



Research Article

Columbian Sharp-Tailed Grouse Nesting Ecology: Wind Energy and Habitat

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ABSTRACT The rapid pace of wind-energy development has increased stakeholder concerns regarding the potential effects on wildlife. Locations targeted for wind-energy development frequently overlap prairie grouse and greater sage-grouse (*Centrocercus urophasianus*) habitats. Research suggests that anthropogenic developments may have negative effects on these species. There is, however, no information published regarding the effect of wind-energy development on Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*), a subspecies that has twice been petitioned for Endangered Species Act protection. To address this need, from 2014 to 2015 we studied Columbian sharp-tailed grouse nesting ecology across restored grasslands in eastern Idaho, USA, where a 215-turbine wind-energy complex had been developed. We monitored 147 nests from 135 females captured at leks 0.1–13.8 km from wind turbines. We used an information-theoretic approach to evaluate the influence of wind-energy infrastructure and habitat characteristics on nest-site selection and daily nest survival. We did not detect any influence of wind-energy infrastructure on nest-site selection or nest survival. Nest-site selection and daily nest survival were influenced by vegetation structure and composition measured at 2 spatial scales. Females selected nest sites with more restored grassland containing >30% forb cover within the nesting core-use area (i.e., 60 ha around the nest) and exhibited a functional response to the availability of that land cover type. Daily nest survival was best predicted by visual obstruction at the nest site and the amount of restored grassland containing >30% forb cover within the nesting core-use area. We recommend wildlife managers continue to implement management practices that will provide bunchgrass-dominated grasslands with >30% forb cover in restored grasslands (e.g., Conservation Reserve Program fields) within Columbian sharp-tailed grouse range. © 2019 The Wildlife Society.

KEY WORDS Columbian sharp-tailed grouse, Conservation Reserve Program, habitat, Idaho, nest selection, nest success, *Tympanuchus phasianellus columbianus*, wind energy.

Wind power is one of the fastest growing sources of electricity supply in the United States. In 2015, the Department of Energy predicted wind power could supply 10% of electricity in the United States by 2020, 20% by 2030, and 35% by 2050 (American Wind Energy Association 2015). The pace and projected growth of wind-energy development has increased concern about the potential effects of this renewable energy source on wildlife (Johnson et al. 2016). Recent estimates suggest hundreds of thousands of birds and bats are killed annually by collisions with wind turbines (Loss et al. 2013, Smallwood 2013, Erickson et al. 2014, Johnson et al. 2016). In addition to collision mortalities, wind-energy development may affect wildlife via habitat loss, increased predation, or

avoidance behavior. These indirect effects of wind-energy development have been documented for multiple bird species (Winder et al. 2014, Mahoney and Chalfoun 2016, LeBeau et al. 2017).

Grassland and shrub-steppe landscapes in the United States are increasingly targeted for wind power development because of the quality of wind resources they can provide. Thus, concerns over potential effects on gallinaceous bird species inhabiting these landscapes have increased (Hovick et al. 2014). Gallinaceous species worldwide are already experiencing long-term declines as a result of habitat loss and fragmentation, disease, invasive species, and anthropogenic activities (North American Bird Conservation Initiative, U.S. Committee 2014, Johnson et al. 2016, Dettenmaier et al. 2017). Although collisions between typically low-flying galliforms and turbine blades are unlikely, indirect effects from anthropogenic features related to wind-energy development have been predicted to occur (Kuvlesky et al. 2007, Pruett et al. 2009).

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Much of the research published regarding the responses of grassland and shrub-steppe gallinaceous species to wind development has focused on greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) and greater prairie-chicken (*Tympanuchus cupido pinnatus*) nesting ecology. In Wyoming, USA, LeBeau et al. (2014) concluded that sage-grouse nest-site selection was not influenced by proximity to turbines, but nest survival decreased in habitats closer to turbines. LeBeau et al. (2017), however, concluded that neither nest-site selection nor nest survival was influenced by wind energy in a longer-term study at the same wind-energy facility. McNew et al. (2014) and Harrison et al. (2017) reported that proximity to turbines did not negatively affect greater prairie-chicken nest-site selection or nest survival in fragmented grasslands in Kansas and unfragmented grasslands in Nebraska, USA, respectively.

To date, no published studies have addressed the potential effects of wind-energy development on sharp-tailed grouse (*Tympanuchus phasianellus*). We initiated this study to investigate the potential influence of wind-energy infrastructure on the nesting ecology of Columbian sharp-tailed grouse (*T. p. columbianus*). We chose to examine the relationship between wind-energy development and nesting ecology because sensitivity analyses have suggested that nest survival is an important contributor to population growth in prairie grouse species (Wisdom and Mills 1997, Hagen et al. 2009, Gillette 2014). We also examined nesting ecology because management prescriptions for Columbian sharp-tailed grouse, including federal farm bill program practices, typically focus on nesting habitat.

The Columbian sharp-tailed grouse, 1 of 6 extant subspecies of sharp-tailed grouse found in North America (Johnsgard 1973), is endemic to shrub-steppe, grassland, mountain shrub, and riparian plant communities in western North America (Connelly et al. 1998). The subspecies currently occupies <10% of its historical range and has been petitioned twice for listing under the Endangered Species Act (U.S. Department of the Interior 2000, 2006). Declines in Columbian sharp-tailed grouse populations are attributed to habitat loss resulting from conversion of native land cover types to cropland, overgrazing by livestock, shrub control, altered fire regimes, invasion of exotic plants, and urban and rural development (Hoffman and Thomas 2007). Until recently, energy development affected <1% of the occupied range (Hoffman and Thomas 2007). Recent expansion and projected growth of wind-energy development into the occupied range necessitates a better understanding of the relationship between wind-energy development and Columbian sharp-tailed grouse ecology (Hoffman et al. 2015).

We hypothesized that female Columbian sharp-tailed grouse would avoid wind turbines when selecting nest sites (Pruett et al. 2009), thereby decreasing the availability of nesting habitat. We also hypothesized that nest survival would be lower in habitat closer to wind turbines as a result of habitat fragmentation and subsidization of nest predators (Dijak and Thompson 2000, Chalfoun et al. 2002). Finally, we hypothesized that vegetation features of restored

grasslands in our study system would influence nest-site selection and nest survival (Meints 1991, Boisvert 2002, Collins 2004). Because we hypothesized that female Columbian sharp-tailed grouse may select nest sites for their brood-rearing potential, we also considered habitat variables and spatial scales relevant to brood-rearing.

