Behavioral Response of Grouse to Wind Energy Turbines:

A Quantitative Review of Survival, Habitat Selection, and Lek Attendance

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Abstract

Grouse (*Tetraoninae spp.*) populations benefit from large intact areas of habitat that satisfy all life cycle requirements and the conservation of these habitats benefits multiple species. Effective conservation requires a thorough understanding of the factors that impact these habitats. Grouse populations are adversely affected by anthropogenic features on the landscape but an overall understanding of the specific effects of wind energy development is lacking. Given the trend in wind energy development, and to better understand and manage grouse species in response to energy development, a quantitative review of studies is necessary. We reviewed studies that evaluated the effect of wind energy facilities on grouse. Our objective was to determine the magnitude of effects of wind turbines on grouse habitat selection, lek attendance, and survival at various distances from wind turbines. We used 10 studies, resulting in 22 study-result combinations, in our meta-analysis. Similar to other anthropogenic features that exist in grouse habitats, grouse habitat selection, survival, and lek attendance were all adversely impacted in habitats in close proximity to wind turbines. However, the magnitude of the effect was small and variable across studies. The results of this analysis build upon previous meta-analyses that estimated effect sizes of other anthropogenic features on grouse populations. Inferences from this study can be applied to future wind energy facilities located in similar habitats and associated with grouse populations similar to those included in this analysis. As additional research is conducted, similarities between study sites and seasonal, species-specific, or behavioral responses will be identified to inform siting of future wind energy facilities in grouse habitats that avoid, minimize, or mitigate impacts. Reducing the impacts of energy development is a necessary step to conserve the habitats of these indicator species upon which many other species also rely.

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Introduction

Grouse (*Tetraoninae spp.*) populations are considered an ideal indicator species for native habitat conservation because they require large intact native habitats to complete their life cycles (Johnsgard 1983, Pruett et al. 2009b, Poani et al. 2002, Sandercock et al. 2011, Rowland et al. 2006). Conservation of these habitats has the potential to benefit not only grouse populations but other species that depend on these habitats for all or part of their life cycles (Suter et al. 2002, Rowland et al. 2006, Copeland et al. 2014). Recent studies have revealed that these habitats are being converted to various land uses and there is growing concern that this habitat loss will lead to or exacerbate species declines (Jones et al 2013, Knick et al. 2013, Leu et al. 2008; McDonald et al. 2009, Northrup et al. 2013, Wilsey et al. 2019). Conserving these habitats has become a priority for many land managers but for effective conservation to take place, a thorough understanding of potential threats to these habitats is needed. Native land conversion, invasive species, wildfires, climate change, and energy development have all been identified as threats to these habitats and has been attributed to habitat loss and grouse population declines (Schroder et al. 2010, Garton et al. 2011, Wilsey et al. 2019). Cumulatively, these threats are likely to continue to persist on the landscape and there is potential that new threats may arise.

Native land conversion, invasive species, and wildfires are all threats that result in direct, quantifiable habitat loss. While energy development has the ability to directly impact grouse species through habitat loss and mortality, the indirect impacts are often difficult to quantify. Yet most management decisions are based on the perceived behavioral response to anthropogenic features associated with energy development (Manier et al. 2014). Thus, a comprehensive evaluation of the effects of energy development infrastructure on grouse populations is necessary to provide land managers the tools necessary for conserving grouse habitats which in turn has the potential to conserve multiple species.

Hovick et al. (2014) examined five studies that evaluated displacement effects and seven studies that evaluated survival rates relative to anthropogenic features associated with energy development. Grouse were displaced and survival rates were negatively impacted by various anthropogenic influences including roads, buildings, transmission lines, and oil and gas development. One type of anthropogenic feature Hovick et al. (2014) could not evaluate was wind turbines due to the lack of studies conducted. Since that synthesis, there have been multiple publications that evaluated the effects of wind energy facilities on grouse populations (e.g., Winder et al. 2015, Harrison et al. 2017, Smith et al. 2017, LeBeau et al. 2017a and b, Proett et al. 2019); however, given the trend in energy development, and to better understand responses and manage grouse species, a quantitative review of these studies is necessary to begin to understand the effects of wind energy infrastructure on grouse populations (Hagen 2010, Hovick et al. 2014, Walters et al. 2014).

Several methods can be used to synthesize the results of multiple studies on a response variable of interest to reach broad generalizations including vote counting and meta-analysis; however, the level of inference depends on the type of synthesis conducted. Recently, Coppes et al. (2019) summarized the effects of wind energy on grouse using a vote counting method and determined that multiple studies reported negative behavioral responses to wind energy facilities. This information is important, but the votes as counted by Coppes et al. (2019) did not provide inference into the magnitude of the effect. In contrast to vote counting, current meta-analytic methods account for variability in the response, sample size, and publication bias allowing the scientist to fully understand the influence of a study in the dataset on the results.

Further, meta-analysis provides an effect size calculation that removes the ambiguity of interpreting the direction of the effect (e.g., vote counting method). There are limits to conducting a meta-analysis including similarity among studies, the number of studies presenting results of interest, adequate information reporting in papers, and unpublished papers that may not have discovered an effect of interest. However, most of these issues can be overcome leading to highly informative and valuable meta-analysis that make important contributions to science as evidenced by papers cited over 500 times (e.g., Aguilar et al. 2006).

