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RESEARCH ARTICLE

Reproductive success of Horned Lark and McCown's Longspur in relation to wind energy infrastructure

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ABSTRACT

Wind energy is a rapidly expanding industry with potential indirect effects to wildlife populations that are largely unexplored. In 2011 and 2012, we monitored 211 nests of 2 grassland songbirds, Horned Lark (*Eremophila alpestris*) and McCown's Longspur (*Rhynchophanes mccownii*), at 3 wind farms and 2 undeveloped reference sites in Wyoming, USA. We evaluated several indices of reproductive investment and success: clutch size, size-adjusted nestling mass, daily nest survival rate, and number of fledglings. We compared reproductive success between wind farms and undeveloped sites and modeled reproductive success within wind farms as a function of wind energy infrastructure and habitat. Size-adjusted nestling mass of Horned Lark was weakly negatively related to turbine density. In 2011, nest survival of Horned Lark decreased 55% as turbine density increased from 10 to 39 within 2 km of the nest. In 2012, however, nest survival of Horned Lark was best predicted by the combination of vegetation height, distance to shrub edge, and turbine density, with survival increasing weakly with increasing vegetation height. McCown's Longspur nest survival was weakly positively related to vegetation density at the nest site when considered with the amount of grassland habitat in the neighborhood and turbine density within 1 km of the nest. Habitat and distance to infrastructure did not explain clutch size or number of fledglings for either species, or size-adjusted nestling mass for McCown's Longspur. Our results suggest that the influence of wind energy infrastructure varies temporally and by species, even among species using similar habitats. Turbine density was repeatedly the most informative measure of wind energy development. Turbine density could influence wildlife responses to wind energy production and may become increasingly important to consider as development continues in areas with high-quality wind resources.

Keywords: wind facility, grassland bird, nest success, turbine density, turbine proximity, habitat

Éxito reproductivo de *Eremophila alpestris* y *Rhynchophanes mccownii* en relación con estructuras de energía eólica

RESUMEN

La energía eólica es una industria en rápida expansión con efectos indirectos potenciales sobre las poblaciones de vida silvestre que no han sido explorados a fondo. En 2011 y 2012 monitoreamos 211 nidos de dos aves de pradera, *Eremophila alpestris* y *Rhynchophanes mccownii*, en 3 granjas eólicas y dos sitios sin desarrollo eólico como referencia en Wyoming. Evaluamos varios índices de inversión y éxito reproductivo: tamaño de la nidada, masa corregida por tamaño de los polluelos, probabilidad diaria de supervivencia de los nidos y número de volantones. Comparamos el éxito reproductivo entre las granjas eólicas y los sitios de referencia, y modelamos el éxito reproductivo en las granjas eólicas en función de la presencia de estructuras de energía eólica y del hábitat. La masa ajustada por tamaño de los polluelos de *E. alpestris* tuvo una relación negativa débil con la densidad de turbinas. En 2011 la supervivencia de los nidos de *E. alpestris* disminuyó 55% al tiempo que la densidad de turbinas aumentó de 10 a 39 dentro de 2 km del nido. Sin embargo, en 2012 la supervivencia de los nidos de *E. alpestris* se predijo mejor por la combinación de la altura de la vegetación, la distancia al borde de la vegetación arbustiva y la densidad de turbinas, y la supervivencia se incrementó débilmente con el incremento en la altura de la vegetación. La supervivencia de los nidos de *R. mccownii* tuvo una relación positiva débil con la densidad de la vegetación en el sitio de anidación cuando se consideró junto con la cantidad de hábitat de pradera en los alrededores y con la densidad de turbinas en un radio de 1 km alrededor de los nidos. El hábitat y la distancia a las estructuras eólicas no explicaron el tamaño de la nidada ni el número de volantones en ninguna de las especies, ni tampoco la masa ajustada por tamaño en *R. mccownii*. Nuestros resultados sugieren que la influencia de las estructuras de energía eólica varía temporalmente y según la especie, aún entre especies que ocupan hábitats similares. Repetidamente, la densidad de las turbinas fue la medida más informativa del desarrollo de infraestructura de energía eólica. La densidad de las turbinas puede afectar las respuestas de la vida

silvestre a la producción de energía eólica y considerarla puede cobrar gran importancia a medida que el desarrollo eólico continúe en áreas con vientos de alta calidad.

Palabras clave: aves de pradera, éxito de nidos, densidad de turbinas, hábitat, instalaciones eólicas, proximidad a turbinas

INTRODUCTION

Extraction of energy from natural resources is a widespread human activity that results in habitat change with potential consequences for fitness and, subsequently, population dynamics of birds and other wildlife (Sergio et al. 2004, Walker et al. 2007, Gilbert and Chalfoun 2011). Extracting energy from new sites and resources, including wind energy, however, will be necessary to meet the predicted 40% increase in global energy demand over the next 21 years (USEIA 2012). Understanding the types and extent of wildlife responses will be critical for effective conservation and management amid a still-growing industry (Loss 2016, Smith and Dwyer 2016).

Some of the highest-quality wind resources in the United States overlap grassland habitat (USEIA 2010). Native grasslands in the United States have experienced extensive fragmentation and conversion to other land cover types (Samson and Knopf 1994, Samson et al. 2004, North American Bird Conservation Initiative, U.S. Committee 2011), which have been associated with precipitous population declines for many grassland-associated bird species (e.g., Butcher and Niven 2007, Sauer et al. 2008, North American Bird Conservation Initiative, U.S. Committee 2014). Activities such as wind energy production that may further reduce or alter grassland habitat therefore merit attention.

Effects of wind energy production and other forms of human-induced habitat change can manifest in both direct and indirect ways. Direct effects of wind energy production, such as turbine collisions, have been extensively estimated (e.g., Péron et al. 2013, Zimmerling et al. 2013, Erickson et al. 2014), but indirect effects, such as decreased reproductive success, remain largely unexplored (e.g., Hale et al. 2014). There are a number of reasons why changes in avian productivity could occur with wind energy development, primarily relating to predation risk and food availability. For example, infrastructure on wind farms can provide refugia for nest predators, such as rodents (R. Brown, PacifiCorp, personal communication), and soil conditions created by construction or reclamation can increase the number of burrowing rodents (Thelander et al. 2003). Increases in rodents or anthropogenic food subsidies (e.g., carcasses from turbine strikes) may attract additional predators that opportunistically depredate nests (Fedriani et al. 2001, Thelander et al. 2003). Additionally, operational turbines produce stimuli such as noise and shadow flicker

that could increase predation risk by masking cues used to detect predators (Rabin et al. 2006).

