

Prairie grouse and wind energy: the state of the science

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Introduction

Electricity generation is one of the leading sources of greenhouse-gas emissions and decarbonization of this sector is a critical part of efforts to limit anthropogenic climate change (Bruckner et al. 2014, Rogelj et al. 2018). Reducing the severity of anthropogenic climate change by avoiding future emissions from fossil-fuel combustion is expected to yield significant long-term benefits for wildlife (Warren et al. 2018), whereas failure to address climate change is likely to lead to widespread wildlife extinctions (e.g., Wiens 2016). Renewable energy sources can contribute to reducing emissions of greenhouse gases; however, development of wind and solar facilities may also have adverse effects on some wildlife species (Kuvlesky et al. 2007, Lovich and Ennen 2011, Allison et al. 2019). With demand for renewable energy growing quickly, understanding the consequences for wildlife, and how to mitigate¹ any negative effects, have become critical questions for conservation biologists to address.

Experience suggests that reducing the risk of negative effects on wildlife populations from increased deployment of renewable energy is possible when informed by reliable empirical information. For example, two decades of research on wind energy and wildlife interactions has led to an improved ability to assess risk and, in some cases, to mitigate effects on raptors, other migratory birds, and bats (e.g., Allison et al. 2019). For groups of wildlife where the scientific foundation is less well-established, however, efforts at risk assessment and mitigation are both more contentious - important stakeholders may disagree on the degree of risk involved in constructing new facilities - and potentially less effective. Although constructing policy that balances risks and benefits to wildlife of developing renewable energy is an inherently value-laden process, and thus beyond the scope of this paper, a shared understanding of the ecological facts informed by current science can serve as an important starting point.

One group for which the potential effects of renewable-energy development may be significant, but about which relatively little is known, is the North American prairie grouse (*Tetraoninae*), including two species of sage-grouse (Greater Sage-grouse [*Centrocercus urophasianus*] and Gunnison Sage-grouse [*C. minimus*]), two species of prairie-chicken (Greater Prairie-Chicken [*Tympanuchus cupido*] and Lesser Prairie-Chicken [*T. pallidicinctus*]), and Sharp-tailed Grouse (*T. phasianellus*). Understanding the effects of wind-energy development on prairie grouse is particularly important because these species are of high conservation concern, some are important game species, and all have geographic distributions that overlap extensively with areas of potentially high-value wind resources that may experience significant development pressure in the coming decades. Indeed, the potential for impacts of wind-energy development was an important factor in the US Fish and Wildlife Service's (USFWS) decision to list Lesser Prairie-Chicken as Threatened under the Endangered Species Act (a decision later vacated by the courts).

¹ Throughout, we use mitigation as a comprehensive term that includes avoidance of impacts, minimization of impacts, and compensation (e.g., offsets) for unavoided impacts.

Despite the potential influence of wind-energy development on prairie grouse populations, a comprehensive review of the current science is lacking. Relevant empirical information is scattered across scientific journals and reports, and no readily accessible summary of the science exists. In part because of this, uncertainty persists as to the nature of the effects of wind-energy development on prairie grouse and what measures would be effective in reducing or offsetting any negative effects. To address this gap, we present a broad, cross-species synthesis of the potential consequences of wind-energy development on prairie grouse. We rely on all sources of information available to us including existing peer-reviewed publications and published reports. In doing so, we build upon a recently published systematic review of the literature on wind energy's effects on grouse around the world (Coppes et al. 2019), but focus specifically on the species endemic to North America's grasslands and shrub-steppe, incorporating research results not available during that review, and drawing on our own collective expertise with these five species.

We begin with a summary of the state of the science surrounding wind energy and its effects on prairie grouse and their habitats in the U.S. and Canada. We then identify the major information gaps that remain, with a focus on identifying research that would improve our understanding of how prairie grouse respond to wind-energy development and inform future conservation actions. Our purpose in providing this synthesis is to outline the empirical basis for assessing risk associated with future wind-energy developments and guide future research towards what we believe are topics that will enhance the scientific basis for conserving prairie grouse in the face of anticipated build-out of wind energy.

Natural history and conservation status

Natural history

Detailed monographs and edited volumes exist for each species (see Connelly et al. 1998, Schroeder et al. 1999, Hagen and Giesen 2005, Knick and Connelly 2011, Johnson et al. 2011, Young et al. 2015, Haukos and Boal 2016), so we present only brief summaries about the natural history of North American prairie grouse.

Distribution

Collectively, prairie grouse occupy shrub-steppe and grasslands of central and western North America. Gunnison Sage-Grouse and Lesser Prairie-Chicken have the smallest geographic distributions. Gunnison Sage-Grouse inhabits sagebrush of western Colorado and eastern Utah and Lesser Prairie-Chicken is limited to the short-grass, mixed-grass, sand sagebrush (*Artemisia filifolia*), and sand shinnery oak (*Quercus havardii*) prairies of the Southern Great Plains. Sharp-tailed Grouse, in contrast, occupies a broad range of grasslands and shrublands from western Quebec to central Alaska and as far south as Colorado. Seven subspecies of Sharp-tailed Grouse have been recognized at various times, of which two are of primary interest from the standpoint of wind-energy development: Plains Sharp-tailed Grouse (*P. t. jamesii*) of

the Great Plains and Columbian Sharp-tailed Grouse (*P. t. columbianus*) of the Great Basin and Columbia Plateau, both of which occupy geographic ranges that overlap with areas of potential interest for development of wind-energy facilities.

In between these distributional extremes are Greater Sage-Grouse and Greater Prairie-Chicken. Greater Sage-Grouse, which do not co-occur with Gunnison Sage-Grouse, occupy sagebrush ecosystems from the high plains east of the Rocky Mountains to the eastern slopes of the Sierra Nevada, and from Alberta and Saskatchewan, Canada, south to Nevada, Utah, and Colorado. Greater Prairie-Chicken once inhabited mixed- and tall-grass prairie from the eastern edge of the Great Plains (from Ontario south through Ohio and Kentucky) to central Saskatchewan, but is now limited to remnant prairie from eastern Colorado to central Illinois. A now-extinct subspecies of Greater Prairie-Chicken, the Heath Hen (*T. c. cupido*), occurred in areas of early-successional vegetation along the New England and mid-Atlantic coasts.

Habitat

Although generally non-migratory, prairie grouse exhibit significant seasonal variation in habitat use that corresponds to different phases of their annual cycles. Among Greater Sage-Grouse, this may include long movements among seasonal ranges (e.g., >100 km in some populations of Greater Sage-Grouse [Connelly et al. 2011, Tack et al. 2012, Newton et al. 2017]). All species have a mating system in which males gather and display for females at traditional locations known as leks. Leks are generally located in relatively open areas of low vegetation where males are highly visible. Nesting habitat, in contrast, tends to consist of relatively tall and dense vegetation. Nests are often constructed within several kilometers of leks. After the eggs hatch, females move with their young to brood-rearing areas that afford a mixture of protective cover and an abundance of insects and forbs. During winter, individuals may move into riparian areas or other areas with greater grass or shrub cover - although this varies considerably among species - that provide access to food and protection from the elements.