Traditional wildlife management meta-analyses that evaluate the response of a particular variable on a species of interest usually involve a comparison of two means with a measure of Hedges, g and Cohen's d (e.g., Hovick et al. 2014). However, as technology has evolved, wildlife monitoring studies have become more advanced to answer more complex questions that investigate the relationship between features on the landscape to various population metrics. The inclusion of these studies in a meta-analysis is necessary to thoroughly understand the effects of anthropogenic features on grouse populations. For example, the search by Hovick et al. (2014) for research publications evaluating the effects of anthropogenic features on grouse populations returned 24 publications, but only 12 fit their analysis criteria. Their criteria excluded studies that evaluated grouse response relative to an anthropogenic feature because they lacked statistics that compared two means (e.g., Aldridge and Boyce 2007, Harju et al. 2010). The excluded studies contained valuable information regarding the effects of anthropogenic features on grouse populations and excluding them may have limited the overall understanding of the effects of anthropogenic features on grouse populations.

The inclusion of regression coefficients in meta-analyses are widely used in the medical and social science fields but have yet to gain traction in the wildlife management field (Peterson and Brown 2005, Becker and Wu 2007). We believe one of the main reasons for this is because there is not a direct way to convert regression coefficients to standard meta-analytic metrics (e.g., Fisher's Z). Peterson and Brown (2005) proposed a formula to convert such metrics but a major assumption of this formula is that all regression coefficients are standardized. Standardized coefficients are rarely reported in the wildlife management field making it difficult to incorporate such studies in a meta-analysis with the Peterson and Brown (2005) formula. However, unstandardized regression coefficients can be synthesized into a magnitude of effect (Becker and Wu 2007) that can be interpreted in a biological meaningful way to support decision making in grouse habitats.

Based on the research evaluating the effects of anthropogenic disturbances on grouse populations, it is clear that anthropogenic features that fragment the landscape have the ability to impact grouse populations (Holloran et al. 2010, Harju et al. 2010, Hovick et al. 2014, Bartuszevige and Daniels 2016). However, a comprehensive evaluation of the spatial extent of this impact is lacking and the inclusion of more representative study designs in our meta-analysis allows us to interpret the magnitude of effect relative to turbines which is useful for decision makers.

The extent and magnitude of these behavior responses likely varies depending on the characteristics of the affected population (e.g., migratory/non-migratory) and is dependent on size, longevity, and density of structures (Naugle et al. 2011). In addition, the magnitude of the effect can vary depending on the life-cycle period of the species (e.g., lekking, nesting, brood-rearing, wintering; see Naugle et al. 2011). For example, grouse may be displaced from suitable nesting habitat due to their avoidance behavior associated with the addition of anthropogenic features to the landscape. This avoidance behavior will likely result in the use of relatively lower quality habitats which may result in population fitness consequences. If grouse are not being displaced and continue to select habitats near anthropogenic features, then there is the potential for those habitats to act as an ecological trap where the habitat appears to be of high quality but the fitness consequences are high (Aldridge and Boyce 2007, Kirol et al. 2015, Hale et al. 2016). A comprehensive understanding of these behavior responses relative to anthropogenic features is necessary to quantify the effects of various anthropogenic features on grouse populations.

In this study we examined previous research that evaluated the effect of wind energy infrastructure, specifically wind turbines, on grouse behavior. We also demonstrated the utility of combining studies that evaluated the response of various population metrics relative to wind turbines to summarize the overall effect of wind turbines on grouse behavior. Future management prescriptions within these habitats should be informed by a suite of information that provides a basis for understanding the extent of impacts, ways to minimize impacts, and adequately quantify necessary mitigation to ensure grouse populations persist on the landscape. Our objective was to determine the magnitude of effects of wind turbines on grouse habitat selection, lek attendance, and survival at various distances from wind turbines.

Methods

We conducted a literature search on September 1, 2019, using Google Scholar to identify studies that evaluated the effect of wind energy facilities on grouse. Our search terms included, grouse, wind, turbine, and prairie-chicken (e.g., [(grouse* and wind*), (grouse* and turbine*)] and [(prairie chicken* and wind*), (prairie chicken* and turbine*)]]). We retained all peer-reviewed literature that evaluated avoidance behavior and survival relative to wind energy development. We then reviewed each of these studies and extracted results specific to habitat selection, lek attendance, and survival relative to proximity to wind turbines because this metric is commonly used to inform habitat management decisions. All studies used in this meta-analysis reported the effect of habitat selection, lek attendance, or survival (i.e., grouse behavior) associated with distance to wind turbine. Here we define habitat selection as a hierarchical process involving a series of innate and learned behavioral decisions made by grouse about what habitat it would use at different scales of the environment (Hutto 1985).

For each study that estimated the effect of wind energy on grouse behavior using distance to turbine, we extracted results and associated sample sizes to assess potential inclusion in a quantitative meta-analysis that synthesized regression coefficients (Becker and Wu 2007). Multiple results included in a single study were referred to as study result-combinations. We ensured the scale of the outcomes were measured equally across the models that evaluated grouse behavior (Becker and Wu 2007). The scale of the focal predictor, distance to wind turbine, was generally in kilometer (km), though we converted from meter (m) to km in two cases. We assumed that individual studies reported results from models with additional covariates chosen critically such that the additional covariates served to control other sources of variation and isolate the effect of distance to turbine. We attempted to include as many study-result combinations as possible to evaluate the effect of distance to turbines on grouse behavior because excluding these studies might have ignored results that were essential to our understanding of the overall effect sizes (Peterson and Brown 2005, Hovick et al. 2014). In addition, excluding such studies decreased precision of the effect size by increasing sampling and non-sampling error (Peterson and Brown 2005).

Survival models measured lek persistence, nest, chick, brood, or adult survival. Lek attendance models evaluated trends in the number of male or female grouse attending leks. Lek persistence was included in the survival evaluation because it evaluated lek activity (active = 1 and inactive = 0) and not the number of individuals attending leks like lek attendance. Habitat selection included measures of resource selection and habitat selection. Studies that reported Cox proportional hazards were inverted to be interpreted as survival. A positive correlation of distance to wind turbine with habitat selection, lek attendance, and survival behavior corresponded to an adverse effect, or behavioral avoidance, of wind turbines on grouse. For example, as the distance to the nearest wind turbine increased, the relative probability of survival and habitat selection and number of males or females attending leks increased.