Altered soils and vegetation in reclaimed areas could also result in different invertebrate communities, the primary food source for grassland songbirds and their nestlings during the breeding season (Kennedy et al. 2009). Changes in predation risk and food availability can also affect parental care behaviors including incubation rhythms and food delivery rates (Fontaine and Martin 2006, Chalfoun and Martin 2010), which can influence hatching rates and offspring quality (Zanette et al. 2011). Increased predation risk or decreased food availability can negatively influence clutch size, brood/nestling mass, nest survival rates, and the number of fledglings produced (Ostfeld and Keesing 2000, Zanette et al. 2000, 2011, Hua et al. 2014). Each of these components contributes to avian productivity and can ultimately affect population growth rates.

Patterns of reproductive success of grassland-associated birds in relation to wind energy have been spatially and temporally variable, with positive (Rubenstahl et al. 2012, Hatchett et al. 2013), neutral (Gillespie and Dinsmore 2014, McNew et al. 2014), and negative responses (LeBeau et al. 2014) reported. Cumulatively, these studies suggest context-dependent responses by species or their nest predators to wind energy infrastructure. Additionally, the most informative measures of wind energy development to assess songbird responses remain unclear. Previous research in human-altered landscapes indicates that proximity to infrastructure, the primary metric used in wind energy development studies, may not always be the most informative metric for predicting responses to disturbance (Kalyn Bogard and Davis 2014, Hethcoat and Chalfoun 2015, Ludlow et al. 2015). Investigations across a broader array of sites, spatial scales, and species are necessary to clarify the scope of wind energy production's influence on avian productivity.

Wyoming, USA is an interesting case study for investigating grassland bird responses to wind energy infrastructure. First, there is high potential for future development of wind energy resources in Wyoming's grasslands. Secondly, the state's grasslands are relatively intact and support mixed-grass and short-grass prairie species that are declining across much of their range (Pocewicz et al. 2009). Finally, in Wyoming's xeric prairie, the sparsely vegetated habitat used by ground-nesting birds extends to the edges of the gravel turbine pads and can include the turbine pads themselves (A. Mahoney

TABLE 1. Age, size, and number of turbines for wind farm study sites in southeastern Wyoming, 2011–2012.

Wind farm	Number of turbines	Area (hectare)	Year constructed
Dunlap Ranch	74	6,295	2009
High Plains/McFadden Ridge	85	4,451	2009
Seven Mile	79	5,665	2008

personal observation). These factors provide an opportunity to assess the influence of wind energy infrastructure on nesting success at a finer-scale than may be possible in other systems where potential nesting substrates are not available in the immediate vicinity of infrastructure.

Our study objective was to examine grassland songbird reproductive success in relation to wind energy development. We quantified a broad suite of reproductive metrics: (1) clutch size, (2) size-adjusted nestling mass, (3) daily nest survival rate, and (4) number of young fledged per successful nesting attempt. We compared the nest success of the 2 most abundant species on our sites, Horned Lark (*Eremophila alpestris*) and McCown's Longspur (*Rhynchophanes mccownii*), on 3 wind farms and 2 undeveloped sites. We modeled nest success within the 3 wind farms with wind energy development and habitat variables. Within wind farms, we considered multiple metrics of wind energy development, including turbine density, proximity to nearest turbine and developed edge, and amount of developed and reclaimed areas, to determine which was most predictive of songbird reproductive success. Combining development and habitat variables allowed us to assess the relative importance of each and to account for variability due to habitat while evaluating the influence of development.

METHODS

Study Area and Site Selection

Study sites were located in the Wyoming Basin Ecoregion in southeastern Wyoming. The Wyoming Basin is an area of transition between prairie grasslands to the east and sagebrush steppe to the west (Chapman et al. 2004). The region is characterized by rolling hills with some rocky ridges. Vegetation varies primarily among mixed-grass prairie, sagebrush steppe, and salt desert shrub habitats based on topography, local soil composition, and precipitation (Shiflet 1994). Our surveys were restricted to shortgrass and mixed-grass prairie habitat, where common plant species included grama and buffalo grasses (*Bouteloua* spp.), sageworts (*Artemisia* spp.), buckwheat (*Eriogonum* spp.), western wheatgrass (*Pascopyrum smithii*), Sandberg's bluegrass (*Poa secunda*), and prairie Junegrass (*Koeleria macrantha*). Elevation ranged from 1,980 to 2,530 m. Livestock grazing is common and widespread in

the Wyoming Basin, and all sites were grazed by cattle using a seasonal rotation grazing system. Sites were a mix of public and private lands. Stocking rates on public lands ranged from 1.6–5.3 ha per animal unit month. Stocking rates on private lands were unavailable but appeared comparable to those on public lands.

In 2011, we selected 2 wind farms, PacifiCorp's Seven Mile Hill (SM) and High Plains/McFadden Ridge (HP) based on the criteria of (1) a minimum of 2 years post-construction to minimize quantifying shorter-term construction-related effects; and (2) presence of grassland habitat. In 2012, we replaced SM with a wind farm with more grassland, PacifiCorp's Dunlap Ranch (DR). Wind farms all used GE 1.5 MW wind turbines, but they varied in age, size, and production capacity (Table 1). Wind farm area was calculated using the boundaries delineated by the facility operator, PacifiCorp, for the turbine build-out at the time of our study. Our preliminary analysis in 2011 of Horned Lark nests indicated a uniformly low survival rate of 6% across the 500 m distance surveyed from wind turbines. We therefore added 2 undeveloped sites in 2012 to estimate avian productivity in areas independent of wind farms and paired these reference sites with HP and DR by calculating the range of values for a suite of geographic and ecological parameters across each wind farm using ArcGIS 10 (ESRI 2011; Appendix Table 6). We generated a list of locations within 32 km of each wind farm with parameter values that fell within the range of values observed for each wind farm. The list of locations was reduced by eliminating areas on private property and those <25 ha. To maintain independence between sites, we eliminated locations closer than 5 km to one another based on the largest average home range of a terrestrial nest predator in our system (coyote [*Canis latrans*]; Mills and Knowlton 1991). We selected two 26 ha reference sites, Control-High Plains (CHP) and Control-Dunlap Ranch (CDR), at random from the remaining candidate sites.