Space use

All prairie grouse show high site fidelity, with adult males joining the lek closest to where they hatched and then remaining faithful to that lek for the duration of their lives (Campbell 1972, Dunn and Braun 1985, Schroeder and Robb 2003, Peck et al. 2012, Fremgen et al. 2017). Indeed, most studies find that, throughout the year, nearly all of the space used by individuals of both sexes is within 10 km of the lek that they attend in spring, although migratory populations wander further afield (Hamerstrom and Hamerstrom 1949, Taylor and Guthery 1980, Aldridge and Boyce 2007, Coates et al. 2013, Gerber et al. 2019). Migratory populations of Greater Sage-grouse may move >100 km between seasonal habitats, whereas Gunnison Sage-grouse typically move shorter distances (up to 40 km) between breeding and wintering habitat. Greater Prairie-Chicken, Lesser Prairie-Chicken, and Sharp-tailed Grouse are not known to have populations that exhibit regular patterns of seasonal migration.

Life-history strategies and population dynamics

Prairie-chickens and Sharp-tailed Grouse exhibit life histories characterized by relatively low adult survival and larger investments in reproduction, with corresponding variation in population growth rates driven by annual variation in survival of eggs and chicks (Hagen et al. 2009, Gillette 2014). Species with these life-history traits are expected to show greater fluctuation in population size (Saether et al. 2013) and prairie-chickens and Sharp-tailed Grouse all tend to exhibit a cyclic boom-or-bust pattern of population growth (Ross et al. 2018).

Sage-grouse, in contrast, have evolved a broadly different life-history strategy, which may have implications for population dynamics and conservation. Compared to other prairie grouse, sage-grouse tend to have high adult survival and low reproductive investment with population growth rates that respond more strongly to variation in adult survival - especially of females - than to variation in reproductive parameters such as clutch size, renesting rate, nest survival, and chick survival (Taylor et al. 2012, Dahlgren et al. 2016). Population growth rates among sage-grouse show relatively high year-to-year consistency (Dahlgren et al. 2016, Coates et al. 2018), although populations cycle over 6-9 year intervals (Fedy and Aldridge 2011), with growth rates varying accordingly.

Conservation status

Gunnison Sage-Grouse is considered Threatened in the U.S. under the federal 1973 Endangered Species Act (ESA). Lesser Prairie-Chicken was briefly listed as Threatened before a court order vacated this rule in response to a lawsuit filed by oil and gas producers and several New Mexico counties. Following subsequent petitions by conservation organizations, and a finding by the USFWS that listing may be warranted, it is once again a candidate for listing, currently under review by the USFWS.

Listing of Greater Sage-Grouse throughout its U.S. range was avoided in 2015 by the implementation of a multi-stakeholder strategy that involved voluntary conservation commitments on private lands and updates to some Federal land-management plans, although recent changes to those plans have led to renewed litigation concerning the protection of the species. Greater Sage-Grouse are considered an endangered species in Canada under the federal Species at Risk Act (Aldridge and Brigham 2003).

Estimated population size of Lesser Prairie-Chickens was 38,637 (90% CI: 20,233 - 49,698) in 2018, about the same as it was in 2012 (Nasman et al. 2018), the first year in which range-wide population surveys were conducted. However, current numbers are substantially less than the approximately 150,000 individuals thought to have constituted the species' population throughout most of the 1970s and 1980s (Garton et al. 2016). Trends in population size are obscured by large annual fluctuations in population size (between 2012 and 2017, year-to-year percent changes in estimated total population size ranged from -48% to +34%) but the general pattern is one of long-term decline since the late 1980s (Garton et al. 2016, McDonald et al. 2017). Most (*ca.* 65%) individuals occur in the population that recently colonized the shortgrass prairie/Conservation Reserve Program (CRP) ecoregion of northwestern Kansas (McDonald et

al. 2017). Three other ecoregional populations found in 1) the sand sagebrush prairie of southwestern Kansas and southeastern Colorado, 2) the mixed-grass prairie of northwestern Oklahoma, northwestern Texas, and south-central Kansas, and 3) the sand shinnery oak prairie of eastern New Mexico and northwestern Texas constitute the remainder of the global population. Genetic data suggest that the population inhabiting the shortgrass prairie/CRP ecoregion was founded by individuals dispersing north from the mixed-grass prairie ecoregion; otherwise, gene flow among ecoregional populations is infrequent (Oyler-McCance et al. 2016).

Rigorous estimates of national and regional population sizes based on systematic survey protocols are lacking for Greater Prairie-Chicken populations but Partners in Flight estimates a total population size at 200,000 - 630,000 (Will et al. 2019). Local extinctions have greatly curtailed the distribution of this species, especially at the northern, southern, and eastern limits of its range (Johnson et al. 2011). Most extant populations show evidence of long-term declines (Johnson et al. 2011). Sharp-tailed Grouse population size is also poorly documented but was estimated by Partners in Flight as 570,000 - 980,000 (Will et al. 2019). Recent, range-wide population trends for this species are also poorly documented, but the substantial range contraction observed during the 20th century (Connelly et al. 1998) suggests an overall decline, at least in southern portions of the species' distribution. Steep declines have also been noted among populations of the Columbian Sharp-tailed Grouse (e.g., Schroeder et al. 2000).

Greater Sage-Grouse range has contracted since the early 1900s, with extirpations occurring in five states and one province (Schroeder et al. 1999, 2004). Declines in population size appear to have continued, primarily in peripheral populations and in the Great Plains ecoregion of Montana, Wyoming, North Dakota, and South Dakota, at approximately 0.8% per year between 1965 and 2015 based on counts of males at leks (WAFWA 2015). This long-term decline is superimposed upon short-term patterns of variation driven by environmental stochasticity in vital rates and medium-term population cycles that occur on a 6-9 year period (Fedy and Aldridge 2011, Fedy and Doherty 2011). Minimum population size of Greater Sage-Grouse as of the beginning of the 2015 breeding season was thought to be approximately 424,000 individuals (WAFWA 2015). Gunnison Sage-Grouse, recognized as a distinct species only recently (Young et al. 2000), have a population estimate of <5,000 individuals (Young et al. 2015). After undergoing substantial declines in recent decades, numbers in the largest remaining population, in Colorado's Gunnison Basin, have stabilized, although the other six populations continue to decline (Young et al. 2015).