STUDY AREA

Our study area was located in Bonneville County, eastern Idaho (Fig. 1). Land ownership included Bureau of Land Management, Bureau of Reclamation, Idaho Department of Lands, Idaho Department of Fish and Game (IDFG), and private lands. The study area landscape was characterized by rolling benchlands (i.e., historically sagebrush-covered transition zone between mountains and valleys) intersected by steep-sloped canyons. Elevations ranged from 1,500 to 2,200 m, increasing from north to south in the study area. The 2 most commonly occurring soils were Ririe silt loam and Torriorthents-rock outcrop complex (Natural Resources Conservation Service 2016). Privately owned benchlands were primarily used for agriculture (typically wheat and alfalfa) or were enrolled in the Conservation Reserve Program (CRP). On Tex Creek Wildlife Management Area (TCWMA), a 14,000-ha big game winter range managed by IDFG situated roughly in the center of the study area, historically farmed lands had been converted to perennial vegetation and were similar in composition and structure to CRP fields.

Common native vegetation across the study area included bluebunch wheatgrass (*Pseudoroegneria spicata*), big sagebrush (*Artemisia tridentata* spp.), antelope bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* spp.), serviceberry (*Amelanchier* spp.), snowberry (*Symphoricarpos* spp.), aspen (*Populus tremuloides*), and willow (*Salix* spp.). Vegetation commonly occurring in CRP fields and TCWMA fields included smooth brome (*Bromus inermis*), intermediate wheatgrass (*Thinopyrum intermedium*), crested wheatgrass (*Agropyron cristatum*), bluebunch wheatgrass (*P. spicata*), big bluegrass (*Poa secunda*), basin wild rye (*Leymus cinereus*), cheatgrass (*Bromus tectorum*), small burnet (*Sanguisorba minor*), blue flax (*Linum lewisii*), yarrow (*Achillea millefolium*), alfalfa, sainfoin, and yellow sweet clover. Common game species within the study area included mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), moose (*Alces alces*), Columbian sharp-tailed grouse, ruffed grouse (*Bonasa umbellus*), and gray partridge (*Perdix perdix*). The climate in the region is classified as continental with a long-term mean annual precipitation of 33 cm and temperatures ranging from an average minimum of -11°C in January to an average maximum of 28°C in July (Western Regional Climate Center 2016).

The wind-energy facilities located within the study area included Wolverine Creek Wind Farm, a 64-megawatt (MW) facility consisting of 43, 1.5-MW turbines (completed in 2005); Goshen North Wind Farm, a 64-MW facility consisting of 83, 1.5-MW turbines (completed in 2010); Horse Butte Wind Farm (Phase 1), a 60-MW facility consisting of 32, 1.8-MW turbines (completed in

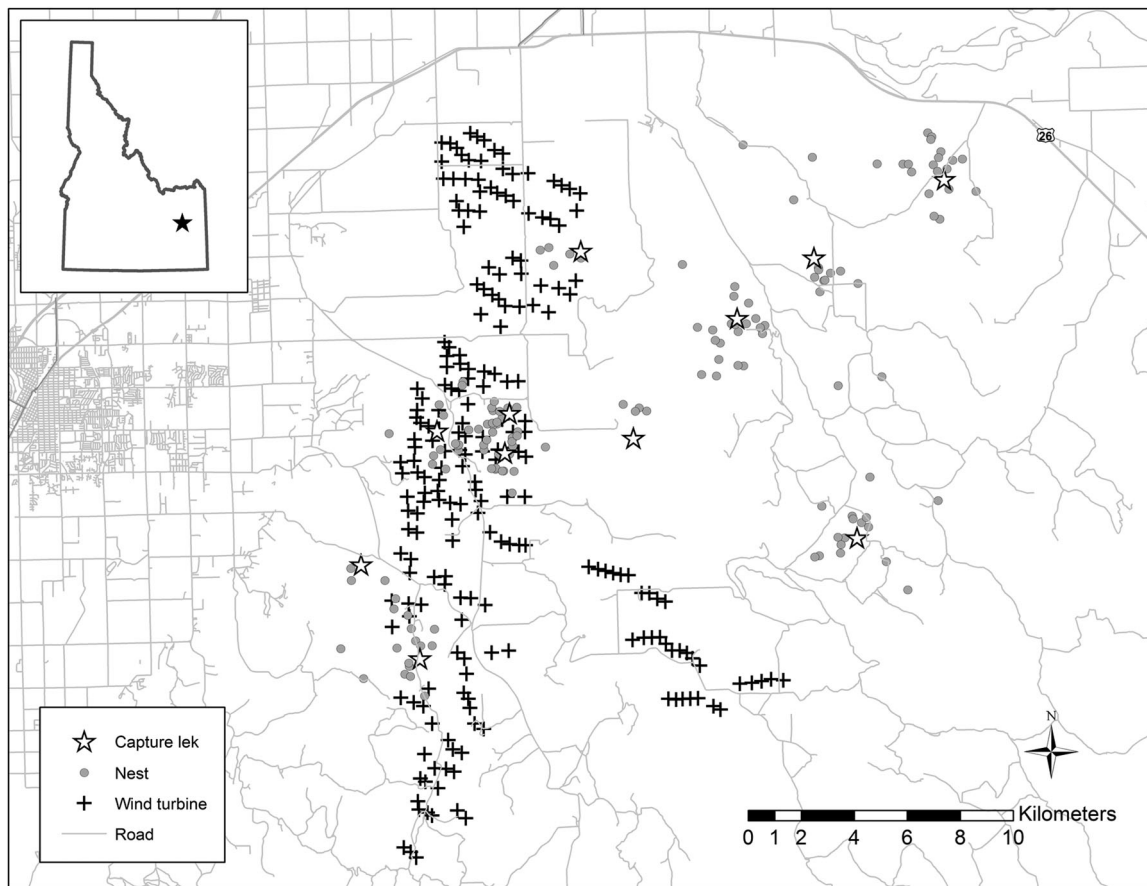


Figure 1. Locations of Columbian sharp-tailed grouse nests ($n = 147$) relative to capture leks ($n = 11$) and wind turbines ($n = 215$) in eastern Idaho, USA, 2014–2015.

2012); and Meadow Creek Wind Farm, a 120-MW facility consisting of 57, 2.1-MW turbines (completed in 2012). Additional wind facility infrastructure included gravel access roads, maintenance buildings, electrical substations, and a small number of overhead transmission lines (most transmission lines within the study area were buried). The wind-energy facilities were developed on leased portions of private land, and excluding turbine pads and associated infrastructure, fields within the turbine complexes were actively farmed or enrolled in the CRP at the time of our study. Wind-developed and undeveloped portions of the study area were a matrix of agriculture and restored grasslands, interspersed with patches of native land cover types. The IDFG documented 39 active Columbian sharp-tailed grouse leks within the study area in 2013 (IDFG, unpublished data), the majority of which were either previously undocumented or not annually monitored.