Nest Monitoring

We conducted nest searching and monitoring during May–July 2011 at HP and SM and May–July 2012 at HP, DR, CHP, and CDR. Nest searching effort was standardized between wind farms and reference sites. Reference sites were searched in their entirety. At wind farms, areas of grassland habitat were surveyed by walking 500 m transects perpendicular to strings of turbines. Nest searching was conducted primarily by rope-dragging, which entailed pulling a 30 m rope along the ground between 2 individuals walking parallel to one another, as well as haphazard and systematic walking and behavioral observations (Winter et al. 2003). Incubating or brooding birds were flushed from the nest due to the disturbance caused by the approaching rope and/or searchers. Nest locations were recorded using a GPS unit (± 4 m

accuracy; Garmin Etrex Venture HC, Garmin, Olathe, KS). Nests were flagged in a random direction by placing a surveyor pin flag and a small spot of spray paint on the ground at 10 and 30 m from the nest (Johnson 2010). Nests were visited every 1–4 days until nests failed or fledged. We concluded that fledging occurred if we observed (1) fledglings of appropriate age nearby; (2) adults with food <10 m from the nest; (3) fecal material on the rim of the nest; or (4) nestlings present within 2 days of fledging age. Nests that fledged one or more young were considered successful (Martin and Geupel 1993). Categorizing nests with nestlings present within 2 days of fledging as successful may result in higher estimates of nest success and number of fledglings than nests visited more frequently. Because we applied the same approach across our study area, however, we expected no systemic bias in comparing nest success or number of fledglings within our study.

Reproductive Metrics

Clutch size can reflect maternal effects (e.g., female quality and investment) and local environmental conditions, such as food availability and predation risk (Zanette et al. 2011, Sofaer et al. 2013, Hua et al. 2014). We recorded the clutch size for all nests observed during the incubation stage on 2 or more consecutive visits. Nestling mass can be positively correlated with post-fledging survival (Suedkamp Wells et al. 2007, Greño et al. 2008, Schwagmeyer and Mock 2008), and mass can also represent parental efforts in nestling provisioning (Zanette et al. 2011). Nestling mass is determined in part by genetics, however, with larger parents producing larger offspring (Garnett 1981). We isolated environmental effects by evaluating mass adjusted for structural size, henceforth called size-adjusted nestling mass. We measured nestling mass, tarsus length, and wing chord. Variability was minimized during this period of rapid growth by measuring broods on the day before pin-break between 1030 and 1330 hr. Based on nests with known hatch and pin-break dates, Horned Lark (4.02 ± 0.04 days [mean \pm SE], $n = 21$) and McCown's Longspur ($4.00 \pm <0.01$ days, $n = 9$) pin-break seems to be a reasonable proxy for age. We estimated the ages of broods with unknown hatch date by comparing feather development with that of known-age broods. Brood age was determined based on the most-developed nestling. Tarsus length and wing chord were measured using digital calipers (to 0.1 mm). Mass (to 0.01 g) was measured using an ABCplus Series digital scale (Adam Equipment Co., Dansbury, Connecticut).

Few nests failed due to causes other than predation, so we limited analysis of the daily survival rate of nests to those nests that either survived or failed due to predation. We estimated the number of young fledged from successful nests as the number of nestlings recorded in

the nest within 2 days of fledging (Martin and Geupel 1993).

Nest Site-Scale Habitat Metrics

To account for potential effects of microhabitat on reproductive success, we measured vegetative habitat characteristics within a 5 m radius of each nest that previous studies found to be associated with grassland bird habitat selection (Fisher and Davis 2010) and/or nesting success (Winter et al. 2005). After the completion of each nesting attempt, a modified 50×30 cm Daubenmire quadrat (Daubenmire 1959) was placed over the nest and 5 m from the nest in each of the cardinal directions. At each sampling point (north, south, east, west, center), we estimated vegetation cover, height, and density. We visually estimated percent ground cover to the nearest 5% within each Daubenmire quadrat for the following classes: grass, forb, shrub, standing dead vegetation, litter, and bare ground (adapted from Winter et al. 2000, Best et al. 1997). We combined grass, forb, shrub, and standing dead vegetation to represent total vegetative cover. We recorded height by visually estimating the height at which 80% of vegetation was growing below and then measured that height using a ruler (Stewart et al. 2001, Fisher and Davis 2010). We recorded relative vegetation density at the center of each Daubenmire quadrat as the number times that vegetation touched a Wiens pole (Wiens 1969) within 10 cm height increments. Because our vegetation was relatively short, we recorded null vegetation density values at heights above 20 cm for the vast majority of nests and therefore used estimates of vegetation density for the first 2 height increments, 0–10 cm and 10–20 cm, in the analyses. We averaged the values of cover, height, and density across the 5 sampling points for each nest.

Neighborhood-Scale Habitat Metrics

Habitat composition and configuration at scales greater than an individual breeding territory have been predictive of nest success for some grassland species (Greenwood et al. 1995, Herkert et al. 2003, Skagen et al. 2005, but see Winter et al. 2005). We defined an area ~ 3 times the size of a large territory as a neighborhood. Based on previously reported territory sizes of Horned Lark and McCown's Longspur in similar habitat in Wyoming and Colorado, we estimated a neighborhood of 4.8 ha (Beason 1995, With 2010). We delineated the neighborhood of each nest using a 124 m radius circular buffer and digitized the land cover within this area at a 1:3,000 scale using Bing Aerial Maps (available through ArcGIS Online). We designated 6 land cover classes: grassland, shrubland, riparian vegetation, developed, reclaimed grassland, and water/ephemeral water. We considered land to be developed if it consisted of a maintained surface (e.g., gravel roads were categorized as developed but unmaintained 2-tracks were not). We

classified areas that underwent grading, contouring, and reseeding after construction disturbance as reclaimed grassland. Using this land cover layer, we calculated grassland area, the density of grassland edge, and distance to nearest shrubby edge in each neighborhood using ArcGIS 10 and Fragstats 4 (McGarigal et al. 2012).

Wind Energy Development Metrics

We quantified wind energy development for each nest using a variety of metrics: (1) turbine density within 500 m, 1 km, 2 km, and 5 km; (2) distance to nearest turbine; (3) distance to developed edge; (4) area developed in the neighborhood; and (5) area reclaimed in the neighborhood. We calculated distance to nearest turbine and turbine density using 2010 Federal Aviation Administration turbine locations for the state of Wyoming (USFWS 2011). We estimated the distance to the nearest developed edge, amount of developed surface area, and amount of reclaimed surface area in the neighborhood of each nest using our digitized land cover layer in ArcGIS 10.

Statistical Analyses

Size-adjusted nestling mass. We followed the approach described by Coslovsky and Richner (2011) to create a measure of nestling size based on morphological measurements. We used the first principal component generated by a principal component analysis of wing chord and tarsus length to represent size and then regressed nestling mass against this measure of size. The residuals of this linear regression represent a nestling's mass relative to the average mass of all nestlings for its size. Size-adjusted nestling mass values are scaled so that 0 represents the average value, such that nestlings with negative size-adjusted mass values are underweight relative to others of their size.