Effects of wind energy on prairie grouse

Anatomy of a wind-energy facility and potential mechanisms of effect on prairie grouse

Construction of wind-energy facilities generally involves building new access roads or improving existing roads and clearing sites on which to place the turbines and associated infrastructure,

potentially including service buildings and substations. Collection and delivery of power generated at the site may also require clearing areas for poles to support power lines, although in some cases these lines may be buried. The amount of land permanently occupied by wind-energy infrastructure is highly variable, ranging from 0.06 - 2.4 ha/MW with an average of 0.3 ha/MW (Denholm et al. 2009). Differences in land cover - for example, forest versus agriculture - and topography at the facility location explain some of the variation in the extent of land-cover change associated with construction of a wind-energy facility (Diffendorfer and Compton 2014), with greater land transformation occurring at facilities built in steep, forested landscapes.

Roads account for most of the direct, permanent ground disturbance at wind-energy facilities in the U.S. (Denholm et al. 2009, Diffendorfer and Compton 2014). Turbine pads, substations, and transmission lines account for most of the remaining area of permanently disturbed land (Denholm et al. 2009). The area of land disturbed temporarily by construction, but not permanently occupied by infrastructure, is more extensive, averaging 0.7 ha/MW (Denholm et al. 2009).

As we review in subsequent sections, patterns of response by prairie-grouse to wind-energy development are not extensively documented and, not surprisingly, mechanisms underlying responses are even less well-understood. Here, we discuss briefly potential pathways by which effects of wind energy may be manifested, recognizing that these are hypotheses based largely on extrapolation from other systems and responses to other anthropogenic structures.

Construction and operation of wind-energy facilities may affect prairie-grouse populations by both direct and indirect pathways. We differentiate between direct and indirect effects using the approach of Hebblewhite (2011). Direct effects of development are those that occur via the direct interaction of people, infrastructure, and the focal species, and may include habitat loss and degradation or direct mortality caused by humans or infrastructure. Direct mortality from collision with turbine blades is not a widespread or significant problem for prairie-grouse; very rarely do they fly high enough to enter the rotor-swept area and collisions with support towers are not commonly recorded (AWWI 2019). The amount of habitat loss or degradation caused by land clearing is relatively small compared to the amount of space used by individual grouse.

Potentially more significant is the functional habitat loss that occurs when individuals avoid using otherwise available habitat around wind-energy infrastructure. Importantly, functional habitat loss occurs even in the absence of changes to land cover. In general, avoidance is thought to be a response to changes in the perceived risk of predation, which itself is presumably driven by some visual or acoustic cue associated with wind-energy infrastructure or associated activities. For example, Pruett et al. (2009b) argued that a cognitive association between tall structures and avian predators might trigger avoidance of wind turbines. Other cues associated with increased human activity, including vehicular traffic, construction noise, or noise produced by turbines during operation, might generate a similar response, as has been suggested to explain avoidance of roads and oil and natural-gas wells by Greater Sage-Grouse (Blickley et al. 2012, Fedy et al. 2015, Holloran et al. 2015).

Avoidance behavior reduces the carrying capacity of an area in the same way as would habitat loss or degradation, being mediated ultimately by some form of density-dependent reduction in recruitment or survival. However, measurable effects on vital rates and population abundance may take longer to manifest and be more difficult to estimate given the sample sizes typical of most studies of prairie grouse, whereas changes in patterns of habitat selection that are indicative of avoidance may be far more immediate and more readily detectable. Behavioral changes are a useful and early sign of effects but must translate into demographic changes if they are to produce population-level consequences. Coupled patterns of avoidance and population decline are apparent from studies of prairie grouse responses to other forms of energy development (Aldridge and Boyce 2007, Holloran et al. 2010, LeBeau et al. 2019). Finally, direct effects of wind-energy development could also operate immediately on vital rates themselves without any intermediate effect on habitat use. For example, noise associated with the construction and operation of wind-energy facilities might also interfere with courtship activities, reducing pairing success (Blickley et al. 2012), or produce sub-lethal, chronic stress responses, potentially suppressing survival or reproductive rates (Ortega 2012).

Indirect effects are those mediated by changes in the abundance or activity of other species, especially predators, that are in turn associated with operation and construction of wind-energy facilities. These effects could arise through changes in the risk of predation by increases in predator abundance or activity (e.g., edge effects) or through associated changes in behavior of prairie grouse. Changes in predator abundance could also lead to behavioral avoidance of areas with higher densities or activity rates of potential predators. In general, indirect effects may be more likely to be evidenced by altered vital rates (e.g., lower rates of nest survival due to greater abundance of nest predators) than are the direct effects of wind-energy development. Predicting the sign and magnitude of these potential effects, however, is difficult as they appear to be strongly context-dependent and few generalizations are evident from studies of other forms of disturbance associated with energy development. For example, whereas above-ground power lines support greater densities of Common Ravens (*Corvus corax*), an important predator of Greater Sage-Grouse nests (Lockyer et al. 2013, Coates et al. 2014, Gibson et al. 2018), potential predators of Sharp-tailed Grouse nests - primarily mammals like striped skunks (*Mephitis mephitis*) or American badgers (*Taxidea taxus*) - appeared to avoid one area in North Dakota with a high density of oil and gas wells (Burr et al. 2017). The only published study to examine the potential effects of a wind-energy development on predators of prairie-grouse found no evidence that occupancy rates of potential predators varied as a function of distance to a turbine (Smith et al. 2017a).

Existing conservation measures at wind-energy facilities

Science-based conservation measures for minimizing effects of wind-energy facilities on grouse populations are lacking. Most existing conservation measures stem either from knowledge of the effects of other anthropogenic disturbances or from basic information on the natural history of prairie grouse. At the broadest level, wind-energy development is discouraged or precluded in core habitats (i.e., areas that support a large percentage of the breeding population or high quality habitat and habitat corridors that connect them) of prairie grouse (see, e.g., Van Pelt et al. 2013, State of Montana 2015). Outside of core habitats, siting of wind-energy facilities is

encouraged in areas already disturbed by agriculture or existing energy infrastructure, the idea being that habitat quality in these areas is already low, that they support relatively few individuals, and that any additional habitat degradation caused by the construction of wind-energy infrastructure will have minimal consequences for rangewide conservation efforts (Obermeyer et al. 2011, Kiesecker et al. 2011, Fargione et al. 2012). Siting facilities in areas already cleared of native vegetation could also reduce carbon emissions from soil disturbance and impacts on habitat of other species (Kiesecker et al. 2019).