METHODS

Capture and Monitoring

We captured female Columbian sharp-tailed grouse during March–May of 2014 and 2015 using walk-in traps and drift fences (Schroeder and Braun 1991). We captured females from 11 leks, 7 of which were used for capture in both years of the study. Capture leks were located 0.1–13.8 km

(median = 1.6 km) from wind turbines (Fig. 1). We selected leks based on size (count of ≥ 10 birds the previous year) and proximity to turbines to maximize capture efficiency and disperse our sample of radio-marked females along the 14-km gradient away from wind turbines. We aged captured females (adult vs. yearling) based on shape and wear of outer primaries (Ammann 1944), weighed them to the nearest 5 g, and banded them with uniquely numbered aluminum leg bands. We fitted females with 9-g, necklace-style, very high frequency radio-transmitters equipped with a mortality switch (Model RI-2D, Holohil Systems, Carp, ON, Canada) and released birds at the capture site immediately after processing. Animal capture and handling protocols were approved by the Utah State University Institutional Animal Care and Use Committee (protocol 2286).

We used ground-based telemetry incorporating portable telemetry receivers and handheld Yagi antennas to monitor radio-marked females 2–3 times per week during the nesting period (Apr–Jul). To estimate pre-nesting and early incubation locations, we used a homing method described by White and Garrott (1990), circling females to within 30–50 m, without flushing, to minimize disturbance (Boisvert 2002, Gillette 2014). We recorded the estimated distance and bearing to each female and the observer's coordinates using handheld Garmin eTrex global positioning systems (GPS; Garmin International, Olathe, KS, USA).

We conducted fixed-wing aerial telemetry flights, to locate radio-marked females that we were unable to locate using ground telemetry methods.

When we found a radio-marked female in the same location on consecutive visits, we presumed she had initiated a nest. Using telemetry, we verified the nest location and flushed the female from the nest to obtain a clutch count for analyses in a concurrent study (Proett 2017). After recording the GPS co-ordinates of each nest, we used telemetry to monitor nests 2–3 times per week from >50 m. We monitored nests from a GPS point, rather than using visual markers, and only approached nests on the initial inspection and to determine nest fate when telemetry indicated the female had left the nest. We classified nests as successful if ≥ 1 egg hatched, based on inspection of eggshell remains (Rearden 1951).

Habitat Variables

We measured microsite habitat characteristics at each nest within 3 days of ascertaining nest fate. We recorded visual obstruction readings (VOR) at the nest by placing a Robel pole in the nest bowl and recording concealment in decimeters (dm) from a distance of 4 m and a height of 1 m (Robel et al. 1970). We randomly assigned a bearing for the first reading; obtained 3 additional readings at 90, 180, and 270 degrees from the initial bearing; and averaged measurements across the 4 transects. We measured overhead concealment by placing a 16-cm diameter cover board, which we modified from Roersma (2001), in the nest bowl and estimating percent concealment to the nearest 5% when viewed from 1 m above the nest. We estimated canopy cover of standing grasses (live or residual), forbs, shrubs, litter, and bare ground by averaging 12, 20 \times 50-cm Daubenmire frame readings (Daubenmire 1959). We estimated canopy cover on an overlapping basis, allowing canopy cover to exceed 100%. We read frames at 0, 3, and 6 m from the nest, along transects separated by 90 degrees.

We also evaluated the influence of macrohabitat on Columbian sharp-tailed grouse nesting ecology by quantifying vegetation configuration within 2 larger scales: nesting core-use area (60 ha) and brood-rearing home range (1,385 ha). The nesting core-use area represents the area used by the female during laying and incubation. Habitat characteristics at this scale have been previously reported to influence prairie grouse nesting ecology (Manzer and Hannon 2005, McNew et al. 2014). Because we did not obtain incubation recess locations during our study, we used recess distances of sharp-tailed grouse from Manzer and Hannon (2005) to delineate the 60-ha core-use area of nesting females. The brood-rearing home range represents the area needed for a female to successfully rear a brood (≥ 1 chick alive) to 42 days post-hatch and was developed using nest-to-brood movements of females in this study (Proett 2017). Ninety percent of females that reared a successful brood in this study area did so within 2,100 m of their nest (1,385 ha area). We assessed the importance of habitat features at this scale because we hypothesized that females may also select nest sites for

their potential as brood-rearing habitat. Previous studies of Columbian sharp-tailed grouse nesting ecology have not assessed the effects of habitat measured at this spatial scale.

To account for >415 ha of grassland cover changes between years, primarily resulting from expired CRP field conversions and changes in vegetation associated with CRP mid-management practices, we developed layers of year-specific land cover type for the study area in a geographic information system (ArcGIS 10.3, Environmental Systems Research Institute, Redlands, CA, USA). We used 2013 and 2015 National Agriculture Imagery Program (NAIP) imagery to manually digitize 10 land cover types (agriculture, aspen, restored grasslands, conifer, development, juniper, riparian, roads, sage-steppe, open water) within 5 km of capture leks. We expanded the area digitized, where necessary, to incorporate nest and brood locations that extended >5 km from capture leks. When land cover identification from NAIP imagery was uncertain, we used field observations to verify land cover types. We used United States government open source road data layers (U.S. Census Bureau 2015) to delineate roads and used NAIP imagery to manually digitize roads where the open source road layers were incomplete. We used the 2014 United States Geological Survey onshore wind turbine location data layer for wind turbine locations (Diffendorfer et al. 2015).

We further categorized restored grasslands (primarily CRP and TCWMA fields) with on-the-ground visual assessments of dominant grass type and forb and shrub canopy cover. We used field-based classifications rather than seeding records because seeding records may not have accurately represented the vegetation composition of fields at the time of our study (particularly in the case of older CRP plantings that included rhizomatous grasses). For each unique patch of restored grassland, we classified the dominant grass into one of the following categories: bunchgrass, rhizomatous grass (smooth brome and intermediate wheatgrass), crested wheatgrass, or cheatgrass. We recorded these grass categories to examine the effect of grass structure on Columbian sharp-tailed grouse nesting ecology; they were representative of grass types commonly found in Idaho CRP fields. Next, we recorded visual estimates of forb and shrub canopy cover within each patch. To account for potential error due to visual estimation, we categorized forb and shrub cover estimates for each patch into 1 of 5 bins: <2%, 2–10%, 11–20%, 21–30%, and >30% cover. We manually digitized each unique patch within the restored grassland land cover type using hand-drawn polygons on field maps as reference. We assigned each polygon with forb and shrub cover estimates using the mean value of the assigned bin (e.g., 11–20% = 15%).