Daily nest survival rate. We estimated daily nest survival rates as a function of energy development and habitat metrics using the nest survival module in RMark (Dinsmore et al. 2002, Laake 2013). RMark acts as an interface with program MARK (White and Burnham 1999) and uses a generalized linear model with logit-link function and binomial errors to evaluate the probability of daily nest survival with covariates and ranks models using Akaike's Information Criterion for small sample size (AIC_c; Burnham and Anderson 2002).

Year. We examined differences in nest success between years using data from HP, the wind farm site surveyed in 2011 and 2012. We randomized the data with 1,000 replications (Manly 2006) to test for a difference in means between years for clutch size, size-adjusted nestling mass, and number of fledglings. We selected this resampling approach because our data were not normally distributed, had unequal variance, and sample sizes were relatively small. When there was no evidence of a difference between

years ($P > 0.05$), or nest sample sizes were too small to permit testing ($n < 8$ nests), we combined data across years.

Wind farm vs. reference sites. Due to small sample sizes (Appendix Table 7), we pooled nests across sites into 2 groups: wind farm (Horned Lark $n = 118$; McCown's Longspur $n = 40$) or reference (Horned Lark $n = 22$; McCown's Longspur $n = 31$). We used a one-tailed randomization test with 1,000 randomizations of the data and an alpha level of $P < 0.05$ to assess whether the mean clutch size or fledgling count per nesting attempt was lower at wind farms than reference sites. To assess size-adjusted nestling mass between wind farm and reference groups, we compared estimated mean and standard error values. We estimated the values using a linear mixed effects model with treatment as the fixed effect and nest as the random effect to account for relatedness of nestlings within a given nest. This and all subsequent modeling was conducted in R 3.0 (R Core Team 2014). To assess whether nest survival was lower at wind farms than reference sites, we pooled nests into wind farm or reference groups. We estimated the mean daily survival rate and 95% confidence interval (CI) for each group (wind farm, reference) using the constant nest survival model in RMark.

Within wind farms. We modeled patterns in grassland bird reproductive success within wind farms as a function of wind energy development, nest site habitat, and neighborhood habitat metrics (Appendix Table 8). Because nest survival may be influenced by different factors across spatial scales (Chalfoun and Schmidt 2012), we utilized a hierarchical approach to model selection. We ranked models within each group of predictors (wind energy, nest site habitat, and neighborhood habitat) using AIC_c. Only uncorrelated predictors (Spearman's rank-order correlation $r_s < 0.5$) were included in a single model. Correlated predictors varied by the response metric being evaluated, yielding different model sets for each response metric (Appendix Table 8). We ranked the models of turbine density at varying radii to determine the most-informative scale and included only the top-ranked turbine density model in the wind energy development model set. The set of wind energy development models consisted solely of univariate models so we could assess which measure of development was most informative. Predictor variables describing habitat at the nest site were all measures of concealment. We hypothesized that responses to different measures of concealment were more likely to be represented by additive models rather than interactions among variables. Therefore, the set of nest habitat models consisted of univariate models and all possible additive models. We hypothesized that the influence of neighborhood habitat predictors could be additive or interactive, so the set of neighborhood habitat models consisted of

TABLE 2. Sample size, mean, and standard error of nest success metrics for Horned Lark and McCown's Longspur on wind farms and undeveloped reference sites in southeastern Wyoming in 2011 and 2012. The sampling unit of clutch size, daily nest survival rate, and number of fledglings (per successful nest) are nests. Nestling and nest sample sizes are given for size-adjusted nestling mass.

		Horned Lark			McCown's Longspur		
		<i>n</i>	Mean	SE	<i>n</i>	Mean	SE
Wind farm	Clutch size	68	2.9	0.1	28	3.4	0.2
	Size-adjusted nestling mass	131 (52 nests)	0.03	0.1	60 (22 nests)	-0.07	0.16
	Daily nest survival rate	93	0.961	0.01	37	0.961	0.009
	Number of fledglings	51	2.4	0.1	19	2.4	0.2
Reference	Clutch size	14	2.9	0.2	22	3.5	0.1
	Size-adjusted nestling mass	24 (11)	-0.11	0.23	34 (13)	0.18	0.22
	Daily nest survival rate	20	0.94	0.02	30	0.939	0.014
	Number of fledglings	8	1.9	0.2	14	2.5	0.3

univariate models and all biologically plausible additive and interaction models.

The top-ranked model from each group was retained to create a final model set consisting of a nest initiation date model that acted as a biologically relevant null model, the highest-ranked development, nest and neighborhood habitat models, and all possible uncorrelated combinations thereof. This model set allowed us to assess the relative predictive power of each group of variables, and, in models that included habitat and development metrics, to assess the influence of development while accounting for habitat. We grouped data across wind farm sites due to limited sample sizes (Appendix Table 7). We used generalized linear models with a Poisson distribution to model clutch size and number of fledglings as a function of development and habitat metrics. No models showed evidence of overdispersion ($P < 0.05$; using the dispersiontest function in package AER; Kleiber and Zeileis 2008). We modeled daily nest survival rate as a function of development and habitat metrics using nest survival models in RMark. We modeled size-adjusted nestling mass using linear mixed-effects models with a Gaussian distribution. Nest was a random effect to account for the relatedness of nestlings from the same nest, and fixed effects were development and habitat predictor metrics.

RESULTS

We monitored 63 Horned Lark and 29 McCown's Longspur nests in 2011 and 77 Horned Lark and 42 McCown's Longspur nests in 2012. The earliest nest initiation dates in 2011 for Horned Lark and McCown's Longspur were May 8 and May 29, respectively. The latest nests of the 2011 season were initiated on July 8 for Horned Lark and July 6 for McCown's Longspur. Nesting began and ended ~2 weeks earlier in 2012. Nestling phenology correlated with a snowy, cold spring in 2011 and a drier, warmer spring in 2012. We observed no instances of nest parasitism by Brown-headed Cowbirds

(*Molothrus ater*), despite their presence within the study area. Predation was the primary cause of nest failure at our sites, accounting for 96% of all nest losses. Nests ($n = 5$) also failed due to abandonment, trampling by cattle, and unknown causes (likely weather-related), resulting in the death of the brood.