When avoidance of grouse habitat is not possible, conservation measures generally focus on minimizing potential effects of infrastructure, usually by establishing setbacks from lek locations. Developing optimal setback distances that can apply across locations and species has proven challenging, however. Prairie grouse tend to nest and raise broods within 10 km of a lek (Holloran and Anderson 2005, Aldridge and Boyce 2007, Winder et al. 2015a) and therefore lek-centered conservation that protects an adequately large area will secure most of the space and resources needed for reproduction. For prairie-chickens, which are mostly non-migratory and tend to remain relatively close year-round to the lek that they attend in spring, lek-centered conservation may prove useful in protecting non-breeding habitat, too (Patten et al. 2011, Boal and Pirius 2012). Focusing protection measures on areas surrounding leks may be less effective for full annual-cycle conservation of sage-grouse, which can move much greater distances between discrete, seasonal home ranges (Aldridge and Boyce 2007, Connelly et al. 2011).

Defining optimal setback distances is also difficult because the distance at which effects of a disturbance can be detected appears highly context dependent and relatively unpredictable (see, e.g., Manier et al. 2014) and because of the complexity of modeling the diminishing gains associated with larger setback distances (e.g., Coates et al. 2013). As a consequence, recommended setbacks vary widely, and most are based on expert opinion rather than empirical estimates of disturbance distances (Powell et al. 2017). For example, Manville (2004) recommended maintaining an 8-km buffer between wind-energy infrastructure and active leks of all species of prairie grouse, whereas Van Pelt et al. (2013) suggested a 2-km buffer for all forms of disturbance around active leks of Lesser Prairie-Chicken. In Wyoming, a 1-km setback around Greater Sage-Grouse leks was established for mines and oil and gas wells in core areas - wind energy is discouraged in core areas - but this distance is reduced to 0.4 km outside of core areas (State of Wyoming 2019). In some cases, recommended setbacks are tailored for specific kinds of disturbances: Montana also prohibits new wind-energy facilities in core areas for Greater Sage-Grouse, but establishes a 6.5-km buffer around leks outside of core areas for wind-energy facilities and a 0.4-km buffer outside of core areas for other forms of development (State of Montana 2015).

Compensatory mitigation is not widely used as a tool for mitigating impacts of wind-energy development on prairie grouse (Jakle 2012). The in-lieu fee program established in the Lesser Prairie-Chicken Range-wide Conservation Plan (Van Pelt et al. 2013) is the most prominent example of using compensation as a tool for offsetting effects of development on prairie grouse, although wind-energy developments constitute a very small percentage of the projects offset by

the ca. 242,000 ha of land managed under this program (Wolfe et al. 2018). Similar efforts have been undertaken for offsetting development impacts to Greater Sage-Grouse, including a habitat bank in Wyoming (LeBeau et al. 2018), Montana's Sage Grouse Habitat Conservation Program (see <https://sagegrouse.mt.gov>), and Utah's habitat credit exchange that allows developers to purchase credits from private landowners who maintain or restore habitat for Greater Sage-Grouse and in doing so offset effects of permanent disturbance elsewhere (see <https://watershed.utah.gov/sgmitigation/>). Opportunities for engaging landowners in habitat restoration that would benefit prairie grouse are numerous, including restoring conifer-invaded shrub-steppe (Baruch-Mordo et al. 2013), improving range-management practices (McNew et al. 2012, Winder et al. 2018), and restoring fire regimes that prevent further loss of native prairie to woody-plant encroachment (Fuhlendorf et al. 2017). When coupled with avoidance and minimization tactics, an increased use of compensatory offsets could improve conservation outcomes for prairie grouse while allowing for the intensity of new wind-energy development needed to meet reduction targets for greenhouse-gas emissions (e.g., Obermeyer et al. 2011).

Studies at wind-energy facilities: research design

Published research on prairie-grouse population ecology relative to wind-energy development has been carried out at five different wind-energy facilities (Table 1). Only Greater Prairie-Chicken has been studied at two different wind-energy facilities (Table 1). No published studies have evaluated the effects of wind-energy development on Gunnison Sage-Grouse or Plains Sharp-Tailed Grouse.

The wind-energy facilities that have hosted research on prairie grouse vary considerably in size (Table 1) and landscape context. Two of the five facilities studied were in relatively intact landscapes, whereas the other three were built in locations with an extensive existing human footprint.

These studies vary considerably in experimental design and duration of observations (Table 1). Only two facilities have hosted studies that collected pre-construction data. LeBeau et al. (2017b) used an unreplicated Before-After/Control-Impact (BACI) design, with control data collected at a site adjacent to the wind facility but far enough from the turbines (mean distance from control leks to a turbine: 11.0 km; range: 7.1 - 16.2 km) to be considered independent of any treatment effect. McNew et al. (2014) and Winder et al. (2014a,b; 2015b) paired a gradient design (Morrison et al. 2008), in which effects are assessed using the response of individuals measured at different distances from the wind turbines, with a before-after framework (i.e., a before-after/gradient [BAG] design). The length of the gradient for these four studies was approximately 28 km.

Table 1. Summary of studies examining wind-energy effects on population ecology of North American prairie grouse.

Location	No. turbines (capacity of facility or complex)	Taxon	Landscape context	Experimental design (study duration [years pre-, post-construction])
Wyoming	79 (118.5 MW)	Greater Sage-Grouse	Intact sage-steppe	BACI ¹ (3, 8) After/Control-Impact ² (0,6) After/Gradient ³ (0,2)
Idaho	215 (366.3 MW)	Columbian Sharp-tailed Grouse	Fragmented Palouse prairie, CRP, and agriculture	After/Gradient ⁴ (0,2)
Kansas	67 (201 MW)	Greater Prairie-Chicken	Fragmented tallgrass prairie and row-crop agriculture	Before-After/ Gradient ^{5,6,7,8} (2,3)
Nebraska	36 (59.4 MW)	Greater Prairie-Chicken	Intact tallgrass prairie	After/Gradient ^{9,10,11} (0,2)
Kansas	200 (400 MW)	Lesser Prairie-Chicken	Fragmented mixed grass prairie and row-crop agriculture	After/Gradient ¹² (0,3)

¹ Before-After/Control-Impact; LeBeau et al. 2017b

²LeBeau et al. 2017a

³LeBeau et al. 2014

⁴Proett et al. 2019

⁵McNew et al. 2014

⁶Winder et al. 2014a

⁷Winder et al. 2014b

⁸Winder et al. 2015b

⁹Harrison et al. 2017

¹⁰Smith et al. 2017a

¹¹Raynor et al. 2019

¹²LeBeau et al. 2020b

The remaining studies all relied on post-construction data only. LeBeau et al. (2017a) relied on an impact-control design, whereas LeBeau et al. (2014), Harrison et al. (2017), Smith et al. (2017a), Raynor et al. (2019), Proett et al. (2019), and LeBeau et al. (2020b) used gradient designs (with lengths of 16 km, 24 km, 23 km, 24 km, 14 km, and 7 km, respectively).