Data Analyses

We developed resource selection functions (RSF; Manly et al. 2002) for nesting female CSTG by contrasting measurements of each variable at nest sites (use) and available sites with mixed-effects logistic regression using package lme4 (Bates et al. 2014) in R (R version 3.3.1, www.r-project.org, accessed 1 Jul 2016). We defined available nesting habitat as grassland or sage-steppe with <30% slope

(Hoffman et al. 2015) within 2.7 km of the lek of capture because 90% of nests in this study fell within a 2.7-km radius of the lek of capture. We then generated 1 point/25 ha of available nesting habitat, resulting in 31–75 available points within each 2.7-km lek buffer. To ensure we had a spatially balanced description of availability, we generated available points using the generalized random tessellation stratified sampling (GRTS) scheme in the package *spsurvey* (Kincaid and Olsen 2016) in R. To account for changes in available nesting habitat between years, and because availability of nesting habitat was constrained by lek of capture, we fit a random lek-year intercept in all models. To avoid multicollinearity, we did not include correlated variables ($|r| \geq 0.65$) in the same model and used Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) to determine which correlated variable moved forward in the following model building process. We considered the most parsimonious model within 2 AIC_c units of the model with the lowest AIC_c score to be our best model for inference. Additionally, we considered more complex models that were within 2 AIC_c of the best model, and included all variables from the best model, to be uninformative and not competitive (because in such cases the inclusion of extra variables leads to a detriment in AIC_c rather than an improvement; Arnold 2010).

We employed a multi-step approach to build and evaluate candidate RSF models with macrohabitat and wind-energy variables (Table 1). In step I, we evaluated univariate models containing each habitat variable measured within each of the 2 macrohabitat scales. If a model performed $\geq 2 AIC_c$ units better than the intercept-only model, we considered the variable to have some support, and included it in our candidate univariate model set. If a variable was supported at both spatial scales, we used AIC_c to select the best spatial

scale for that variable and moved only that scale forward in the process. To determine our best habitat model in step II, we compared the univariate candidate model set with a set of additive models constructed from all non-correlated combinations of variables contained in the univariate candidate model set. To assess the influence of wind-energy development in step III, we compared the best habitat model to a set of models adding each wind turbine density variable to the best habitat model and to univariate wind turbine density models (Dinsmore et al. 2002, Webb et al. 2012). Step IV in our process compared the top model from step III to a generalized functional response model (GFR; Matthiopoulos et al. 2011) containing different parameterizations of all variables from our step III top model. The GFR model we evaluated (model O1 in Matthiopoulos et al. 2011) used a random lek-year intercept and interactions between the variable of interest and its availability within the focal area surrounding leks to evaluate whether nest-site selection was a linear function of the availability of the variable. We conducted the GFR comparison as the last modeling step in our process to make our nest-site selection results as applicable as possible to other restored grassland landscapes that likely have varying habitat configurations.

We evaluated the predictive ability of the fixed effects in our best model from step IV with leave-one-out cross validation. In this process, we held out 1 data point, constructed the fixed-effects model using the remaining data points, and used the resulting model coefficients to predict the relative probability of selection for the left-out data point. This process proceeded iteratively until each point (nest sites and available locations) had been left out and predicted. We then sorted the relative probability of selection values for the available locations from lowest to

Table 1. Predictor variables used to model nest-site selection and daily nest survival of Columbian sharp-tailed grouse, eastern Idaho, USA, 2014–2015.

Variable	Description	Scale ^a	Analysis ^b
Habitat			
VOR	Visual obstruction at 4 m from nest (dm)	M	DNS
Over	Overhead concealment 1 m above nest (%)	M	DNS
Grass	Total live and residual grass canopy cover (%)	M	DNS
Bunch_m	Bunchgrass canopy cover (%)	M	DNS
Crest_m	Crested wheatgrass canopy cover (%)	M	DNS
Rhizo_m	Rhizomatous grass canopy cover (%)	M	DNS
Forb	Forb canopy cover (%)	M	DNS
Shrub	Shrub canopy cover (%)	M	DNS
Litter	Litter (%)	M	DNS
Bare	Bare ground (%)	M	DNS
Bunch	Restored grassland dominated by bunchgrass (ha)	CU, HR	Both
Crest	Restored grassland dominated by crested wheatgrass (ha)	CU, HR	Both
Rhizo	Restored grassland dominated by rhizomatous grass (ha)	CU, HR	Both
Forb < 2	Restored grassland with < 2% forb cover (ha)	CU, HR	Both
Forb > 30	Restored grassland with > 30% forb cover (ha)	CU, HR	Both
Shrub > 2	Restored grassland with > 2% shrub cover (ha)	CU, HR	Both
Roads	Road density (ha)	CU, HR	Both
Wind energy			
Turb_dist	Distance to turbine (m)	N/A	DNS
Turb_dens	Number of turbines within respective scale buffer	CU, HR	Both

^a M = microsite (6-m radius); CU = core-use area (437-m radius); HR = brood-rearing home range (2,100-m radius).

^b DNS = variable used in daily nest survival analysis only; both = variable used in daily nest survival and nest-site selection analyses.

highest and grouped them into 10 ranked bins, with approximately equal number of available locations in each bin ($n = 107$). We then recorded the number of nests with relative probability of selection values falling into each bin and compared bin rank and nest frequency with a Spearman's rank correlation coefficient (r_s). Models with good predictive ability would have a strong positive correlation between bin rank and nest frequency (i.e., $r_s > 0.6$; Boyce et al. 2002).

We employed a similar multi-step approach to assess the influence of habitat features and wind-energy development on daily nest survival (DNS). We estimated the effects of explanatory variables on DNS using generalized linear models in the RMark package (Laake 2014) for R, which implements Program MARK (White and Burnham 1999). In addition to the variables used in our nest-site selection analysis, we also considered the effects of microsite habitat variables and an additional wind-energy variable (distance to wind turbine [m]; Table 1). Because many radio-marked females in our study likely never interacted with a wind turbine during the breeding season, we felt turbine density was more appropriate than distance to turbine for nest-site selection analyses (i.e., directional movements by birds inhabiting the portion of the study area without turbines could have been misinterpreted as avoidance or attraction to turbines). Conversely, some nest predators are capable of moving large distances and their density may be related to anthropogenic disturbance (e.g., corvids), so the inclusion of a distance to turbine variable made biological sense for the DNS analysis.

Before initiating the stepwise approach, we explored both linear and quadratic relationships between microsite habitat variables and DNS and used AIC_c to select the best form for each microsite habitat variable. The only other deviation from the previously described model building and selection process was the addition of a comparison of a model allowing annual variation in DNS to a null model (Step I for this process). If the annual variation model outperformed the null model, an annual variation term would be included in all ensuing models.