Wind Farm vs. Reference Sites

Horned Lark reproductive success was not lower at wind farms than reference sites as measured by mean clutch size ($P = 0.54$), number of fledglings ($P = 0.98$), size-adjusted nestling mass, and daily nest survival rate (Table 2). A post-hoc examination of the data showed weak evidence of a higher average number of Horned Lark fledglings per successful nest at wind farms than reference sites (one-tailed randomization test $\bar{x}_{\text{wind-ref}} = 0.5$, $P = 0.06$; Table 2).

No measures of McCown's Longspur reproductive success differed between wind farm and reference sites, including mean clutch size ($P = 0.38$), number of fledglings ($P = 0.42$), size-adjusted nestling mass, and daily nest survival rate (Table 2).

Within Wind Farms

Nests were located across a range of observed values for development, nest-site, and neighborhood-scale habitat characteristics, with Horned Lark tending to nest closer to turbines and developed edges and in areas with higher amounts of developed and reclaimed surfaces than McCown's Longspur (Table 3). The best-supported models of nest success (those within 2 AIC_c units of the top model) varied by species and response variable (Table 4 and 5). Many of the top-ranked models, however, did not predict a directional response in nest success, with 95% CIs of the slope that crossed zero. Additionally, many of the top-ranked models were uninformative, with AIC_c scores within 2 units of the top-ranked model resulting from the addition of an uninformative predictor to the top-ranked model (Arnold 2010). Henceforth, we report only informative models that were positively or negatively related to

TABLE 3. Mean \pm standard error and ranges of predictor variables for nests within 500 m of a turbine in southeastern Wyoming, 2011–2012.

Category	Nest success predictor variable	Horned Lark		McCown's Longspur	
		Mean \pm SE	Range	Mean \pm SE	Range
Development	Distance to Turbine (m)	185 \pm 12	4 to 490	264 \pm 20	29 to 490
	Turbine Density (500 m, 1 km, 2 km, 5 km)	26.4 \pm 1.3	1 to 85	26.8 \pm 2.3	1 to 85
	Distance to Developed Edge (m)	130 \pm 11	<1 to 730	188 \pm 20	10 to 504
	Amount of Developed Area (m ² in neighborhood)	1,062 \pm 111	0 to 4,581	570 \pm 171	0 to 3,543
	Amount of Reclaimed Area (m ² in neighborhood)	5,242 \pm 568	0 to 35,234	2,457 \pm 739	0 to 13,370
Nest-site habitat	Veg Density 0–10 cm, 10–20 cm	1.08 \pm 0.08	0 to 5	1.39 \pm 0.18	0 to 6.4
	Veg Cover (%)	38 \pm 1	6 to 68	50 \pm 2	19 to 72
	Veg Height (0.5 cm)	7.8 \pm 0.3	3.3 to 18.6	7.8 \pm 0.40	3.8 to 16.0
Neighborhood habitat	Amount of Grassland Habitat (m ²)	21,286 \pm 1,981	19 to 48,278	29,992 \pm 3,678	385 to 48,305
	Distance to Shrub Edge (m)	133 \pm 15	2 to 537	91 \pm 10	10 to 197
	Edge Density (m/ha)	0.02 \pm 0.001	<0.00 to 0.05	0.02 \pm 0.002	0.00 to 0.04

nest success (see Appendix Table 9 and 10 for the slope and 95% CIs of nest success estimated by each model of wind energy infrastructure).

Patterns of Horned Lark clutch size and number of fledglings were not related to any development, nest-site habitat, or neighborhood habitat characteristics. Horned Lark size-adjusted nestling mass was weakly negatively related to turbine density within a 5 km radius of the nest ($\beta = -0.02$; 95% CI: $-0.038, -0.002$; Figure 1). The top-ranked model for nest survival of Horned Lark nests within each model set (development, nest-site habitat, and

neighborhood habitat) was consistent in both 2011 and 2012 turbine density within 2 km of the nest, nest-site vegetation height, and distance to nearest shrubby edge. However, the ranking and predictive power in the final model set that combined these variables differed between years. In 2011, Horned Lark daily nest survival was negatively related to turbine density within a 2 km radius ($\beta = -0.06$; 95% CI: $-0.12, < -0.00$; Figure 2). The probability of a nest surviving the entire nesting period (~ 20 days) ranged from 0.74 at turbine density of 10 to 0.21 at turbine density of 39. In 2012, however, turbine

TABLE 4. Best-supported models ($\Delta AIC_c < 2.00$) of nest success for Horned Lark at wind farms in southeastern Wyoming, 2011–2012, ranked based on the difference from the top model in Akaike's Criterion corrected for small sample size (ΔAIC_c). K is the number of parameters, and w_i is the model weight. The AIC_c values of the top model for each metric of nest success were: Clutch size = 194.29; Size-adjusted nestling mass = 284.48; Daily nest survival rate in 2011 = 153.90; Daily nest survival rate in 2012 = 102.38; Number of fledglings = 147.71.

Nest success metric	Model	ΔAIC_c	K	w_i	
Clutch size	Veg Density 10–20 cm	0	2	0.28	
	Reclaimed Area	0.46	2	0.23	
	Distance to Shrub Edge	1.35	2	0.14	
	Nest Initiation Date	1.4	2	0.14	
Size-adjusted nestling mass	Turbine Density 5 km	0	4	0.62	
	Turbine Density 2 km	0	2	0.24	
Daily nest survival (2011)	Turbine Density 2 km * Veg Height	1.25	4	0.17	
	Turbine Dens 2 km + Veg Height + Dist to Shrub	1.92	4	0.12	
	Turbine Dens 2 km + Veg Height + Dist to Shrub	0	4	0.2	
Daily nest survival (2012)	Veg Height	0.36	2	0.17	
	Turbine Density 2 km * Veg Height	0.77	4	0.14	
	Constant Survival (null model)	0.85	1	0.13	
	Distance to Shrub Edge	1.43	2	0.1	
	Turbine Density 2 km	1.58	2	0.09	
	Nest Initiation Date	2	2	0.07	
	Number of fledglings	Turbine Density 2 km	0	2	0.27
		Vegetation Cover	0.25	2	0.24
Nest Initiation Date		0.47	2	0.21	
Distance to Shrub Edge		0.48	2	0.21	

TABLE 5. Best-supported models ($\Delta AIC_c < 2.00$) of McCown's Longspur nest success within wind farms in southeastern Wyoming, 2011–2012. Shown are models with the number of parameters (K) and their Akaike model weight (w_i). The AIC_c value of the top model for each nest success metric were: Clutch size = 94.72; Size-adjusted nestling mass = 148.52; Daily nest survival rate = 125.12; Number of fledglings = 61.51.