All things being equal, inferences offered by studies that incorporate pre-construction data, include some form of control, and that are based on longer time-series are considered more

robust than those derived from studies that lack pre-construction data, control areas, or are conducted over relatively short periods of time. Long study durations are especially important for species like prairie grouse that exhibit high site fidelity and that may therefore show a delayed response to changes in habitat quality, including lagged declines in lek attendance or recruitment to leks (e.g., Monroe et al. 2017).

Studies at wind-energy facilities: evidence for effects

Adult Survival

Survival of adult female Greater Prairie-Chicken (Winder et al. 2014b, Smith et al. 2017), Greater Sage-Grouse (LeBeau et al. 2014, LeBeau et al. 2017a), and Lesser Prairie-Chicken (LeBeau et al. 2020) measured at 0-3, 8-9, 1-2, 1-6, and 1-3 years post-construction, respectively, did not vary as a function of distance to a wind turbine. Some evidence suggests a positive effect of wind-energy facilities on adult female survival: Winder et al. (2014) found that annual survival of Greater Prairie-Chickens was substantially greater during the 3-year post-construction period than the 2-year pre-construction period (57% v. 32%), and LeBeau et al. (2017a; 2019) found survival of Greater Sage-Grouse and Lesser Prairie-Chicken was greater in areas that contained a higher density of wind-energy infrastructure (roads and turbine pads). Explanations for higher post-development survival are speculative but generally involve potential negative effects of development on common predators of prairie grouse (i.e, a positive indirect effect on grouse; Winder et al. 2014b, Smith et al. 2017, LeBeau et al. 2017a).

Reproduction

Nest survival for Greater Prairie-Chicken was not affected by the development of a 201-MW wind-energy facility (McNew et al. 2014). Harrison et al. (2017) and Proett et al. (2019) found no relationship between distance to a wind turbine and nest survival of Greater Prairie-Chicken and Sharp-tailed Grouse, respectively, but did not collect pre-construction data and thus it remains uncertain whether patterns of nest survival were affected by construction and operation of the facilities at which they worked. LeBeau et al. (2014) reported that survival of Greater Sage-Grouse nests and broods declined with proximity to a wind turbine, but an analysis of a larger sample from a longer time-series collected at the same facility found no effect of distance to a wind turbine on either nest or brood survival (LeBeau et al. 2017a). These contrasting findings from the same location highlight the challenges associated with drawing conclusions about prairie-grouse demography from samples collected over short time periods. In addition, although existing research showed no evidence of deleterious effects of wind-energy development on nest survival, the lack of pre-construction data (except for McNew et al. 2014), and lack of studies evaluating brood survival hinders our ability to draw definitive conclusions about the effects of wind-energy development on reproductive success.

Abundance and habitat use

Efforts to assess effects of wind-energy development on lek counts are limited and results mixed. Winder et al. (2015b) found no significant effect of proximity to a turbine on the

probability of Greater Prairie-Chicken lek persistence nor any differences in the probability of pre- and post- construction lek persistence when the study area was considered as a whole. Rates of change in the number of males attending leks were also unaffected by construction and operation of the wind-energy facility. However, when a subset of leks within 8 km of a turbine were analyzed separately, persistence was lower for leks closer to turbines. The decline in probability of persistence was steepest within approximately 3 km of a turbine. Among Greater Sage-Grouse, LeBeau et al. (2017b) found no effect of a 118.5-MW wind-energy facility on the trends in the number of males attending leks from pre- to post-development within a control and treatment area. Although the average number of males attending leks declined from pre-construction levels at 3 treatment leks (ranging from 1.5 - 4.1 km from a turbine), similar declines were also estimated to have occurred at control sites (leks \geq 6.3 km from the nearest turbine).

Nest-site selection by Greater Prairie-Chicken, Sharp-tailed Grouse, Greater Sage-Grouse, and Lesser Prairie-Chicken was unaffected by wind turbines, suggesting vegetation structure at this scale of selection is more influential than the presence of wind energy infrastructure (McNew et al. 2014, Harrison et al. 2017, LeBeau et al. 2017a, Proett et al. 2019, LeBeau et al. 2020).

At larger spatial scales, patterns of habitat use by male and female Lesser Prairie-Chickens at a site in Kansas were unrelated to the presence of wind turbines (LeBeau et al. 2020). Female Greater Prairie-Chickens in Kansas were not displaced by construction of a wind-energy facility but, following construction, tended to increase use of those parts of their breeding-season home range farther from a turbine (Winder et al. 2014a). Space use during the non-breeding season was not affected by construction and operation of the facility. Raynor et al. (2019) did not find a relationship between distance to a turbine and relative probability of space use or habitat selection during the breeding season among female Greater Prairie-Chickens at a site in Nebraska, although this study did not benefit from pre-construction data.

LeBeau et al. (2017a) found that areas with a greater proportion of land disturbed by infrastructure at a wind-energy facility were less likely to be used by female Greater Sage-Grouse during brood-rearing and post-brood-rearing periods. Effects on selection of brood-rearing habitat were stronger in the later years of the study, suggesting a lag time in response of at least 3 years.

In a meta-analysis of all published studies on wind energy and prairie grouse, LeBeau et al. (2020a) found substantial variation in the effect of proximity to a turbine on both habitat selection and lek attendance. For both parameters, point estimates of the effect size suggested small, negative effects of proximity to a turbine, but were bounded by wide confidence intervals that were also consistent with neutral or positive effects. Uncertainty was greatest in regard to the effects on habitat selection.

Studies at wind-energy facilities: data limitations

Three key limitations characterize existing research. First, evidence from other fields of science suggests that the results of any individual study may yield unreliable inferences about causal relationships (Johnson 2002, Ioannidis 2005, Moonesinghe et al. 2007, Nichols et al. 2019), yet replication of studies examining interactions between prairie grouse and wind energy at different facilities is rare. Second, many studies lack pre-construction data, meaning that estimates of effect are valid only if distributions of response variables in control and treatment areas differ solely due to the presence of wind turbines, or if those effects can be isolated statistically. Wind-energy facilities are not located randomly within a landscape, and thus it is likely that a whole suite of environmental factors, some related to the facility and some not, will vary with distance to a turbine. Without pre-construction data (i.e., a Before-After Gradient design) it can be difficult to account for such factors.

Finally, most studies base inference on relatively short time-series, yet short-term responses to wind-energy development may not provide insight into long-term consequences. Indirect effects mediated by changes in habitat may take years to manifest in the form of altered vital rates and population-level responses, and site fidelity may delay the appearance of avoidance behavior. Some studies of prairie grouse response to other forms of disturbance suggest that it may take 10 or more years for effects to manifest, yet to date no published studies at wind-energy facilities have followed outcomes for this long.

Extrapolating from studies of other anthropogenic disturbances

If the ecological effects of wind-energy facilities and other forms of disturbance - notably oil and gas infrastructure, power lines, and roads - on prairie grouse are underlain by similar processes, then research on these other stressors may offer further insight into the potential effects of wind energy. Here, we summarize what existing research tells us about the effect of other potential anthropogenic stressors on prairie grouse and consider how we can use this information to improve our ability to assess and mitigate risks associated with wind-energy development.