The initial steps in our hierarchical model building process allowed us to examine the influence of habitat variables related to the composition and structure of vegetation typically found in CRP plantings in eastern Idaho. To avoid data dredging, we chose to identify the best measurement scale for each variable and then identify the top performing multi-scale habitat model constructed from variables that had some univariate support. Our final steps allowed us to examine the relative importance of wind-energy variables while accounting for the variation in nest-site selection or DNS explained by the vegetation composition and structure that occurred within the landscape. We acknowledge that a statistically superior model could be identified by considering all possible covariate combinations (Bromaghin et al. 2013) but given the tendency of AIC_c to favor models with spurious effects (Aho et al. 2014), we opted for this more ecologically based and parsimonious approach to model building and selection (Franklin et al. 2000).

RESULTS

We radio-marked 135 Columbian sharp-tailed grouse females and monitored 147 nests (119 first nests and 28 renests) during 2014 and 2015. Fifty-two percent of nests were located under grass, 27% were located under forbs, and 21% were located under shrubs. Apparent nest success (i.e., the number of successful nests divided by the total number found) for the 2-year study period was 46% (45% for first nests and 50% for renests). We included nests of females that were killed while incubating ($n = 6$) in our nest survival analyses as failed nests. We censored all renests ($n = 28$) and 2015 nest attempts of females radio-marked in 2014 ($n = 12$) from our nest-site selection analyses because it was unknown if they returned to and bred at the lek of capture.

Nest-Site Selection

We used 107 nests in our nest-site selection analyses ($n = 51$ in 2014, $n = 56$ in 2015). The top univariate habitat model was the amount (ha) of restored grassland containing >30% forb cover within the core-use area (Table 2). Also, at the core-use area scale, the amount of restored grassland dominated by bunchgrasses and the amount of restored grassland containing <2% forb cover had support for inclusion in additive habitat models. The amount of restored grassland dominated by bunchgrasses, however, was highly correlated with the amount of restored grassland containing >30% forb cover, so only the forb cover variable moved forward in the model building process. The amount of restored grassland containing >30% forb cover was also the most supported variable measured within the brood-rearing home range and 4 additional variables measured within the brood-rearing home range had support for inclusion in multivariate habitat models. The amount of restored grassland dominated by crested wheatgrass was correlated with the amount of restored grassland containing <2% forb cover within the brood-rearing home range, so only the forb cover variable moved forward in the model building process.

Four models were within 2 AIC_c of the top additive habitat model describing nest-site selection in step II of our model building process. The univariate model of the amount of restored grasslands with > 30% forb cover within the core-use area was among the 4 models and each of the other, more complex models contained that variable. Therefore, we considered the univariate model to be the top model to move forward in the process. In step III of the model building process, the univariate habitat model outperformed all models that contained wind-energy variables. The only additive models that were within 2 AIC_c of the top univariate habitat model contained uninformative wind-energy parameters with 95% confidence intervals on parameter estimates that overlapped 0 (turbine density in core-use area 95% CI = $-0.42-0.08$, turbine density in brood-rearing home range 95% CI = $-0.46-0.30$) and were therefore not considered competitive.

A GFR model with interactions and first-order expectations of the amount of restored grassland with >30% forb

Table 2. Candidate models from each step of our model selection process for resource selection models describing Columbian sharp-tailed grouse nest-site selection, eastern Idaho, USA, 2014–2015. We used Akaike’s Information Criterion with second-order bias correction (AICc) to rank models in 4 steps (step I: models ≥ 2 AICc less than intercept-only model; step II: models ≤ 2 AICc from top model; steps III–IV: all models considered). K = number of parameters, Dev = deviance, Δ AICc = difference in AICc between the model of interest and the top model, and w = Akaike weight.

Step ^a	Group	Model ^{b,c}	K	Dev	AIC _c	Δ AIC _c	w
I	Univariate habitat	Forb > 30_CU	3	697.9	703.9	0.0	0.53
		Bunch_CU ^d	3	698.9	704.9	1.0	0.33
		Forb > 30_HR ^d	3	701.5	707.5	3.6	0.09
		Forb < 2_HR	3	704.7	710.7	6.7	0.02
		Bunch_HR ^d	3	706.3	712.3	8.4	0.01
		Forb < 2_CU ^d	3	706.7	712.7	8.8	0.01
		Crested_HR ^d	3	706.7	712.7	8.8	0.01
		Shrub > 2_HR	3	707.7	713.7	9.8	0.01
II	Multi-scale habitat	Forb > 30_CU + Forb < 2_HR	4	695.5	703.5	0.0	0.37
		Forb > 30_CU	3	697.9	703.9	0.5	0.29
		Forb > 30_CU + Shrub > 2_HR ^c	4	697.1	705.9	1.6	0.16
		Forb > 30_CU + Shrub > 2_HR + Forb < 2_HR ^c	5	695.2	705.2	1.7	0.16
III	Multi-scale habitat + wind	Forb > 30_CU	3	697.9	703.9	0.0	0.43
		Forb > 30_CU + Turb_dens_CU ^c	4	696.1	704.1	0.2	0.39
		Forb > 30_CU + Turb_dens_HR ^c	4	697.8	705.8	1.9	0.17
		Turb_dens_HR	3	711.0	717.0	13.1	<0.01
		Turb_dens_CU	3	712.3	718.3	14.4	<0.01
IV	GFR ^f	Forb > 30_CU + Forb > 30_CU _{exp} + Forb > 30_CU × Forb > 30_CU _{exp}	5	691.2	701.2	0.0	0.79
		Forb > 30_CU	3	697.9	703.9	2.7	0.21

^a Step I compared models ($n = 16$) consisting of a single habitat covariate measured within 2 spatial scales to an intercept-only model. Step II compared additive, multi-scale habitat models ($n = 7$) combining variables from the step I candidate model set. Step III compared the most parsimonious model within 2 AIC_c of the top model from step II to the same model with wind-energy variables added and univariate wind-energy models ($n = 5$). Step IV compared the most parsimonious model within 2 AIC_c of the top model from step III to a functional response model containing all variable(s) from the same model.

^b All models include a random lek-year intercept.

^c Forb > 30_CU = restored grassland with >30% forb cover within core-use area (ha); Bunch_CU = restored grassland dominated by bunchgrass within core-use area (ha); Forb > 30_HR = restored grassland with >30% forb cover within brood-rearing home range (ha); Forb < 2_HR = restored grassland with <2% forb cover within brood-rearing home range (ha); Bunch_HR = restored grassland dominated by bunchgrass within brood-rearing home range (ha); Forb < 2_CU = restored grassland with <2% forb cover within core-use area (ha); Crested_HR = restored grassland dominated by crested wheatgrass within brood-rearing home range (ha); Shrub > 2_HR = restored grassland with >2% shrub cover within brood-rearing home range (ha); Turb_dens_CU = number of wind turbines within core-use area, Turb_dens_HR = number of wind turbines within brood-rearing home range.

^d Variable eliminated from proceeding to step II because it was either outperformed by its other measurement scale or it was highly correlated with a better-performing variable.