Nest success metric	Model	ΔAIC_c	K	w_i
Clutch size	Turbine Density 5 km	0.00	2	0.26
	Grassland Area	0.38	2	0.22
	Vegetation Density 10–20 cm	0.50	2	0.20
	Nest Initiation Date	0.54	2	0.20
Size-adjusted nestling mass	Grassland Edge Density	0.00	4	0.20
	Turbine Density 500 m	0.04	4	0.20
Daily nest survival	Turbine Dens 1 km + Veg Dens 10–20 cm + Grassland Area	0.00	4	0.22
	Veg Density 10–20 cm	0.31	2	0.19
	Turbine Density 1 km * Veg Density 10–20 cm	1.16	4	0.12
	Turbine Density 1 km	1.23	2	0.12
	Veg Density 10–20 cm * Grassland Area	1.47	4	0.11
	Nest Initiation Date	1.51	1	0.10
Number of fledglings	Veg Density 10–20 cm	0.00	2	0.29
	Amount of Developed Area	0.56	2	0.22
	Grassland Edge Density	0.64	2	0.21
	Nest Initiation Date	1.12	2	0.16

density within a 2 km radius (8 to 28 turbines in the areas surveyed) alone was not predictive of nest survival ($\beta = -0.06$; 95% CI: $-0.16, 0.04$). Instead, the highest ranked model of nest survival was the additive model of turbine density within 2 km, vegetation height, and distance to shrub edge. In this additive model, the confidence intervals of the slopes crossed zero for the turbine density and distance to shrub edge predictors, but vegetation height was positively related to nest survival when the other terms were present ($\beta = 0.27$; 95% CI: 0.01, 0.53).

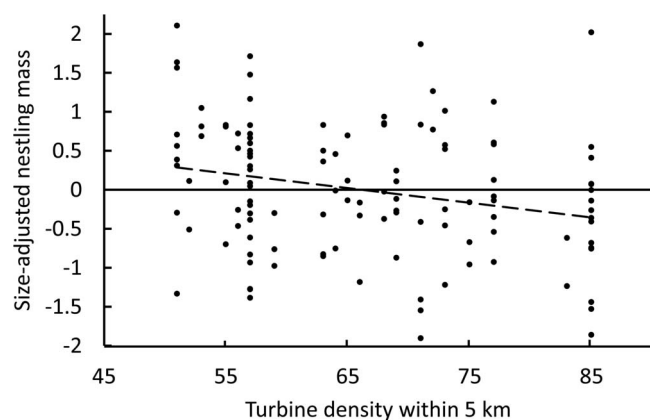


FIGURE 1. Horned Lark size-adjusted nestling mass in relation to the density of turbines within a 5 km radius of the nest on wind farms in southeastern Wyoming, 2011–2012. Points represent nestlings and the dashed line represents the predicted relationship based on a general linear mixed model with turbine density as the fixed effect and nest as a random effect to account for relatedness of nestlings within a given nest. The average size-adjusted mass for a given size is scaled to 0, so nestlings represented by points >0 were heavy for their size, and those <0 were light given their size.

McCown's Longspur clutch size, size-adjusted nestling mass, and number of fledglings were not described well by our development, nest-site habitat, or neighborhood habitat models, with 95% CIs of the slopes of all top-ranked models crossing zero and low R^2 values ($<20\%$). McCown's Longspur nest survival rates were best predicted by an additive model of turbine density within 1 km, vegetation density, and grassland area. The 95% CIs of the slope estimates of turbine density and grassland area both crossed zero, whereas vegetation density was negatively related to daily nest survival when the other terms were considered ($\beta = -1.02$; 95% CI: $-1.90, -0.14$). The univariate model of vegetation density at 10–20 cm height

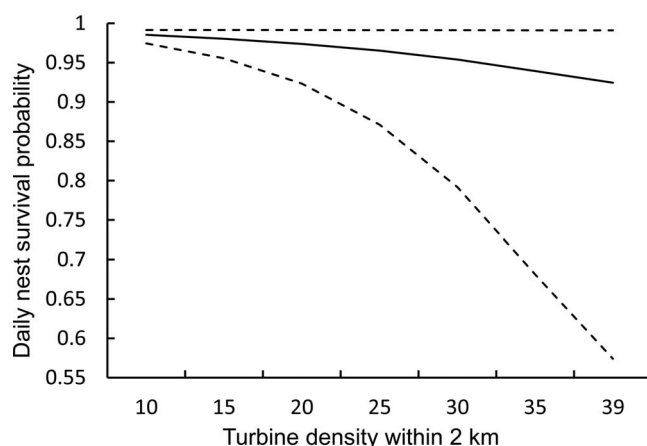


FIGURE 2. The probability of daily survival of Horned Lark nests on wind farms in southeastern Wyoming in 2011 decreased with wind turbine density within a 2 km radius, as modeled using nest survival models in RMark. Dashed lines represent 95% confidence intervals.

was also well supported, with a similar weakly negative pattern of daily nest survival with increasing vegetation density ($\beta = -0.83$; 95% CI: $-1.64, -0.01$).

DISCUSSION

In addition to direct mortality, the alteration of habitat for wind energy could indirectly affect songbird reproductive fitness via multiple pathways, including predation risk and food availability. We found that wind turbine density at broad scales (1–5 km) was more predictive of nesting productivity than any other measure of wind energy development. The size-adjusted nestling mass and, in 2011, the nest survival of Horned Lark decreased as turbine densities increased. The nest survival of McCown's Longspur decreased with increasing density of vegetation when considered together with turbine density and the amount of grassland habitat in the neighborhood of the nest. No measures of wind energy development predicted patterns in clutch size and number of fledglings of either species, however, or the size-adjusted nestling mass of McCown's Longspur. Given the expansion of wind energy development, identifying concomitant patterns of reproductive success will be necessary to accurately assess potential threats to local wildlife populations, particularly for species such as songbirds whose population growth rates can be strongly influenced by reproductive rates (Stahl and Oli 2006).

We found no evidence of lower reproductive success for either species at the coarse-scale comparison of wind farms to reference sites. Unexpectedly, the mean number of Horned Lark fledglings per successful nest attempt at wind farms was slightly higher, averaging 1 additional fledgling for every 2 nests. Although variation in predation, behavior, and micro-environmental conditions could benefit the survival of eggs or young at wind farms, we offer the caveat that, due to logistical constraints, our comparison was limited to 3 wind farms and 2 reference sites and may not be representative of other sites or years.