Oil and gas extraction

Substantially more research has been published concerning the impacts of oil and gas extraction on prairie grouse than has been published about wind energy. Oil and gas development results in functional habitat loss in proximity to wells and associated infrastructure and declines in the size, density, and stability of leks near oil and gas development (Pitman et al. 2005, Doherty et al. 2008, Walker et al. 2007, Pruett et al. 2009a, Holloran et al. 2010, Hagen et al. 2011, Dinkins et al. 2014, Timmer et al. 2014, Plumb et al. 2019). The distances to which these effects extend from oil and gas infrastructure appear highly variable both within and among species, likely related to differences in the nature of the development as well as grouse population structure and underlying habitat quality. For example, Pitman et al. (2005) estimated that Lesser Prairie-Chickens avoided nesting within 140 m of oil and gas wells at one site in Kansas, but showed no avoidance at another site, perhaps due to differences in noise levels or visual disturbance associated with drilling at the two locations. Hagen et al. (2011) reported

larger avoidance distances: female Lesser Prairie-Chickens reduced their use of areas within 320 m of oil and gas wells during the summer. Holloran et al. (2010) found even stronger effects among Greater Sage-Grouse, with nesting females avoiding areas within 950 m of natural-gas wells. In addition, males were less likely to recruit to leks within 3 km of wells. Functional loss of wintering habitat due to the presence of oil and gas infrastructure is also apparent among Greater Sage-Grouse, with birds avoiding areas within several kilometers of active wells (Carpenter et al. 2010, Holloran et al. 2015). In addition to species-, season-, and site-specific effects, such as visibility of disturbances (Aldridge and Boyce 2007), avoidance distances are probably also shaped by variation in well density, which itself is consistently and negatively associated with measures of habitat use and lek attendance, persistence, and density (Doherty et al. 2008, Walker et al. 2007, Holloran et al. 2010, Timmer et al. 2014, Green et al. 2017).

Effects of oil and gas development on vital rates of prairie grouse populations are less well known. Aldridge and Boyce (2007) found no effect on nest survival of Greater Sage-Grouse but showed strong avoidance of any anthropogenic development, whereas Sharp-tailed Grouse nest survival was greater in an area of North Dakota with a high density of oil wells (0.8 - 1.0/km²) than in an area that contained only a single well (density <0.01/km²), which the authors attributed to a higher density of meso-predators at the less disturbed site (Burr et al. 2017). Survival of chicks and yearlings of Greater Sage-Grouse in Alberta and Wyoming declined with increasing development of oil and gas (Aldridge and Boyce 2007, Holloran et al. 2010), despite the fact that broods avoided areas with a high density of visible wells in Alberta (Aldridge and Boyce 2007).

Why prairie grouse respond negatively to oil and gas development is unclear, but acoustic and visual disturbance may play a role, at least in explaining changes in habitat use. Attendance of males at Greater Sage-Grouse leks experimentally exposed to recorded sounds of natural-gas drilling and road traffic declined relative to control leks, with a significantly greater decline observed at leks exposed to road noise compared to drilling noise (Blickley et al. 2012). Although not conclusive, results in Dzialak et al. (2012), Fedy et al. (2015), and Holloran et al. (2015) suggest that reducing human activity levels at wells can reduce avoidance by Greater Sage-Grouse, further supporting the idea that noise and visual disturbances associated with active oil and gas development may underlie functional habitat loss (Aldridge and Boyce 2007). Stipulations that limit certain kinds of activity - typically drilling or construction - during sensitive periods of the year near leks or critical winter habitat have not been effective, however, in avoiding impacts of oil and gas development (Walker et al. 2007, Doherty et al. 2008), suggesting either that a) stipulated setback distances are too small or that b) infrequent but chronic human activity throughout the year is as detrimental as acute, noisy activities during particular seasons.

The effects of oil and gas infrastructure on prairie grouse may not be immediately apparent (but see Blickley et al. 2012), especially among longer-lived sage-grouse. Most studies report that declines in numbers begin approximately 4 years after oil and gas wells are constructed (Walker et al. 2007, Doherty et al. 2010, Harju et al. 2010, Carpenter et al. 2010, Gregory and Beck 2014, Green et al. 2016), perhaps because philopatric adults tolerate disturbance but are not

replaced by new recruits after they die. Leks attended by small numbers of males may show more immediate declines in response to oil and gas development (Gregory and Beck 2014).

Research on effects of oil and gas development and production tends to suffer from some of the same problems facing studies of wind-energy development, especially a lack of strong experimental designs that include controls and pre-construction data. Many studies also rely on relatively short durations of data collection, which may be problematic given that time lags in responses to development are common. Replication of study findings is generally better.

Power lines

Prairie grouse are less likely to use otherwise available habitat near power lines and tend to have lower reproductive success in proximity to power lines (Pitman et al. 2005, Hagen et al. 2011, Wisdom et al. 2011, Gibson et al. 2018, Kohl et al. 2019, Plumb 2019, LeBeau et al. 2019). As with oil and gas development, however, the magnitude of reported effects varies considerably among studies. Pitman et al. (2005) estimated that Lesser Prairie-Chickens avoided placing nests within 144-263 meters of high-voltage transmission lines mounted on 30-m-tall metal pylons, and Hagen et al. (2011), using data from the same areas, estimated that females were less likely to select summer habitat within 662-709 m of transmission lines. Kohl et al. (2019) found that the probability of habitat use for nesting or brood-rearing by Greater Sage-Grouse declined within 1.1 and 1.2 km, respectively, of transmission lines. Declines in lek attendance among male Greater Sage-Grouse were steeper among leks within 5 km of a transmission line (Gibson et al. 2018). Effects on vital rates extended even further, but also showed considerable variability: nest survival of Greater Sage-Grouse was lower within 12.5 km of transmission lines in one study (Gibson et al. 2018), and within 2.4 km in another (Kohl et al. 2019). Habitat selection and survival were negatively impacted by transmission lines but the extent of the impact varied by habitat suitability and proximity to leks (LeBeau et al. 2019). Population persistence among Greater Sage-Grouse was negatively associated with distance to a power line (Wisdom et al. 2011). Some of this apparent variation may reflect differences among species- and life-stage specific differences in sensitivity to power lines. Another likely source of variation in effect size among studies is the size of the power line and associated disturbance. Transmission lines, with a wider cleared right-of-way and taller support structures, had stronger effects on Greater Sage-Grouse than did low-voltage distribution lines mounted on shorter towers (Kohl et al. 2019).