We modeled the slope coefficients for distance to wind turbine on habitat selection, lek attendance, and survival separately using a generalized linear random-effects model to account for multiple studies with varying number of study-result combinations. This model was analogous to the random effects models recommended by Raudenbush 2009, Viechtbauer 2010, and Nakagawa and Santos 2012 with heterogeneity fixed using the inverse of the standard error of beta. The generalized linear random-effects model accounted for non-independence of reported effect sizes from the same study with a random effect term and provided population-level inference.

$$\boldsymbol{\beta}_{ij} = \mu + \alpha_i + e_{ij} \quad where \;\; i = 1, \dots, k; \;\; j = 1, \dots, n_p, \\ \alpha_i \sim N(0, {\sigma_\alpha}^2), e_{ij} \sim N(0, \sigma^2)$$

where β_{ij} was the regression coefficient for distance to turbine for the jth result within the ith study, μ was the population overall mean (mean effect size), α_i was the random effect of the ith study, and e_{ij} was the residual deviation. The k studies each have n_p corresponding effect sizes and variances. The models were fit using the package nlme in R version 3.61 (Pinheiro et al. 2019). The resulting mean slope effect size was predicted along with approximate confidence intervals (alpha level = 0.10) and p-values were calculated from effect sizes and corresponding standard errors assuming a normal distribution. An overall effect size with a positive slope was interpreted as an adverse effect for each of the habitat selection, survival and lek attendance outcomes. The magnitude and direction of the modelled mean effect was interpreted for each outcome. A forest plot was generated to visually inspect the effect sizes and associated standard errors from each study-result combination relative to the overall modeled effect size. These plots contain standard error ranges, rather than confidence intervals, for each regression coefficient to depict the weights used to estimate the overall mean (larger lines denote coefficients with less weight); the standard error and confidence intervals are shown for the modelled effect size.

We tested for influential study-result combinations using Cook's distances (Cook 1977). Large Cook's distances were evaluated to detect study-result combination influences and any study-result combinations determined to be influential were removed from the analysis (Cook and Weisberg 1982).

Publication bias is often an issue in meta-analysis because significant results are generally more likely to be published than non-significant results. We used funnel plots as a graphical tool to assess the presence of publication bias in the dataset (Sterne et al. 2001, Nakagawa and Santos. 2012). The funnel plot showed publication bias as asymmetry on the graph of effect size (x-axis) versus precision (y-axis). If the studies were not evenly distributed on the left and right of the plot, then there was evidence of publication bias and the results of the meta-analysis might have been biased.

Results

Our Google Scholar search returned over 350 matches. After review of all 350 matches, we retained 15 studies that evaluated avoidance behavior, lek attendance, or survival relative to wind energy developments (Table 1). These studies investigated the response of five species of grouse (greater sage-grouse; *Centrocercus urophasianus*; n=3), black grouse (*Tetrao tetrix*; n=1), red grouse (*Lagopus lagopus scoticus*; n=3), greater prairie-chicken (*Tympanuchus cupido*; n=7), and Columbian Sharp-Tailed Grouse (*Tympanuchus phasianellus columbianus*; n=1). Of these 15 studies, 10 included results that directly evaluated grouse behavior relative to distance to wind turbine. The black grouse and red grouse studies were excluded from the synthesis because they did not present results that evaluated habitat selection, lek attendance, or survival relative to distance to wind turbine. We excluded one greater prairie-chicken study that evaluated nest site selection and nest survival relative to wind turbines because this study did not report coefficients associated with post-construction response to distance to wind turbine (McNew et al. 2014). The overall number of study-result combinations was 22 but varied from one to six for each study and came from four unique study locations in Idaho, Kansas, Nebraska, and Wyoming (Table 1).

Table 1. Studies retained from the Google search and number of study structure combinations included in the meta-analysis

Study Reference	Location	Species	Study Design	Studied Behavior	Study-result Combinations
Pearce-Higgins et al. 2009	United Kingdom	Red grouse	A	Habitat Selection	0
Douglas et al. 2011	United Kingdom	Red grouse	A	Habitat Selection	0
Pearce-Higgins et al. 2012	United Kingdom	Red grouse	A	Habitat Selection	0
LeBeau et al. 2014	Wyoming, USA	Greater sage-grouse	ACI	Survival	3
McNew et al. 2014	Kansas, USA	Greater prairie-chicken	BAI	Habitat Selection and Survival	0
Winder et al. 2014b	Kansas, USA	Greater prairie-chicken	BACI	Survival	1
Winder et al. 2014a	Kansas, USA	Greater prairie-chicken	BACI	Habitat Selection	2
Winder et al. 2015	Kansas, USA	Greater prairie-chicken	BACI	Survival (Lek persistence)	1

Zwart et al. 2015	United Kingdom	Black grouse	BA	Survival	0
Smith et al. 2016	Nebraska, USA	Greater prairie-chicken	A	Lek Attendance	1
Harrison et al. 2017	Nebraska, USA	Greater prairie-chicken	A	Habitat Selection and Survival	2
LeBeau et al. 2017a	Wyoming, USA	Greater sage-grouse	BACI	Lek Attendance	4
LeBeau et al. 2017b	Wyoming, USA	Greater sage-grouse	ACI	Habitat Selection and Survival	6
Smith et al. 2017	Nebraska, USA	Greater prairie-chicken	A	Survival	1
Proett et al. 2019	Idaho, USA	Columbian sharp-tailed grouse	A	Survival	1