Horned Lark size-adjusted nestling mass and 2011 rates of nest survival decreased with wind turbine density at broader scales, within 5 km and 2 km of nests, respectively. Spatial patterns in nestling mass and nest survival can be driven by many factors, including predation risk, food availability, and parental behaviors (Naef-Daenzer et al. 2000, Ostfeld and Keesing 2000, Zanette et al. 2000, 2011, Frid and Dill 2002, Massaro et al. 2008). Areas of high turbine density may be risky for birds because rodent species that depredate nests are often more abundant near energy development and roads (Adams and Geis 1983, Rytwinski and Fahrig 2007, Abernethy 2011, Hethcoat and Chalfoun 2015). We therefore expected reduced nest survival near turbines, but personnel at the wind farms in our study combatted rodent infestations by setting traps

at the bases of turbines (R. Brown personal communication), likely reducing the number of mice and therefore the probability that increased predation rates would be observed in relation to turbine proximity. Future assessments of wildlife responses to turbine proximity should attempt to account for such management actions.

For Horned Lark, the strength of the relationship between turbine density and nest survival varied between years. Annual differences in nest survival can occur in ecosystems with variable rodent populations and diverse predators, particularly given pulsed resources associated with fluctuating weather conditions (Ostfeld and Keesing 2000), such as those we observed between the 2 years of this study. Although identification of nest predators was not a goal of our study, we anecdotally observed a broad suite of potential predators, including chipmunks, ground squirrels, swift fox (*Vulpes velox*), coyote, Western Meadowlark (*Sturnella neglecta*), and raptors such as American Kestrel (*Falco sparverius*).

Food availability can also directly influence nestling mass (Naef-Daenzer et al. 2000, Zanette et al. 2000) and indirectly affect nest survival (Ostfeld and Keesing 2000). For example, invertebrates, the primary food source of nestlings, could be affected by the introduction of invasive plants often associated with disturbance (Samways et al. 1996, Gerber et al. 2008). Any one or combination of changes in risk or food availability could account for reduced nestling mass, nest survival, and annual variation in nest survival.

Nest survival of McCown's Longspur decreased with increasing vegetation density at 10–20 cm height, particularly when considered with turbine density within 1 km and the amount of grassland habitat within the neighborhood of the nest. Increased vegetation density would seem to provide more concealment to nests, conferring greater protection from predation (Martin 1993). However, higher vegetation density has been correlated with increased nest predation in grasslands by small mammals (Dion et al. 2000) that may use areas of higher vegetation density for cover, food resources, or ease of burrowing. Birds, however, may detect and react to predators later in areas with denser vegetation, possibly making nests easier to locate (Lima 1993). We speculate that turbine density could change the magnitude of the response to vegetation density because of the potential to mask signals used by birds to detect danger and the potential for increased activity of nest predators.

To date, some of the observed positive or neutral patterns of reproductive success for birds at wind farms (e.g., Rubenstahl et al. 2012, Hatchett et al. 2013, Gillespie and Dinsmore 2014, McNew et al. 2014) do not mirror those documented with some other types of energy development (Gilbert 2010, Northrup and Wittemyer 2013, Hethcoat and Chalfoun 2015, but see Francis et al.

2011). These findings may be attributable to differences between wind energy and other types of industrial-scale energy development. For instance, the common mono-pole-style tower provides few surfaces suitable for perching or nesting by avian predators, and post-construction vehicle traffic rates on wind farm roads can be far less than those in oil and gas fields. For example, on Dunlap Ranch, each wind turbine is visited 2 times per year for scheduled maintenance (PacifiCorp 2009), whereas active natural gas wells on the Jonah Infill Drilling Project in western Wyoming are visited ~122 times per year for scheduled maintenance (BLM 2006). Additionally, management efforts such as rodent trapping to combat infestation of turbines at the wind farms in our study could reduce the number of nest predators near turbines. Differences such as these may account for variable songbird nesting responses to different types of energy development (Smith and Dwyer 2016).

A comprehensive understanding of avian responses to the wind energy industry is still lacking. We present evidence that the standard measure of wind energy development, turbine proximity, may not adequately quantify effects of infrastructure. In our study, models with turbine density at scales of 1–5 km were repeatedly the most informative models, suggesting that intensity of development may have a greater influence on songbird productivity than proximity to a single turbine. We propose that future studies consider the inclusion of turbine density as a means of quantifying wind energy development, particularly as regions of high quality wind resources become more developed. Additionally, our research demonstrates annual variation in the effects of infrastructure on avian reproductive success. For example, infrastructure may only have negative consequences during years of high predator abundance or stressful climatic conditions. To isolate temporal environmental variation from development effects and to better assess general trends, longer-term studies that incorporate higher numbers of wind farms and garner higher nest sample sizes are necessary. Finally, our study suggests species-specific responses to wind energy infrastructure in mixed-grass prairie habitat that have not been documented in previous songbird nesting success research in other ecoregions. Regional variation in bird response to wind energy infrastructure may preclude extrapolation across systems.

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APPENDIX

APPENDIX TABLE 6. Parameters used to pair undeveloped sites with wind farm sites in southeastern Wyoming in 2012. USGS: US Geological Survey; WYGISC: Wyoming Geographic Information Science Center; WYNDD: Wyoming Natural Diversity Database; WGFD: Wyoming Game and Fish Department; TNC: The Nature Conservancy; BLM: Bureau of Land Management.

Parameter	Value	Data layer source
Cover type	Grassland	USGS National Land Cover Database 2006 Land Cover for Wyoming 30 m
Elevation	7,000–8,000 ft. (averaged across sites)	WYGISC Digital Elevation Model for Wyoming 90 m
Topographic slope and roughness	Averaged across sites	WYGISC Digital Elevation Model for Wyoming 90 m
Within McCown's Longspur distribution/range	High Probability of Occurrence	WYNDD McCown's Longspur Predicted Distribution Model Map
Minimum distance from wind farm	5 km	Average coyote home range in sagebrush/grassland habitat (Mills and Knowlton 1991)
Anthropogenic surface disturbance	None or 2-tracks	WGFD and TNC Anthropogenic Disturbance for Wyoming 30 m
Minimum size	25 ha	Based on work force capabilities
Landownership	Public	BLM Land ownership for Wyoming at 1:24,000

APPENDIX TABLE 7. Sample sizes of nests in southeastern Wyoming at High Plains (HP), Seven Mile (SM), and Dunlap Ranch (DR) wind farms, and undeveloped reference sites Control-High Plains (CHP) and Control-Dunlap Ranch (CDR) during the 2011 and 2012 nesting season for all reproductive success response metrics by species, year, and site.