Unlike oil and gas development, the negative effects of power lines on prairie grouse habitat use and demography are probably not mediated by human activity. Collisions with power lines can be a significant source of mortality in some locations (Beck et al. 2006, Wolfe et al. 2007), but changes in predator abundance and behavior are likely more important in general (Gibson et al. 2018). For example, power lines support higher densities of common ravens (*Corvus corax*), an important predator of Greater Sage-Grouse nests (Lockyer et al. 2013, Coates et al. 2014, Gibson et al. 2018).

Replication of study findings regarding the effects of power lines is generally good, although the ability of these studies to identify causal relationships is limited by the tendency for co-location

of power lines and roads and because of the reliance on observational studies lacking pre-construction data and true controls.

Roads

Reported effects of roads on prairie grouse are inconsistent even within a study (e.g., Pitman et al. 2005, McNew et al. 2013) and effects probably depend strongly on the characteristics of the road, including traffic volume and width of the right-of-way. For example, Gunnison Sage-Grouse avoided nesting within 8 km of major highways (Aldridge et al. 2012), whereas unimproved roads in Kansas had no consistent effect on nest placement of Lesser Prairie-Chicken (Pitman et al. 2005). Lesser Prairie-Chickens avoided nesting within 252-465 m of improved roads, however, and females showed reduced probability of using areas within 715-990 m of an improved road (Pitman et al. 2005, Hagen et al. 2011). Harrison et al. (2017) found that Greater Prairie-Chickens were less likely to select nest sites that were within 700 m of roads, which in this study area included two paved, two-lane highways and many smaller paved and unpaved roads. Traffic noise led to significant declines in abundance of male Greater Sage-Grouse at leks and had a stronger negative effect than did drilling noise (Blickley et al. 2012). No studies have isolated any effect of roads on vital rates of prairie grouse.

Potential mechanisms by which roads may affect prairie grouse are myriad (Kociolek et al. 2011), but include loss of habitat within the road footprint; direct mortality from collisions with motor vehicles; changes in activity, abundance, or species composition of predator assemblages (e.g., Chalfoun et al. 2002); changes in structure or species composition of adjacent vegetation that reduces suitability for grouse; or disturbance associated with the noise or sight of passing vehicles. Of these, only the aversion to traffic noise has been demonstrated experimentally to affect prairie grouse, reducing lek attendance by male Greater Sage-Grouse (Blickley et al. 2012).

The effect of roads on prairie grouse is difficult to generalize because these potential effects are likely strongly dependent on the characteristics of the road, surrounding habitat, and perhaps the individualistic response of different species. Isolating effects of roads per se, excepting the obvious effects of collision mortality, is also challenging because roads rarely occur independently of other anthropogenic disturbances.

What can other forms of disturbance tell us about the effects of wind energy?

The relative dearth of research conducted on prairie grouse at wind-energy facilities has motivated an interest in using the more extensive body of research on impacts of other anthropogenic stressors on these species for insight into the potential effects of wind-energy and appropriate conservation measures to mitigate them. Based on our review, we conclude that studies of how prairie grouse respond to other forms of anthropogenic disturbance are unlikely to be any more revealing of specific effects, such as disturbance distances or extent of functional habitat loss, than the early studies of habitat use that helped define buffer distances still enforced today (e.g., Wallestad and Schladweiler 1974). However, we also recognize that

wind-energy development is likely to continue within the range of prairie grouse, that development will occur before we have addressed all of the key information gaps regarding the effects of wind energy, and that conservation measures, even if they are best considered as working hypotheses rather than definitive statements of fact, will be needed. Below, we explain why the results of studies of other stressors, in particular oil and gas development, may be difficult to generalize. Having established these caveats, we then identify generalities from studies of other stressors that we use to generate several hypotheses about the potential effects of wind energy.

We see at least two major obstacles to generalizing the effects of other stressors. First, at least qualitatively, we find little evidence that prairie grouse respond to wind-energy facilities - as constructed to date - in the same way that they respond to other anthropogenic stressors. Functional habitat loss and depressed vital rates that characterize oil and gas development, power lines, and some roads are not apparent to the same extent at the few wind-energy facilities that have been studied. This supposition should be tested by formal meta-analysis in which effect sizes of different anthropogenic stressors on specific demographic responses are compared directly.

Second, although roads, powerlines, and oil and gas development have generally negative effects on survival and habitat use of prairie grouse (Hagen 2010, Hovick et al. 2014), the magnitude of these effects and distance at which they are detectable is highly variable among species and locations (see also Northrup and Wittemyer 2013, Gregory and Beck 2014, Manier et al. 2014). This implies a high degree of context-dependency, where the effects of any particular disturbance will depend on a host of idiosyncratic biotic and abiotic factors. If true, this suggests that usefully generalizing effects from one location to another, let alone from one type of disturbance to another, will prove difficult without a stronger grasp on the mechanisms at work. We conclude that quantifying specific and possibly unique effects of wind-energy development, to the extent that such data are useful in generating improved conservation measures, will only be revealed by further study at wind-energy facilities.

That said, what can we learn from studies of other stressors? First, that the density of infrastructure matters. For example, the deleterious effects of oil and gas development tend to increase with well density (Doherty et al. 2008, Green and Aldridge 2017) and in some cases are only detectable after a certain threshold of well density is passed (Doherty et al. 2010, Harju et al. 2010). Construction of wind-energy facilities may result in direct loss of habitat and habitat fragmentation at extents comparable to those associated with oil and gas extraction (Jones and Pejchar 2013), and thus some of the insights gained from research on oil and gas development may inform our understanding of wind energy's potential effects. Theory and empirical data also suggest at least some degree of generality in how different species respond to different forms of habitat loss and habitat fragmentation (Didham et al. 2012, Betts et al. 2014). This suggests that future studies should account not just for proximity to a turbine, but also the density of wind-energy infrastructure on the landscape. It also highlights the need for caution in predicting the cumulative effects of wind-energy build-out from studies examining responses of local populations to single, isolated wind-energy facilities.

Second, that roads and above-ground power lines have deleterious effects on prairie grouse, and that minimizing both when constructing new wind-energy facilities may reduce impacts on grouse. Approaches might include, for example, repurposing existing roads, limiting public access to any new roads, reducing the size and traffic volume of roads within a project area, and by burying power lines.

Third, setback distances established for oil and gas development should not be applied to wind-energy facilities as existing data do not support the hypothesis that responses to these two stressors are equivalent. The limited data available to date from studies at wind-energy facilities suggest that impacts are most pronounced within 3 km of a turbine for Greater Prairie-Chicken (Winder et al. 2015b) and within 1.5 km of a turbine for Greater Sage-Grouse (LeBeau et al. 2017b). We emphasize that whether these response thresholds apply to other species and facilities in other landscapes is unknown. They should be treated as tentative and adjusted as needed when more data are collected.