A = After development study design
BACI = Before-After-Control-Impact study design
ACI = After-Control-Impact study design
BA = Before-After study design

Habitat Selection

Three studies, resulting in five study-result combinations, were included in the weighted random-effects model to estimate the magnitude of effect of wind turbines on habitat selection. We found little evidence that proximity to wind turbines negatively affected habitat selection (average β = 0.032; 90% CI: -0.086, 0.151; Figure 1). The relative probability of habitat selection increased by 3 to 16% (upper 90% CI) for everyone km increase from distance to wind turbine. Across all the studies we included in our analysis, the magnitude of effect ranged from no effect (β = -0.07) on greater sage-grouse nest site selection (LeBeau et al. 2017b) to a 22% increase in greater prairie-chicken nest site selection for every one km increase from distance to wind turbines (Harrison et al. 2017). The two study sites that evaluated habitat selection outside of the nesting season, Kansas and Wyoming, found evidence of avoidance behavior during the breeding period (GRPC; β=0.075; 8% increase for every km; Winder et al. 2014b and GRSG; β=0.198; 22% increase for every km; LeBeau et al. 2017b).

The Cook’s distance indicated that one of the study-result combinations was overly influential in the model (GRPC non-breeding space use; Winder et al. 2014a, Cook’s D = 15.38) and was removed from the dataset. Inspection of asymmetry in the funnel plots did not provide evidence of publication bias (Figure 2).

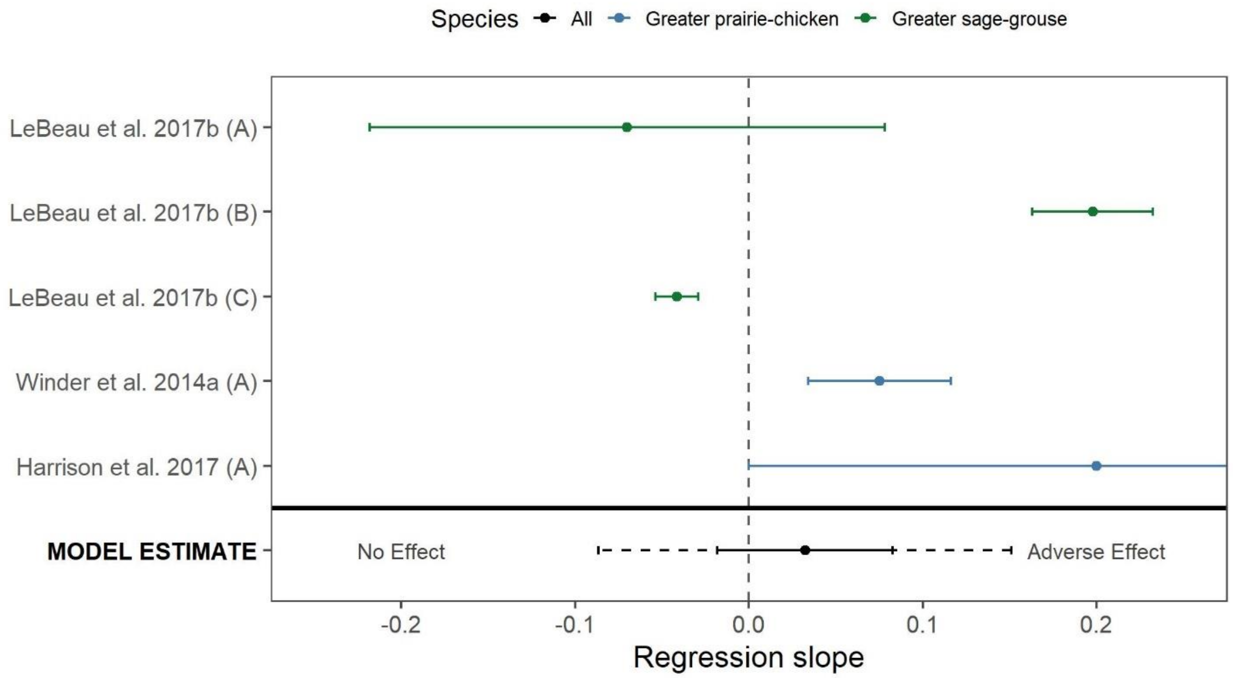

Figure 1. Regression slopes (mean +/- standard error in solid line) for the effect of distance from turbine on habitat selection from each study included in the analysis and the overall estimated mean slope (0.032, 90% confidence interval in dashed line). Colors indicate the focal species. Study details are provided in Appendix A1. Note that the SE bar for Harrison et al. 2017 extends beyond the limit of the plot; we cropped the plot for visual clarity.