^e Model contains uninformative parameters (Arnold 2010) and therefore was not considered competitive.

^f GFR = Generalized functional response model. Subscript exp represents the expectation for that variable in each sampling instance, as described by Matthiopoulos et al. (2011).

cover within the core-use area performed better than the best model from step III. The GFR model indicated selection for restored grasslands with >30% forb cover within the core-use area increased as availability of that land cover type within 2.7 km of the lek increased (Fig. 2 and Table 3). Cross validation suggested the fixed effects-only GFR model had poor predictive ability ($r_s = 0.21$, $P = 0.56$), with about 41% of nests falling in low to medium ranked bins (1–5) and 59% of nests falling within medium to high ranked bins (6–10), suggesting other variables we did not consider were significantly influencing nest-site selection.

Daily Nest Survival

Our nest survival analysis included 147 nests ($n = 59$ in 2014, $n = 88$ in 2015). Our DNS estimate was 0.972 and the overall survival estimate for the 27-day incubation period was 0.465. Daily nest survival did not differ between years, eliminating the need for an annual variation term in subsequent models. There was support for modeling linear, rather than quadratic, forms of all microsite habitat variables.

Our univariate model comparison suggested VOR, percent overhead concealment at the nest, the amount of

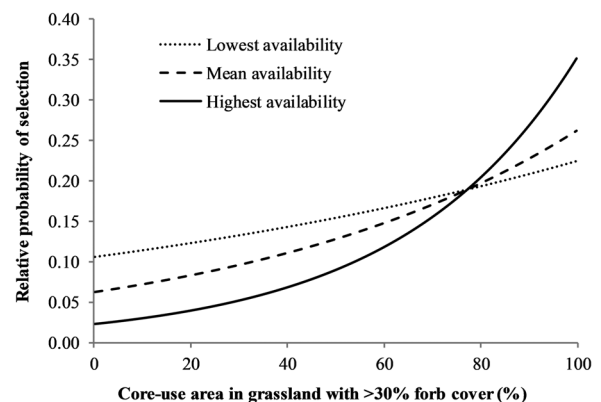


Figure 2. Relationship between relative probability of selecting a nest site and the percent of the core-use area in grasslands containing >30% forb cover—for portions of the landscape with the highest, average, and lowest availability of that cover type—for Columbian sharp-tailed grouse in eastern Idaho, USA, 2014–2015. We converted the modeled area (ha) to percent of the core-use area buffer on the x -axis to aid interpretation and held the non-plotted covariates from the top model at their means.

Table 3. Coefficient estimates (β) and standard errors (SE) from the best models describing nest-site selection and daily nest survival of Columbian sharp-tailed grouse, eastern Idaho, USA, 2014–2015.

Variable ^{a,b}	β	SE
Nest-site selection		
Forb > 30_CU	0.372	0.178
Forb > 30_CU _{exp}	-0.865	0.377
Forb > 30_CU: Forb > 30_CU _{exp}	0.349	0.285
Nest survival		
VOR	0.158	0.060
Forb > 30_CU	0.016	0.007

^a Forb > 30_CU = restored grassland with >30% forb cover within core-use area (ha), VOR = visual obstruction at 4 m from nest (dm).

^b Subscript exp represents the expectation for that variable in each sampling instance, as described by Matthiopoulos et al. (2011).

restored grassland containing >30% forb cover within the core-use area, and the amount of crested wheatgrass-dominated grasslands within the core-use area had some utility in explaining DNS (Table 4). We found no evidence that any of the variables measured within the brood-rearing home range affected DNS. The most explanatory additive habitat model contained VOR and the amount of grassland containing >30% forb cover within the core-use area, and all 4 competitive models in the habitat model set included those variables. Adding wind-energy variables to the best additive habitat model did not improve model fit, suggesting wind-energy variables did not affect DNS. The estimated effects of wind-energy variables in those models were moreover imprecise, with 95% confidence intervals on parameter estimates overlapping zero (turbine distance 95%

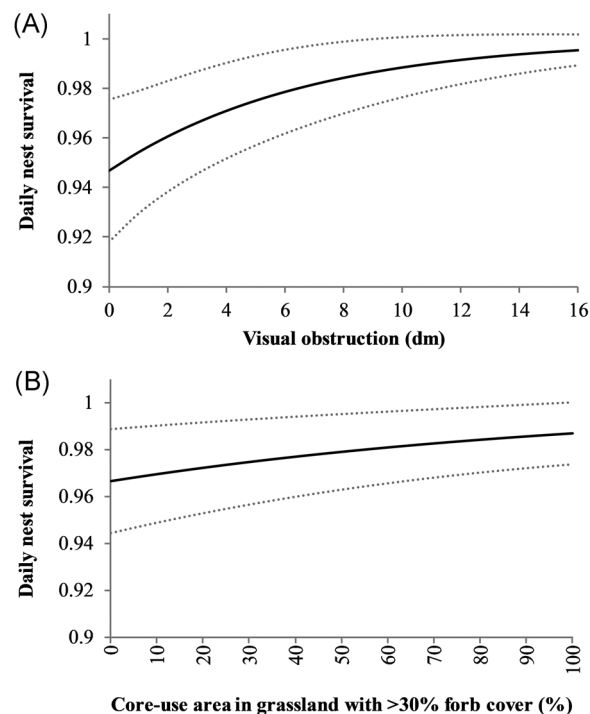


Figure 3. Effects of A) visual obstruction and B) percent of core-use area in grasslands containing >30% forb cover on daily nest survival (\pm 95% CI) of Columbian sharp-tailed grouse, eastern Idaho, USA, 2014–2015. We converted the modeled area (ha) to percent of the core-use area buffer on the x-axis to aid interpretation and held the non-plotted covariates from the top model at their means.

Table 4. Candidate models from each step of our model selection process for generalized linear models describing daily nest survival of Columbian sharp-tailed grouse nests ($n = 147$) in eastern Idaho, USA, 2014–2015. We used Akaike’s Information Criterion with second-order bias correction (AICc) to rank models in 4 steps (steps I–II: models ≥ 2 AICc less than intercept-only model; steps III: models ≤ 2 AICc from top model; step IV: all models considered). K = number of parameters; Dev = deviance; Δ AICc = difference in AICc between the model of interest and the top model; and w = Akaike weight.

