We can only speculate as to why adult survival was higher closer to the facility but it is likely related to lower densities of avian predators. Avian predator density was lower closer to turbines within the SMH study area ($\beta = 0.014$; 90% CI = 0.014–0.015; C. W. LeBeau, Western EcoSystems Technology, Inc., unpublished data).

Our results indicated there was substantial temporal variability in nest, brood, and summer survival for all nests, broods, and summer females during the study period. In an attempt to control for this variability, we included year as a stratum and subsequently included a separate baseline hazard for each year. Because sage-grouse demography and abundance are largely influenced by annual variation in resource availability (Blomberg et al. 2012), we suspect the unexplained annual variation observed in our survival estimates was most likely associated with our imperfect ability to describe annual environmental conditions with covariates. The number of broods we could monitor was dependent on a female successfully hatching ≥ 1 egg during the nesting period. Low nest success years resulted in fewer broods to monitor, indicating the importance of a separate baseline hazard for each year. In addition to unexplained annual variability, we controlled for as much natural variability as possible by developing a rigorous natural model containing only non-anthropogenic factors. The effect of the SWEF on survival, if present, may be small relative to the natural variability within the study area (e.g., lek of capture, weather patterns), which makes it difficult to detect an effect.

The lack of other studies investigating effects of wind energy development to sage-grouse habitat selection and survival limits our ability to make inferences about the cumulative impacts of wind energy development on sage-grouse, but we were able to describe some effects wind energy developments may have on sage-grouse populations. Although we attempted to account for possible confounding factors, there is a chance that we did not detect important interactions between environmental features and habitat selection and survival patterns. The lack of preconstruction data may have produced some uncertainty in the interpretation of our results. Nonetheless, our results demonstrate that wind energy development has some implications to sage-grouse populations during the brood-rearing and summer periods.

MANAGEMENT IMPLICATIONS

Future wind energy developments should consider the potential effects of wind energy development on sage-grouse habitat selection patterns and survival parameters. Current USFWS Land-Based Wind Energy Guidelines do not have specific sage-grouse or prairie grouse avoidance measures for wind energy developers but the Guidelines do suggest impacts will be similar to those from other anthropogenic structures (USFWS 2012). Based on our analysis, future wind energy developments located in similar habitats with a similar disturbance footprint to our facility (0.7% within 1.20 km of the facility) should consider the potential impacts of wind energy development on sage-grouse habitat selection patterns and survival parameters ≤ 1.20 km from any occupied nesting, brood-rearing, or summer habitats. Even though we did not detect a negative effect of the facility during the nesting period and a positive effect on female survival, we are cautious to present any management recommendations that support these results because the lack of additional supporting studies and the variability in habitats and sage-grouse population characteristics throughout their range. Overall facility size may vary while still achieving a similar disturbance footprint. Additional studies investigating potential impacts of connectivity between habitats will be important to understand if facilities disrupt movements and will aide future wind project siting. Monitoring of multiple spatially distributed study sites would provide further information on impacts and cumulative effects of wind energy development on sage-grouse populations.

ACKNOWLEDGMENTS

We thank personnel from Hi-Allen Ranch and PacifiCorp Energy for allowing us access to study areas. We appreciate field assistance provided by J. Eddy, A. Hansen, P. Hansen, R. Hay, T. Higgins, M. Karsch, A. Kircher, J. Loos, A. Malone, J. Parson, T. Rintz, M. Salava, G. Shedd, B. Smith, and E. Vasquez. We thank J. Dahlke of Wyoming Wildlife Consultants for providing project management support. We thank T. Fulbright. D. Gibson, and anonymous reviewers for their reviews and suggestions that markedly improved our manuscript. We thank the National Wind Coordinating Collaborative and Sage-Grouse Research Collaborative, Avian Power Line Interaction Committee, American Wind Energy Association, EDP Renewables North America (formerly Horizon Wind Energy), Iberdrola Renewables, Margaret and Sam Kelly Ornithological Research Fund, PacifiCorp Energy, Bates Hole-Shirley Basin, South-Central, and Southwest Wyoming Sage-grouse Local Working Groups, U.S. Department of Energy, University of Wyoming Agricultural Experiment Station, University of Wyoming School of Energy Resources, and the Wyoming Reclamation and Restoration Center for providing funding support.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Anderson, P. K., and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. Annals of Statistics 10:1100–1120.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology 77: 215–227.

Batary, P., and A. Baldi. 2004. Evidence of an edge effect on avian nesting success. Conservation Biology 18:389–400.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Berry, J. D., and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. Journal of Wildlife Management 49:237–240.

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3: Article 55. https://doi.org/10.1890/E S11-00304.1

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Buchanan, C. B., J. L. Beck, T. E. Bills, and S. N. Miller. 2014. Seasonal resource selection and distributional response by elk to development of a natural gas field. Rangeland Ecology and Management 67:369–379.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000. Effects of predation and hunting on adult sage grouse (Centrocercus Urophasianus) in Idaho. Wildlife Biology 6:227–232.

Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53–67 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology, volume 38. University of California Press, Berkeley, USA.

Copeland, H., A. Pocewicz, D. E. Naugle, T. Griffiths, D. Keinath, J. Evans, and J. Platt. 2013. Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. PLoS ONE 8(6):e67261.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B-Statistical Methodology 34:187–220.

Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2014. Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. Condor: Ornithological Applications 116:629–642.

Doherty, K. E., D. E. Naugle, H. E. Copeland, A. Pocewicz, and J. M. Kiesecker. 2011. Energy development and conservation tradeoffs: systematic planning for greater sage-grouse in their eastern range. Pages 505–516 *in* S. T. Knick, and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, USA.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6(10):e26273. doi:10.1371/journal.pone.0026273

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, and J. B. Winstead. 2012. Temporal and hierarchical spatial components of animal occurrence: conserving seasonal habitat for greater sage-grouse. Ecosphere 3(4):30.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

Erickson, W. P., G. D. Johnson, M. D. Strickland, D. P. Young Jr., K. J. Sernka, and R. E. Good. 2001. Avian collisions with wind turbines: a summary of existing studies and comparisons to other sources of bird collision mortality in the United States. National Wind Coordinating Collaborative (NWCC) Publication and Resource Document. Prepared for the NWCC by WEST, Inc., Cheyenne, Wyoming, USA.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038–1041.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gill, J. P., M. Townsley, and G. P. Mudge. 1996. Review of the impacts of wind farms and other aerial structures upon birds. Scottish Natural Heritage Review No. 21. Scottish Natural Heritage, Battleby, United Kingdom.

Gregory, A. J., and J. L. Beck. 2014. Spatial heterogeneity in response of male greater sage-grouse lek attendance to energy development. PLoS ONE 9(6):e97132. doi:10.1371/journal.pone.0097132.

Guisan, A., S. B. Weiss, and A. D. Weiss. 1999. Glm versus CCA spatial modeling of plant species distribution. Plant Ecology 143:107–122.

Hagen, C. A. 2010. Impacts of energy development on prairie grouse ecology: a research synthesis. Transactions of North American Wildlife and Natural Resource Conference 75:96–103.

Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (volume 38). University of California Press, Berkeley, USA.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Holloran, M. J., B. C. Fedy, and J. Dahlke. 2015. Winter habitat use of greater sage-grouse relative to activity levels at natural gas well pads. Journal of Wildlife Management 79:630–640.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Homer, C. G., C. L. Aldridge, D. K. Meyer, M. J. Coan, and Z. H. Bowen. 2009. Multiscale sagebrush rangeland habitat modeling in southwest Wyoming. U.S. Geological Survey Open-File Report 2008-1027, Reston, Virginia, USA.

Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. J. Schell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. International Journal of Applied Earth Observation and Geoinformation 14:233–244.

Hovick, T. J., R. D. Elmore, D. K. Dahlgren, S. D. Fuhlendorf, and D. M. Engle. 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. Journal of Applied Ecology 51:1680–1689.

Hovick, T. J., R. D. Elmore, D. K. Dahlgren, S. D. Fuhlendorf, and D. M. Engle. 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. Journal of Applied Ecology 51:1680–1689.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004*a*. Modeling survival: application of the Andersen-Gill model to Yellowstone grizzly bears. Journal of Wildlife Management 68:966–978.

Johnson, C. J., S. E. Nielse, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Johnson, G. D., M. K. Perlik, W. P. Erickson, and M. D. Strickland. 2004*b*. Bat activity, composition and collision mortality at a large wind plant in Minnesota. Wildlife Society Bulletin 32:1278–1288.

Johnson, G. D., and S. E. Stephens. 2011. Windpower and biofuels: a green dilemma for wildlife conservation. Pages 131–157 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete data. Journal of the American Statistical Association 53(282):457–481.

Kirol, C. P., J. L. Beck, S. V. Huzurbazar, M. J. Holloran, and S. N. Miller. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:968–990.

Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, U.S.A. Ecology and Evolution 3:1539–1551.

Kuvlesky, W. P. Jr., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, and F. C. Bryant. 2007. Wind energy development and wildlife conservation: challenges and opportunities. Journal of Wildlife Management 71:2487–2498.

LeBeau, C., J. L. Beck, G. D. Johnson, and M. J. Holloran. 2014. Short-term impacts of wind energy development on greater sage-grouse fitness. Journal of Wildlife Management 78:522–530.

Liebezeit, J. R., J. Kendall, S. Brown, C. B. Johnson, P. Martin, T. L. McDonald, D. C. Payer, C. L. Rea, B. Streever, A. M. Wildman, and S. Zack. 2009. Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska. Ecological Applications 19:1628–1644.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage-grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Mahoney, A., and A. D. Chalfoun. 2016. Reproductive success of horned lark and McCown's longspur in relation to wind energy infrastructure. Condor: Ornithological Applications 118:360–375.