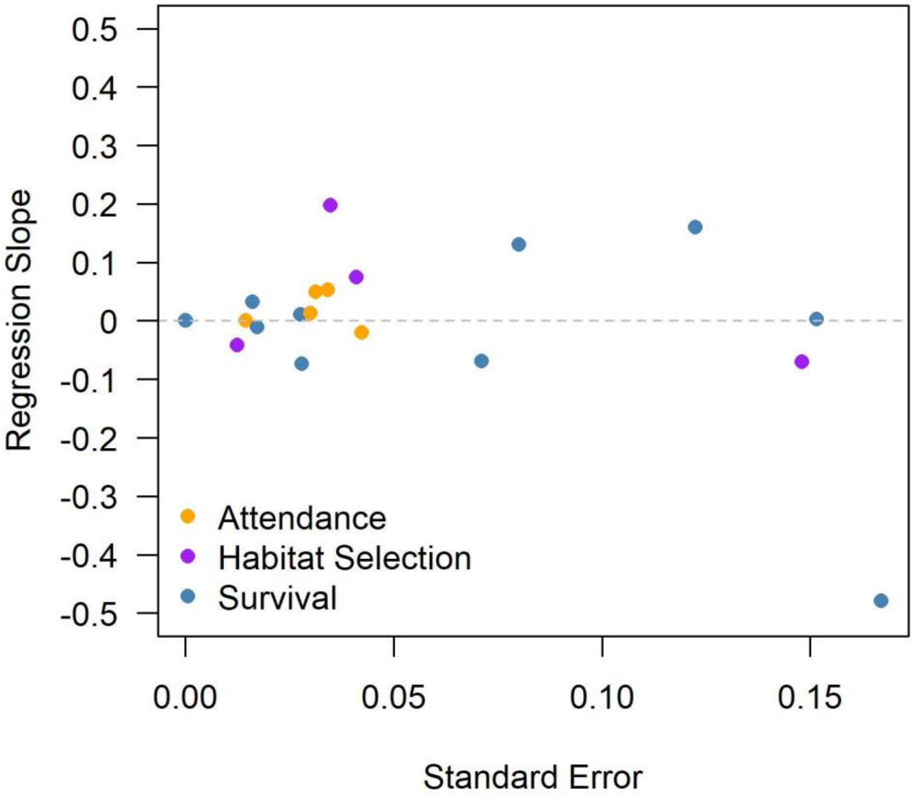

Figure 2. Funnel plot used to evaluate publication bias in our meta-analysis evaluating the magnitude of effect of distance to wind turbines on grouse behavior

Survival

Seven studies, resulting in 11 study-result combinations, were included in the weighted random-effects model to estimate the magnitude of effect of wind turbines on survival. Similar to habitat selection, we found little evidence that proximity to wind turbine negatively affected grouse survival (average β = 0.038; 90%CI: -0.0096, 0.0864; Figure 3). The relative probability of survival increased by 4% to 9% (upper 90% CI) for every one km increase from distance to wind turbine The reported effects ranged from -0.03 (GRSG; LeBeau et al. 2017b), interpreted as no effect, to 0.48 (GRSG; LeBeau et al. 2014), indicating a large adverse effect (38% increase in survival with every km) occurring during the brood rearing period. Nest survival relative to wind turbines was evaluated at three study sites: Idaho, Nebraska and Wyoming. The reported effects of wind turbines from these three study sites on nest survival were small ranging from 0.01 (GRSG; LeBeau et al. 2017b) interpreted as a 1% increase to 0.10 (CSTG; Proett et al. 2019) approximately an 11% increase in nest survival with every one km increase in distance from turbines. Brood survival was only evaluated at one study site where a short-term negative effect was detected two years following development (β = 0.479; 38% increase for every km; LeBeau et al. 2014) but the magnitude of effect was relatively small (β = 0.069; 6% increase for every km) during the longer six year study period (LeBeau et al. 2017b). Female survival was evaluated at three study sites with the reported magnitude of effect greatest on GRPC at the Nebraska study site (β = 0.16; 17% increase for every km; Smith et al. 2017) but relatively small to no effects at the Wyoming study site (GRSG; β = -0.011; LeBeau et al. 2014 and β = -0.033; LeBeau et al. 2017b) and the Kansas study site (GRPC: β = 0.003; Winder et al. 2014b). Lek persistence was negatively affected by proximity to wind turbines at one study site (β = 0.13; 14% increase in the relative probability of a lek persisting [i.e., active vs inactive] for every km; Winder et al. 2015).

The Cook's distance indicated that none of the study-result combinations were overly influential (e.g., Cook's D <0.51). Inspection of asymmetry in the funnel plots did not provide evidence of publication bias (Figure 3).