Step ^a	Group	Model ^b	K	Dev	AIC _c	Δ AIC _c	w
I	Annual variation	Intercept-only	1	523.6	525.6	0.0	0.58
		Year	2	522.2	526.2	0.6	0.42
II	Univariate habitat	VOR	2	517.5	521.5	0.0	0.26
		Over	2	517.8	521.8	0.3	0.23
		Forb > 30_CU	2	518.9	522.9	1.5	0.13
		Crest_CU	2	519.5	523.5	2.0	0.10
		VOR + Forb > 30_CU	3	510.8	516.8	0.0	0.20
III	Multi-scale habitat	VOR + Forb > 30_CU + Crest_CU ^c	4	508.9	516.9	0.1	0.19
		VOR + Forb > 30_CU + Over ^c	4	509.4	517.4	0.5	0.15
		VOR + Forb > 30_CU + Crest_CU + Over ^c	5	507.7	517.7	0.9	0.13
		VOR + Forb > 30_CU	3	510.8	516.8	0.0	0.38
IV	Multi-scale habitat + wind	VOR + Forb > 30_CU + Turb_dist ^c	4	509.6	517.6	0.8	0.26
		VOR + Forb > 30_CU + Turb_dens_HR ^c	4	510.0	518.0	1.2	0.21
		VOR + Forb > 30_CU + Turb_dens_CU ^c	4	510.8	518.8	2.0	0.14
		Turb_dens_CU	2	522.6	526.6	9.8	<0.01
		Turb_dens_HR	2	523.4	527.4	10.6	<0.01
		Turb_dist	2	523.5	527.5	10.7	<0.01

^a Step I compared a model incorporating variation between years to an intercept-only model. Step II compared univariate models ($n = 24$) of variables measured within 3 spatial scales to an intercept-only model. Step III compared additive, multi-scale habitat models ($n = 14$) combining all variables from the candidate model set identified in step II. Step IV compared the most parsimonious model within 2 AICc of the top model from step III to the same model with wind-energy variables added and univariate wind-energy models ($n = 7$).

^b VOR = visual obstruction at 4 m from nest (dm); Over = overhead concealment 1 m above nest (%); Forb > 30_CU = restored grassland with >30% forb cover within core-use area (ha); Crested_CU = restored grassland dominated by crested wheatgrass within core-use area (ha); Turb_dist = distance to wind turbine (m); Turb_dens_HR = number of wind turbines within brood-rearing home range; Turb_dens_CU = number of wind turbines within core-use area.

^c Model contains uninformative parameters (Arnold 2010) and therefore, was not considered competitive.

CI = -2.04×10^{-05} – 9.11×10^{-05} , turbine density in brood-rearing home range 95% CI = -0.37 – 0.33 , turbine density in core-use area 95% CI = -0.04 – 0.01). The estimated DNS ($\pm 95\%$ CI) from the best model increased from 0.947 ± 0.029 (23% nest success) at a VOR of 0 dm to 0.997 ± 0.006 (92% nest success) at a VOR of 16 dm (Fig. 3A and Table 3). The estimated DNS from the best model increased from 0.970 ± 0.022 (44% nest success) to 0.988 ± 0.013 (72% nest success) when the portion of the core-use area containing restored grasslands with $>30\%$ forb cover increased from 0% to 60% (ha converted to % of the core-use area to ease interpretation; Fig. 3B and Table 3).

DISCUSSION

We hypothesized that Columbian sharp-tailed grouse would avoid wind-energy infrastructure when nesting and have lower nest survival closer to turbines but found no support for either hypothesis. The primary factors influencing nest-site selection and nest survival were vegetation structure and composition. Females selected nest sites in grasslands with higher forb cover within the nesting core-use area. Nest survival was positively influenced by the amount of visual obstruction at the nest site and the amount of grassland with higher forb cover within the nesting core-use area.

Our nest-site selection results are similar to those of McNew et al. (2014) and Harrison et al. (2017) who reported no influence of wind-energy development on nest-site selection in greater prairie-chickens. Similarly, LeBeau et al. (2014, 2017) reported no influence of wind-energy development on nest-site selection in sage-grouse. Our results do not support the prediction of Pruett et al. (2009) that prairie grouse would avoid wind turbines and differ from studies by Pittman et al. (2005) and Holloran (2005) that documented avoidance of energy-related infrastructure (though not wind energy) by prairie-chickens and sage-grouse, respectively.

Grouse behavioral responses to energy development during the nesting season may vary based on differences in associated infrastructure (Manier et al. 2014). For instance, oil and gas developments may trigger predator avoidance behaviors because they provide potential perches and nesting platforms for raptors and corvids (Prather and Messmer 2010, Messmer et al. 2013). Energy developments using overhead transmission lines also provide raptor and corvid perches (Connelly et al. 2000, Prather and Messmer 2010) and may trigger similar responses. Because most transmission lines associated with wind development in our study area were buried, vertical infrastructure consisted primarily of wind turbines, which lack suitable perches for raptors and corvids. This lack of subsidized predator perches may have contributed to the results we observed.

Variation in disturbance levels or features associated with roads may also explain differences in observed grouse behavioral responses. Greater prairie-chickens avoided major roads when nesting in Kansas (McNew et al. 2014) and also avoided roads in Nebraska where high traffic volume was documented (Harrison et al. 2017). We did not detect a negative response of nesting Columbian

sharp-tailed grouse to roads in our study, although we combined all road types into a single road variable, which may have influenced our ability to detect an effect. In general, roads in our study area consisted primarily of wind turbine access roads, with restricted public access, and poorly maintained county roads, both of which were lightly traveled during the nesting season. Additionally, many wind turbine access road edges were seeded with forb-rich seed mixes as a mitigation practice. These features may have contributed to the results we observed, or alternatively, nesting Columbian sharp-tailed grouse may be less sensitive to roads than other prairie grouse species.

Columbian sharp-tailed grouse in our study selected specific vegetation characteristics within restored grasslands for nesting. Nest microsite habitat characteristics selected by Columbian sharp-tailed grouse are well-documented (McDonald 1998, Meints 1991, Boisvert 2002, Collins 2004, Stonehouse et al. 2015). At the microsite scale, Columbian sharp-tailed grouse tend to select nest sites with higher grass canopy cover (McDonald 1998, Boisvert 2002, Collins 2004, Stonehouse et al. 2015), higher VOR (Meints 1991, Boisvert 2002, Collins 2004), less bare ground (Meints 1991, Collins 2004), and taller forbs (Stonehouse et al. 2015). Selection of nest sites with more vegetation cover suggests that decisions made by Columbian sharp-tailed grouse when selecting nest microsites may be related to concealment from visually oriented predators (Lima 2009).

Animals may select different habitat components at different spatial scales and patterns detected at one scale cannot always reliably be scaled-up or scaled-down (Weins 1989, Schneider 1994). To detect patterns that may occur at larger spatial scales and provide results applicable to the scales at which habitats are typically managed, we assessed the effects of habitat variables measured within the core-use area of nesting females and the home range of brood-rearing females. Our results suggested that Columbian sharp-tailed grouse females selected for grassland patches with $>30\%$ forb cover within the core-use area and showed a functional response (Myserud and Ims 1998) to the availability of that cover type, with strength of selection increasing with availability. The documentation and description of this functional response should allow results from this study be applied to other landscapes where the configuration and abundance of restored grasslands may differ from the landscape we studied.