Manly, B. F. J. 2006. Randomization, bootstrap and Monte Carlo methods in biology. Third edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Manly, B. F. J., L. L. McDonald, and D. Thomas, editors. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London, United Kingdom.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson, editors. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht, The Netherlands.

McDonald, T. L., B. F. J. Manly, R. M. Nielson, and L. V. Diller. 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. Journal of Wildlife Management 70:375–383.

McNew, L. B., L. M. Hunt, A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2014. Effects of wind energy development on nesting ecology of greater prairie-chickens in fragmented grasslands. Conservation Biology 28:1089–1099.

Naugle, D. E., K. E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland. 2011. Energy Development and greater sage-grouse. Pages 489–503 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (volume 38). University of California Press, Berkeley, USA.

Nonne, D., E. Blomberg, and J. Sedinger. 2013. Dynamics of greater sage-grouse (*Centrocercus urophasianus*) populations in response to transmission lines in central Nevada. Progress report: year 10. Department of Natural Resources and Environmental Sciences, University of Nevada, Reno, USA.

Northrup, J. M., and G. Wittemyer. 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecology Letters 16:112–125.

Nur, N., A. L. Holmes, and G. R. Geupel. 2004. Use of survival time analysis to analyze nesting success in birds: an example using loggerhead shrikes. Condor 106:457–471.

Pearce-Higgins, J. W., L. Stephen, A. Douse, and R. H. W. Langston. 2012. Greater impacts of wind farms on bird populations during construction than subsequent operation: results of a multi-site and multi-species analysis. Journal of Applied Ecology 49:386–394.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. Avoidance behavior by prairie grouse: implications for wind energy development. Conservation Biology 23:1253–1259.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Sappington, M. J., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419–1426.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus Urophasianus*). Account 425 *in* A. Poole and F. Gill, editors. The birds of North America. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Shaffer, J. A., and D. A. Buhl. 2016. Effects of wind-energy facilities on grassland bird distributions. Conservation Biology 30:59–71.

Smith, K. T., C. P. Kirol, J. L. Beck, and F. C. Blomquist. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:article 15.

Taylor, R., J. D. Tack, D. E. Naugle, and L. S. Mills. 2013. Combined effects of energy development and disease on greater sage-grouse. PLoS ONE 8(8):e71256. doi: 10.1371/journal.pone.0071256

Therneau, T. M. 2015. coxme: mixed effects Cox models. R package version 2.2-4. http://CRAN.R-project.org/package=coxme. Accessed 6 Jul 2014.

Therneau, T. M., and P. M. Grambsch. 2000. Modeling survival data: extending the Cox model. Springer-Verlag, New York, New York, USA.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.

Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early broodrearing habitat use and productivity of greater sage-grouse in Wyoming. Western North American Naturalist 66: 332–342.

U.S. Fish and Wildlife Service [USFWS]. 2004. Prairie grouse leks and wind turbines: US Fish and Wildlife Service justification for a 5-mile buffer from leks; additional grassland songbird recommendations. Division of Migratory Bird Management, Arlington, Virginia, USA.

U.S. Department of Energy. 2008. 20% wind energy by 2030: increasing wind energy's contribution to U.S. electrical supply. Office of Scientific and Technical Information, Oak Ridge, Tennessee, USA.

U.S. Fish and Wildlife Service [USFWS]. 2012. Final Land-Based Wind Energy Guidelines. March 23, 2012. USFWS, Washington, D.C., USA. http://www.fws.gov/cno/pdf/Energy/2012_Wind_Energy_Guidelines_final.pdf

U.S. Geological Survey. 2011. National Land Cover Database NLCD, Multi-Resolution Land Characteristics Consortium (MRLC). USGS Earth Resources Observation and Science (Eros) Center, Sioux Falls, South Dakota, USA.

U.S. Geological Survey. 2015. National Elevation Dataset (NED). Raster digital data. USGS, Sioux Falls, South Dakota, USA.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile Virus in the Powder River Basin, Montana and Wyoming, USA. Dissertation. University of Montana, Missoula, USA.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

Walters, K., K. Kosciuch, and J. Jones. 2014. Can the effect of tall structures on birds be isolated from other aspects of development? Wildlife Society Bulletin 38:250–256.

Western Regional Climate Center. 2014. Medicine Bow, Wyoming (486120). Period of Record Monthly Climate Summary, Period of Record: 11/08/1881 to 12/18/2014. http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy6120. Accessed 12 Dec 2014.

Winder, V. L., A. J. Gregory, L. B. McNew, and B. K. Sandercock. 2015. Responses of male greater prairie-chickens to wind energy development. Condor 117:284–296.

Winder, V. L., L. B. McNew, A. J. Gregory, L. M. Hunt, S. M. Wisely, and B. K. Sandercock. 2014*a*. Space use by female greater prairie-chickens in response to wind energy development. Ecosphere 5(1):3.

Winder, V., L. B. McNew, L. M. Hunt, A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2014*b*. Effects of wind energy development on seasonal survival of greater prairie-chickens. Journal of Applied Ecology 51: 395–405.

Associate Editor: Timothy Fulbright.