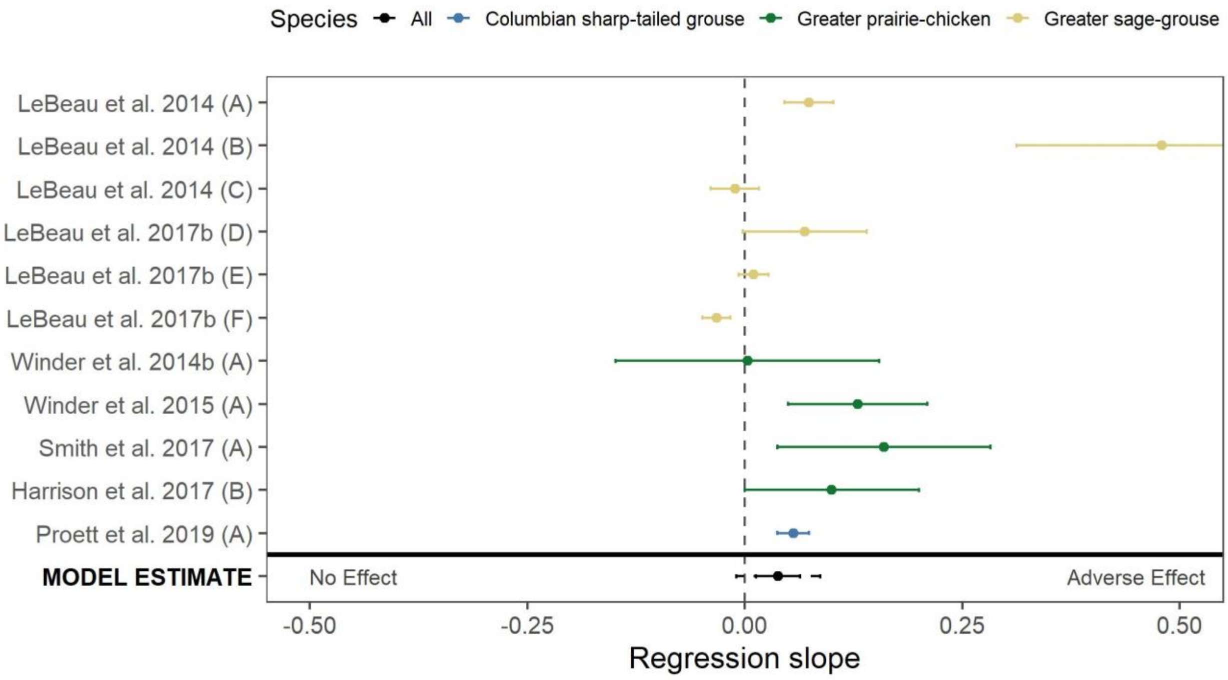

Figure 3. Regression slopes (mean +/- standard error in solid line) for the effect of distance from turbine on survival from each study included in the analysis and the overall estimated mean slope (0.038, 90% confidence interval in dashed line). Colors indicate the focal species. Study details are provided in Appendix A1. Note that the SE bar for LeBeau et al. 2014 (B) extends beyond the limit of the plot; we cropped the plot for visual clarity.

Lek Attendance

Two studies, resulting in five study-result combinations, were included in the random-effects model to estimate the magnitude of effect of wind turbines on lek attendance. Similar to the other grouse behaviors, we found little evidence that proximity to wind turbine negatively affected grouse survival (average β = 0.017; 90% CI: -0.014, 0.047; Figure 5) as male and female lek attendance increased by approximately 2% to 5% (upper 90% CI) for every one km increase in distance from turbines. The reported effects ranged from -0.02 at seven years post development (interpreted as 2% decrease for every km) to 0.05 at six years post development (interpreted as a 5% increase for every km) for GRSG (LeBeau et al. 2017a). Most of the results indicate that the number of male and females attending leks at two study sites in Nebraska and Wyoming did not seem to be negatively affected by proximity to wind turbines (LeBeau et al. 2017a and Smith et al. 2016).

The Cook's distance indicated that none of the study-result combinations were overly influential (e.g., Cook's D <0.55). Inspection of asymmetry in the funnel plots did not provide evidence of publication bias (Figure 4).

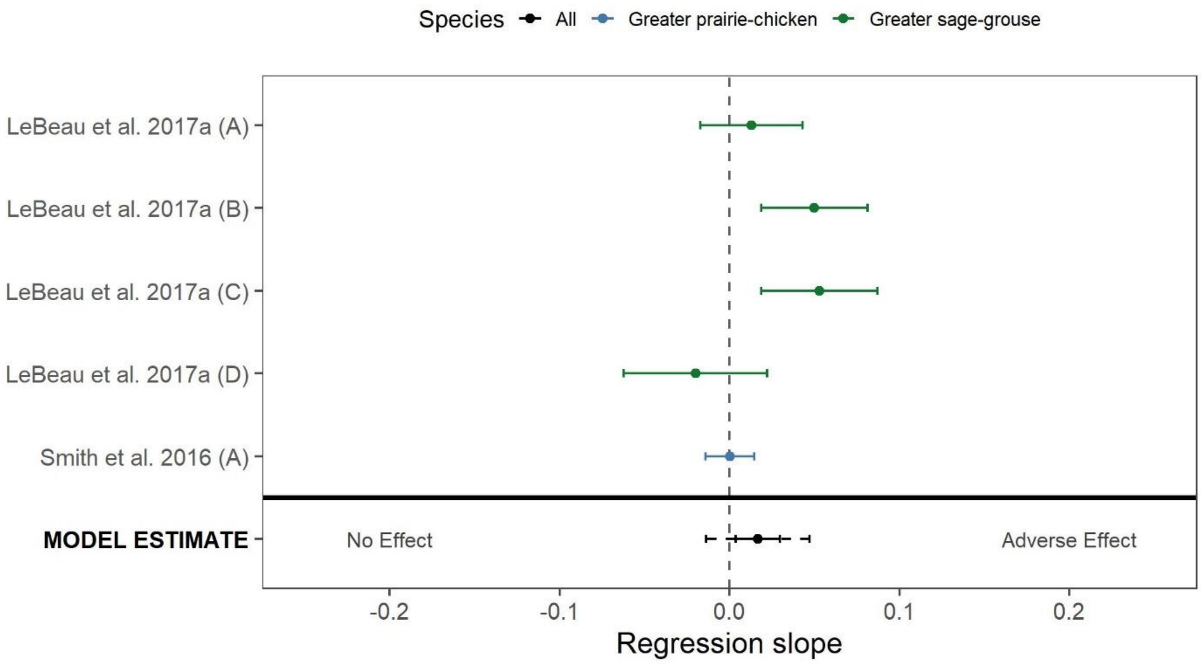

Figure 4. Regression slopes (mean +/- standard error in solid line) for the effect of distance from turbine on lek attendance from each study included in the analysis and the overall estimated mean slope (0.017, 90% confidence interval in dashed line). Study details are provided in Appendix A1.

Discussion

Similar to grouse response to other anthropogenic features (e.g., roads, oil and gas development), habitat selection, lek attendance, and survival were adversely impacted by wind turbines based on the modeled positive means; however, the magnitude of the effect was small and variable across studies. This small effect was likely attributable to the lack of studies that found distance to turbine as an important predictor of grouse behavior. Out of the 10 research studies included in the meta-analysis, authors from two studies reported and interpreted a total of three study-result combinations that demonstrated proximity to wind turbines negatively impacted grouse behavior (Winder et al. 2014a, LeBeau et al. 2014). Winder et al. (2014a) found that greater prairie-chicken space use was negatively affected by distance to wind turbine during the breeding period as distance to wind turbine was included in their final model and was significant at the 95% confidence level. LeBeau et al. (2014) reported lower greater sage-grouse nest and brood survival in habitats closer to wind turbines two years following development as distance to wind turbine was included in their final model and significant at the 90% confidence level. The other reported study-result combinations were results that authors reported to support evidence that distance to wind turbines did not negatively affect grouse behavior or were results that were not included in the best supporting models. Results from this meta-analysis supported findings from other studies that showed distance to wind turbines was not a strong predictor of grouse behavior, and further, that no adverse effects were found in relation to distance to wind turbines on grouse behavior.