Species	Nest success metric	2011		2012			
		HP	SM	HP	DR	CHP	CDR
Horned Lark	Clutch size	37	2	12	16	8	6
	Size-adjusted nestling mass	30	0	14	11	4	7
	Daily nest survival rate	53	2	13	9	5	7
	Number of fledglings	26	1	13	8	2	5
McCown's Longspur	Clutch size	21	0	4	3	21	1
	Size-adjusted nestling mass	16	0	2	4	12	1
	Daily nest survival rate	27	0	4	6	29	1
	Number of fledglings	13	0	2	2	7	1

APPENDIX TABLE 8. Candidate models used to quantify the relationship between nest success metrics of Horned Lark and McCown's Longspur with wind energy development, nest site habitat, and neighborhood habitat predictor variables within 3 wind farms in 2011 and 2012 in mixed-grass prairie in Wyoming. Only uncorrelated (Spearman's rank-order correlation $\rho < 0.5$) variables were included in a single model.

Model Set	Model	Horned Lark Response Metric				McCown's Longspur Response Metric			
		Clutch size	Size-adjusted nestling mass	Nest survival rate	Number of fledglings	Clutch size	Size-adjusted nestling mass	Nest survival rate	Fledge count
Turbine density	Turbine Density 500 m	x	x	x	x	x	x	x	x
	Turbine Density 1 km	x	x	x	x	x	x	x	x
	Turbine Density 2 km	x	x	x	x	x	x	x	x
	Turbine Density 5 km	x	x	x	x	x	x	x	x
Wind Energy Development	Top-ranked Turbine Density Model	x	x	x	x	x	x	x	x
	Distance to Turbine Reclaimed Area	x	x	x	x	x	x	x	x
	Developed Area	x	x	x	x	x	x	x	x
	Distance to Developed Edge	x	x	x	x	x	x	x	x
Nest Site Habitat	Veg Height	x	x	x	x	x	x	x	x
	Veg Cover	x	x	x	x	x	x	x	x
	Veg Density 0–10 cm	x	x	x	x	x	x	x	x
	Veg Density 10–20 cm	x	x	x	x	x	x	x	x
	Veg Height + Veg Cover	x	x	x	x	x	x	x	x
	Veg Height + Veg Density 0–10 cm	x	x		x	x	x		x
	Veg Height + Veg Density 10–20 cm						x		x
	Veg Cover + Veg Density 0–10 cm		x	x		x		x	
	Veg Cover + Veg Density 10–20 cm	x	x	x	x	x	x	x	x
	Veg Density 0–10 cm + Veg Density 10–20 cm	x	x		x	x	x		x
Neighborhood Habitat	Distance to Shrub Edge	x	x	x	x	x	x	x	x
	Grassland Edge Density	x	x	x	x	x	x	x	x
	Grassland Area	x	x	x	x	x	x	x	x
	Dist To Shrub Edge + Grassland Edge Dens			x				x	
	Dist To Shrub Edge + Grassland Area	x	x	x	x	x	x	x	x
	Dist To Shrub Edge + Grassland Area + Dist. To Shrub Edge*Grassland Area	x	x	x	x	x	x	x	x
	Dist To Shrub Edge + Grassland Edge Density + Dist To Shrub Edge*Grassland Edge Density	x	x	x	x	x	x	x	x
Final Model Set	Top-ranked model of each model set and all uncorrelated combinations thereof.								

APPENDIX TABLE 9. Estimates of the slope and 95% confidence interval of measures of nest success for Horned Lark as a function of wind energy development metrics on wind farms in southeastern Wyoming in 2011 and 2012. Only results for the top-ranked model of turbine density for each nest success response variable are shown (clutch size = 500 m, size-adjusted nestling mass = 5 km, nest survival rate 2011 and 2012 = 2 km, number of fledglings = 2 km). Nest survival rates are untransformed estimates using a logit link function.

Wind energy development metric	Horned Lark nest success response metric				
	Clutch size	Size-adjusted nestling mass	Nest survival rate 2011	Nest survival rate 2012	Number of fledglings
Turbine density	0.06 (−0.07, 0.18)	−0.02 (−0.04, −0.003)	−0.059 (−0.115, −0.002)	−0.061 (−0.165, 0.042)	0.01 (−0.01, 0.03)
Distance to turbine	−0.04 (−0.37, 0.31)	0.04 (−0.45, 0.53)	−0.112 (−1.077, 0.852)	0.439 (−0.896, 1.774)	0.11 (−0.37, 0.63)
Reclaimed area	0.00 (−0.00, 0.00)	0.00 (−0.00, 0.00)	0.000 (−0.000, 0.000)	−0.000 (−0.000, 0.000)	0.00 (−0.00, 0.00)
Developed area	0.00 (−0.00, 0.00)	−0.00 (−0.00, 0.00)	−0.000 (−0.000, 0.000)	−0.000 (−0.001, 0.000)	0.00 (−0.00, 0.00)
Distance to developed edge	−0.00 (−0.18, 0.19)	0.17 (−0.12, 0.46)	−0.131 (−0.734, 0.472)	0.185 (−0.417, 0.786)	−0.02 (−0.25, 0.21)

APPENDIX TABLE 10. Estimates of the slope and 95% confidence interval of measures of nest success for McCown's Longspur as a function of wind energy development metrics on wind farms in southeastern Wyoming in 2011 and 2012. Only results for the top-ranked turbine density model for each nest success response variable are shown (clutch size = 5 km, size-adjusted nestling mass = 500 m, nest survival rate = 1 km, number of fledglings = 5 km). Nest survival rates are untransformed estimates using a logit link function, and the nesting period for McCown's Longspur in our study averaged 21 days.

Wind energy development metric	McCown's Longspur nest success response metric			
	Clutch size	Size-adjusted nestling mass	Nest survival rate	Number of fledglings
Turbine density	−0.01 (−0.02, 0.01)	−0.19 (−0.39, 0.04)	0.125 (−0.044, 0.294)	−0.01 (−0.03, 0.02)
Distance to turbine	0.17 (−0.46, 0.85)	0.07 (−1.06, 1.35)	0.155 (−1.394, 1.703)	0.21 (−0.73, 1.26)
Reclaimed area	0.00 (−0.00, 0.00)	0.00 (−0.00, 0.00)	0.000 (−0.000, 0.000)	−0.00 (−0.00, 0.00)
Developed area	0.00 (−0.00, 0.00)	0.00 (−0.00, 0.00)	0.000 (−0.001, 0.001)	−0.00 (−0.00, 0.00)
Distance to developed edge	0.03 (−0.42, 0.52)	−0.22 (−1.03, 0.74)	−0.424 (−1.757, 0.909)	0.23 (−0.49, 1.04)