Forb cover within the core-use area is important to Columbian sharp-tailed grouse nest-site selection. Goddard et al. (2009) documented sharp-tailed grouse selecting shrub-steppe over residual grass within the patch scale (250-m radius) for first-nest attempts in fragmented habitats of northeastern British Columbia, Canada. They attributed selection of that land cover type to the concealment attributes provided by shrubs. Forb cover in our study area may provide similar concealment benefits but we suspect that the benefits of higher forb cover for incubating females go beyond concealment. The core-use area we evaluated represents the assumed extent of habitat available to females during incubation recess movements.

Nesting season diets of Columbian sharp-tailed grouse consist primarily of grasses and forbs, with forbs dominating as the season progresses (Hoffman and Thomas 2007). The females we studied may have selected grassland patches with higher forb abundance to meet the nutritional requirements of egg-laying and incubation.

Because we found a strong correlation between bunchgrass and grassland forb cover within the core-use area, we cannot rule out the possibility that nesting CSTG were actually selecting bunchgrass cover or a combination of bunchgrass dominance and forb cover when placing their nests. The structural attributes of bunchgrasses, relative to sod-forming exotic grasses, may provide a variety of benefits to CSTG, including better residual cover for nest concealment, diverse thermal environments (Carroll et al. 2015), and improved mobility resulting from greater interspacing between plants (Marten et al. 2015).

We found variables measured within the core-use area to be better predictors of nest-site selection than variables measured within the brood-rearing home range. We hypothesized that CSTG females would select nest sites for their potential as brood rearing habitat. Our results suggest Columbian sharp-tailed grouse may not make nest-site decisions that consider brood-rearing habitat or that the variables we considered were not important at the brood-rearing home range scale.

Similar to our nest-site selection results, we found no evidence of wind-energy infrastructure affecting Columbian sharp-tailed grouse nest survival. These results are similar to those of McNew et al. (2014) and Harrison et al. (2017) who found no influence of wind-energy infrastructure on greater prairie-chicken nest survival in Kansas and Nebraska, respectively. Both studies found nest survival was influenced by vegetation rather than wind-energy infrastructure. LeBeau et al. (2014) documented decreased sage-grouse nest survival as distance to turbines decreased at a wind-energy facility in Wyoming, but LeBeau et al. (2017) found no effect in a longer-term study at the same study site.

We hypothesized that Columbian sharp-tailed grouse nest survival would decrease near turbines because of increased predation resulting from anthropogenic features or habitat fragmentation (Stephens et al. 2004, Liebezeit et al. 2009). For instance, corvid abundance could increase near turbines if collision mortalities resulted in subsidized food resources and meso-carnivores could benefit from either subsidized food resources or improved access resulting from turbine roads (Tigas et al. 2002). Post-construction mortality surveys provide evidence of subsidized food resources (bird and bat carcasses) within wind-developed portions of our study (Tetra Tech, unpublished report), but the influence of those subsidies on predator distribution and density is unknown.

Nest survival of Columbian sharp-tailed grouse in our study increased with more visual obstruction around the nest and more restored grassland with high forb cover within the nesting core-use area. Previous studies have also documented higher VORs associated with successful Columbian sharp-tailed grouse nests (McDonald 1998,

Boisvert 2002, Collins 2004), suggesting the importance of concealment from visually oriented predators at the microsite scale. No previous studies of Columbian sharp-tailed grouse nest survival have documented the importance of forb cover within the nesting core-use area. Higher forb cover within the core-use area may create a more effective visual barrier, making nests harder for predators to detect (Arnold et al. 2007), or may provide foraging and concealment benefits to females during incubation recesses. An increase in the abundance of this forb-rich grassland cover type may also reduce the foraging efficiency of nest predators that have developed a search image for it (i.e., larger patches of homogeneous land cover are more inefficient to search than smaller, conspicuous patches; Whittingham and Evans 2004).

We were able to explore the effects of wind energy on Columbian sharp-tailed grouse nesting ecology only around pre-existing wind farms over a 2-year period; therefore, we must acknowledge some potential limitations of our study. Because our study was not a before-after control-impact design, we were unable to assess potential changes in nesting behavior or demographics pre- and post-development. Additionally, longer-term studies may be necessary to better assess demographic responses of upland birds to development (LeBeau et al. 2014, 2017). Our study was initiated 2 years after the most recent wind-energy development and 9 years after completion of the first wind farm within the study area. It is possible that this time lag may have been sufficient for Columbian sharp-tailed grouse to acclimate to the presence of the wind-energy infrastructure, masking any initial effects of its development. Although nest survival has been identified as an important factor influencing population growth in Columbian sharp-tailed grouse (Gillette 2014), investigations of adult survival, brood and chick ecology, and lek attendance patterns are needed to assess overall effects of wind energy on populations.

Differences in size and scale of energy developments may contribute to whether effects on nesting ecology occur (Harrison et al. 2017). The number of turbines ($n = 215$) in our study area was large relative to previous grouse and wind-energy studies (McNew et al. 2014, Harrison et al. 2017, LeBeau et al. 2017), yet, consistent with those studies, we failed to observe an effect on nesting ecology. Nevertheless, we recommend caution when extrapolating our study results to other wind development sites, which may differ in turbine number, turbine capacity (MW), configuration, or the amount of associated infrastructure. Finally, we acknowledge that nesting Columbian sharp-tailed grouse could respond differently to wind-energy developments in landscapes with different land cover attributes.

MANAGEMENT IMPLICATIONS

Nesting prairie grouse may be less sensitive to wind-energy development than other forms of energy development or anthropogenic infrastructure. Additional research on Columbian sharp-tailed grouse adults, broods, chicks, or leks

would provide further insights into potential effects of wind-energy development on populations. Efforts to manage Columbian sharp-tailed grouse nesting habitats in eastern Idaho should focus on creating or maintaining parcels of bunchgrass-dominated, perennial grasslands with >30% forb canopy cover and with residual vegetation for nest concealment. Nest survival estimates from our study suggest that CRP and other restored grasslands can provide viable nesting habitat for Columbian sharp-tailed grouse in eastern Idaho. Our results also provide evidence of the potential benefits of CRP-SAFE, a subprogram of CRP, for nesting Columbian sharp-tailed grouse. In Idaho, CRP-SAFE seed mixes contain a higher diversity of grasses and forbs, intended to improve nesting and brood-rearing cover. Plantings achieving bunchgrass-dominated stands with forb canopy cover levels above 30% should result in measurable increases in Columbian sharp-tailed grouse nest survival.

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