Our analysis benefited from the inclusion of studies that evaluated grouse behavior relative to wind turbines while taking into consideration other landscape features that might have been influencing grouse behavior which provides a more accurate representation of the potential impacts. By focusing on grouse response in relation to distance to turbines, we were able to summarize and interpret the magnitude of an effect that could be used in habitat management decisions. However, while distance to turbine has been a common response variable evaluated due to its ease of interpretation, it may not accurately measure the behavioral responses of grouse to wind turbines. For example, the proportion of disturbance associated with wind turbine pads and roads consistently out-performed models with distance to wind turbines in a sage-grouse study in Wyoming (LeBeau et al. 2017b), and turbine density was included in a set of competing models of nest survival and habitat selection models for Columbian sharp-tailed grouse in Idaho (Proett et al. 2019). This suggests that density of infrastructure associated with wind energy facilities may be a better predictor of behavioral responses than distance to wind turbines that later of which aligns with the majority of studies reporting minimal adverse effects. Future studies should consider a measure of density along with distance to turbines to thoroughly understand the behavioral responses of grouse to wind turbines.

The study-result combinations that were included our analysis were restricted to the fixed-effect of distance to turbine; studies that compared mean effects between treatment and control areas were not considered. The studies and resulting study-structure combinations that did not meet our study inclusion requirements could have influenced our interpretation of the results. For example, male black grouse attending leks in close proximity to turbines were displaced (Zwart et al. 2015) and red grouse occupancy and distribution were negatively affected by wind turbines (Pearce-Higgins et al. 2012). While three other studies did not find any effect of wind turbines on red grouse abundance or greater prairie-chicken nest site selection and survival (Pearce-Higgins et al. 2009, Douglas et al. 2011, McNew et al. 2014). The results from these studies align with the results of our meta-analysis where the magnitude of effects were small and varied among studies.

The effects of distance to turbines on grouse behavior may vary based on season or life-cycle. Hovick et al. (2014) found a consistent adverse effect of anthropogenic features on grouse populations during multiple life-cycle periods. However, the majority of research evaluating the effects of wind turbines on grouse population metrics were conducted during the breeding period. The one non-breeding study-result combination evaluated in our analysis was found to be highly influential in the estimate of habitat selection mean effect size. Greater prairie-chicken space use during the non-breeding period was not affected by wind turbines but due to the variance of the estimate reported by Winder et al. 2014a, it had the potential to bias the overall effect. By removing this study-result combination from the habitat selection analysis, we were able to reduce this potential bias. But doing so limited our analysis of habitat selection relative to wind turbines to the breeding period only. Therefore, additional studies are needed to evaluate grouse responses to wind turbines during the non-breeding periods.

While our results reflected behavioral responses during the breeding period, there were a few population vital rates that were measured consistently among study sites. The nesting time period was evaluated at all four study sites (McNew et al. 2014, LeBeau et al. 2014, 2017b, Harrison et al. 2017, Proett et al. 2019). Nest site selection and survival was not adversely affected by proximity to wind turbines suggesting that females were decided to select nest site locations based on site-specific habitat types rather than the presence of wind turbines. In addition, it appears this decision does not result in negative consequences to this population fitness parameter.

Female survival was the other population parameter that has been evaluated at multiple study sites (Winder et al. 2014a, Smith et al. 2016, LeBeau et al. 2014, 2017b). Similar to nest survival, the presence of wind turbines did not appear to negatively impact female survival. Nest and female survival are important population parameters that influence population viability because they are measures of population recruitment (Taylor et al. 2012, Dahlgren et al. 2016). Recruitment can be indexed through lek counts, and the lack of adverse impacts to nest and female survival likely contributed to the lack of negative impacts on lek attendance. However, it is important to note that the majority of the studies included in this analysis occurred over relatively short time frames. Long-term lek trend information is needed to thoroughly understand population level effects (Harju et al. 2010, Dahlgren et al. 2016). In addition, brood survival was not sufficiently evaluated in these studies. Brood survival can be important to overall population viability and should be investigated further (Dahlgren et al. 2016).

Similar to season, the effects of distance to turbines on grouse behavior may vary based on species specific responses. However, the purpose of this analysis was to evaluate the overall magnitude of effect associated with this species as a group. Our analysis considered three North American grouse species. Studies of grouse species of conservation interest including lesser prairie-chicken and plains sharp-tailed grouse populations were not included because no studies were found during our search. The lack of studies directly measuring the effects of wind turbines on lesser prairie-chicken and plains sharp-tailed grouse populations limit our ability to make inferences to these species; however, these species exhibit similar behavior and occupy similar habitats as the studied grouse populations and it is inferred that these species will exhibit similar responses to wind energy development as the studied grouse species. However, further research is necessary to estimate potential impacts to these species and species-specific responses.

The number of study-result combinations included in the analysis was relatively high but it is important to note that these effects came from four separate study locations. The results from these studies represent the affected grouse population, wind facility characteristics, and level of existing habitat fragmentation on the landscape among other biotic and abiotic features. A detailed assessment of these characteristics should be used to develop landscape and site-specific scale siting tools to help inform siting of future wind energy developments in grouse habitats. In addition, it is important to note that these studies do not consider the cumulative effects of multiple wind energy facilities on the landscape as these study sites are great distances apart. It is unknown how multiple facilities on the landscape would affect a grouse population, but we assume the impact would be similar to other forms of development that fragment the landscape.

Without the inclusion of studies with regression coefficients, our sample size would have been reduced substantially from 22 to nine study-result combinations, reducing the robustness of the analysis. However, by focusing on the studies with regression coefficients in our analysis we had to make some assumptions (Becker et al. 2007). We assumed that all study-result combinations were important population parameters affecting grouse population viability and that one response was not more important than another even though adult female survival might be an important contributor to grouse populations (Taylor et al. 2012). We also assumed all other coefficients associated with additional covariates included in the regression models (e.g., shrub or grass cover) were held constant. Despite these challenges, recent studies (e.g., Becker et al. 2007 and Peterson and Brown 2005) have advocated for the synthesis of regression slopes in meta-analysis because many studies only include regression slopes in their results, as in common in the ecological field.

The results of this analysis build upon meta-analyses previously conducted to estimate effect sizes of other anthropogenic features on grouse populations. Previous analyses lacked assessments of the effect sizes associated with wind energy facilities due to the limited number of studies that existed at that time (e.g., Hagen 2010, Hovick et al. 2014). An important step in understanding the impacts of wind energy development on grouse populations is to place the impacts observed in this study in context with other forms of anthropogenic structures so that managers can be informed while conserving grouse habitats. Future analyses should build upon Hovick et al. (2014) by incorporating studies that report regression coefficients and provide relative effect sizes for various anthropogenic features including wind energy development.

Until then, inferences from this study can be applied to future wind energy facilities located in similar habitats and associated with similar grouse populations as the populations included in this analysis. As additional research is conducted, similarities between study sites and seasonal, species-specific, or behavioral response will be identified to inform siting of future wind energy facilities in grouse habitats that avoid, minimize, or mitigate impacts. Reducing the impacts of energy development is a necessary step to conserve the habitats of these indicator species upon which many other species also rely.

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Appendix A Summary of grouse studies included in the meta-analysis estimating effect sizes associated with grouse behavior relative to wind turbines.

Appendix A. Study-result combination used in the meta-analysis to estimate the magnitude of effect of distance to wind turbines on grouse habitat selection, survival, and lek attendance. Study-result combination Winder et al. 2014b (B) was removed from the overall modelled mean due to potential bias

Study	Species	Location	Model Type	Model Estimate	SE	Sample Size
Habitat Selection						
Harrison et al. 2017 (A)	GRPC	Nebraska	Discrete choice – nest selection	0.00020	0.00020[a]	91
LeBeau et al. 2017b (A)	GRSG	Wyoming	Discrete choice – nest selection	-0.07000	0.14805 [a]	104
LeBeau et al. 2017b (B)	GRSG	Wyoming	Discrete choice – brood selection	0.19780	0.03480	42
LeBeau et al. 2017b (C)	GRSG	Wyoming	Discrete choice – summer selection	-0.04150	0.01240	125
Winder et al. 2014a (A)	GRPC	Kansas	Resource Utilization Function – breeding	0.07500	0.04100	102
Winder et al. 2014a (B)	GRPC	Kansas	Resource Utilization Function – non breeding	0.00020	0.00020	37
Lek Attendance						

LeBeau et al. 2017a (A)	GRSG	Wyoming	General linear mixed model – Neg. Binomial male lek attendance (4 yrs post-development)	0.01300	0.03010 [a]	14
LeBeau et al. 2017a (B)	GRSG	Wyoming	General linear mixed model – Neg. Binomial male lek attendance (5 yrs post-development)	0.05000	0.03130 [a]	14
LeBeau et al. 2017a (C)	GRSG	Wyoming	General linear mixed model – Neg. Binomial male lek attendance (6 yrs post-development)	0.05300	0.03410 [a]	14
LeBeau et al. 2017a (D)	GRSG	Wyoming	General linear mixed model – Neg. Binomial male lek attendance (7 yrs post-development)	-0.02000	0.04230	14
Smith et al. 2016 (A)	GRPC	Nebraska	General linear mixed model – Poisson female lek attendance	0.00030	0.01450	15
Survival						
Harrison et al. 2017 (B)	GRPC	Nebraska	Daily nest survival – nest survival	0.00010	0.00010	91
LeBeau et al. 2014 (A)	GRSG	Wyoming	Cox proportional hazards regression – nest survival	-0.07400[b]	0.02800	95

LeBeau et al. 2014 (B)	GRSG	Wyoming	Cox proportional hazards regression – brood survival	-0.47900 [b]	0.16700	31
LeBeau et al. 2014 (C)	GRSG	Wyoming	Cox proportional hazards regression – female survival	0.01110 [b]	0.02770	116
LeBeau et al. 2017b (D)	GRSG	Wyoming	Cox proportional hazards regression – brood survival	-0.06900 [b]	0.07110 [a]	123
LeBeau et al. 2017b (E)	GRSG	Wyoming	Cox proportional hazards regression – nest survival	-0.01030 [b]	0.01720	302
LeBeau et al. 2017b (F)	GRSG	Wyoming	Cox proportional hazards regression – female survival	0.03260 [b]	0.01620	511
Proett et al. 2019 (A)	CSTG	Idaho	General linear model - nest survival	0.00006	0.00002	147
Smith et al. 2017 (A)	GRPC	Nebraska	Logistic exposure survival – female survival	0.16000	0.12245	62
Winder et al. 2014b (A)	GRPC	Kansas	Binomial model – female survival	0.00300	0.15153	220
Winder et al. 2015 (A)	GRPC	Kansas	logistic regression – annual probability of lek persistence	0.13000	0.08000	23

[a] Standard errors were calculated from confidence intervals assuming a normal distribution

[b] Cox proportional hazard regression coefficients were inverted to interpret survival rather than risk