Fourth, lagged responses to disturbance are typical for prairie grouse. Monitoring and research thus should extend for at least five years post-construction, and longer wherever possible. Because the cost of annual, long-term research and monitoring is often prohibitive, researchers might consider revisiting sites that have existing data to determine whether conclusions drawn from initial research remain valid after grouse have been exposed to operating turbines for a longer period of time. Space-for-time study designs are likely to be problematic given the significant heterogeneity in responses of prairie grouse that have been observed in studies of other stressors.

Finally, studies of other stressors indicated that responses of local populations to disturbance are context dependent. We do not yet understand which factors drive variation in the response to disturbance, but they may include size of the local grouse population, extent of available habitat, levels of existing disturbances, and landscape context. It is therefore unlikely that developers building new facilities within prairie grouse habitat can avoid impacts by applying a single set of criteria for setbacks or timing of activities. Buffers useful in protecting one population may prove inadequate when applied to another. Until we can better predict the conditions that underlie this heterogeneity, wind-energy development that occurs within areas occupied by prairie grouse will best promote conservation of these species by evaluating projects on a case-by-case scenario, adopting buffers that reflect the best science available, by monitoring responses over an adequate length of time, and by offsetting any effects revealed by monitoring.

Wind-energy effects: research needs

An important take-home from this review is the need for replication: we simply do not have enough studies at wind-energy facilities to draw strong conclusions across species, habitat types, and time. Although almost any additional research will prove valuable, studies that include the following elements will be especially useful.

Address time lags in response to wind-energy facilities

Strong site fidelity among prairie grouse and slow changes in plant and animal communities (e.g., predators) over time may introduce substantial lags in the response to disturbance, so research needs to be conducted on relatively long temporal scales, ideally long enough to measure responses across multiple generations. Studies conducted over periods less than 5 years - as is the case with most existing research on prairie grouse and wind energy - may produce inaccurate estimates for responses to disturbance and other landscape-scale changes, especially if effects on grouse are mediated by changes in abundance or behavior of other species (e.g., mesopredator release). For example, effects of human development on risk-foraging tradeoffs in predators can change non-linearly over space and time as predators become acclimated to human activities (Smith et al. 2015, 2017b).

Exactly how long studies should extend is uncertain, but time lags of up to 10 years have been noted in studies of impacts of oil and gas development on Greater Sage-grouse (Harju et al. 2010). Ideally, studies should incorporate longer periods of data collection both before and after construction and in both control and impact sites. Recognizing that long-term studies are often difficult to fund, investigators might consider alternative approaches, such as revisiting sites of earlier studies to determine whether initial conclusions remain valid after grouse populations have been exposed to operating facilities for longer periods of time. For example, resampling Greater Prairie-Chickens at the Kansas facility studied by McNew et al. (2014) and Winder et al. (2014a, b; 2015b), or Greater Sage-Grouse at the Wyoming facility studied by LeBeau et al. (2014; 2017a,b), both of which have some pre-construction data available, would offer an outstanding opportunity to consider long-term effects.

Conduct studies that sample at multiple spatial extents to scale-up to population-level understanding of wind-energy effects

Understanding the effect of wind-energy development on population growth rate requires sampling at the appropriate spatial scale. Effects measured at the local level (e.g., lek location) may not be indicative of changes at the population level, for example due to source-sink dynamics (Runge et al. 2006). Studies that sample at multiple spatial extents can address this concern by integrating the potentially divergent response of many local sub-populations. O'Donnell et al. (2019) present a promising approach for creating empirical definitions of prairie-grouse populations based on hierarchical clustering of leks: individual leks are clustered into groups that define a subpopulation, subpopulations are clustered into larger groups that define a population of potentially interacting subpopulations, populations are clustered to define a meta-population, and so on. This approach could be used to identify appropriate targets for sampling, assessing trends across scales, and would allow for stronger inference about the connection between local changes measured around a wind facility and changes at the population level (e.g., Fuhlendorf et al. 2002).

For example, future studies could ask whether trends in numbers of lekking males varied among sub-populations or populations that were exposed to different intensities of wind-energy

development. Doing so would allow for an evaluation of the association between density of development and population change, which has proven important in studies of other anthropogenic stressors. Studies of local responses to wind-energy facilities would form part of the sampling effort, helping improve our understanding of site-level impacts, but would be supplemented by samples drawn from leks in other sub-populations. Defining these hierarchical clusters for all species of prairie-grouse, using the methods established in O'Donnell et al. (2019) and cross-walking with existing management units, would be a useful first step.

Consider cumulative effects

Existing studies find no evidence of substantial short-term negative effects to prairie grouse from wind-energy development but they tell us little about the possibility for incremental effects of additional development, as has been observed in studies of oil and gas development (summarized in Naugle et al. 2011). As we note above, this may be best accomplished by supplementing studies of impacts at individual sites with samples drawn from a larger spatial extent that consider the nested nature of leks, sub-populations, populations, and meta-populations. Doing so will not only advance our understanding of local impacts but will directly address the potential for non-linear effects of increasing density of wind-energy facilities on the landscape. Although outside the scope of this paper, future research on cumulative effects should consider the role of new wind-energy facilities as one of many possible anthropogenic stressors, none of which are likely to exert effects independently of the others (e.g., Kirol et al. 2020).

Measure fitness outcomes, not its individual components

Future research should shift the focus from individual vital rates to integrated measures of fitness, potentially providing a more comprehensive assessment of the demographic effects of wind energy and its ultimate effect on rates of population growth. For example, small and statistically non-significant impacts to multiple vital rates (e.g., nest survival, renesting rates, brood survival, chick survival) may collectively result in significant impacts to population viability. Particularly for lekking grouse species, integrated population models (IPMs) that combine multiple sources of demographic information, such as various vital rate estimates from individually marked birds in combination with lek data (see Coates et al. 2018), could be used to provide more robust estimates of population growth and refine vital rates estimates to better understand links to population trends.

Address understudied species

We currently do not have a strong enough understanding of the effects of wind energy on prairie grouse to use the response of one species to predict responses in another. None of the prairie grouse are especially well-studied in regards to the effects of wind-energy development, but some are even less so; focused work is needed on the most understudied species, particularly Sharp-tailed Grouse (one study of nest survival at one complex of wind facilities) and Lesser Prairie-Chicken (one study over several years at one facility). Sharp-tailed Grouse has the

advantage of being relatively widely distributed and having a larger, more stable population, thus making it potentially more amenable to study. Lesser Prairie-Chicken is of high conservation concern, has a geographic range that includes extensive areas of potentially high-value wind resources, and has been subject of considerable research effort during the past decade, which will serve as baseline information to critically assess any effects due to wind-energy development.

Improve conservation measures

Although we emphasize a need to develop a more holistic understanding of how prairie grouse are affected by wind-energy development, we also recognize the need for better information on how to avoid, minimize, and offset effects of individual facilities. A variety of strategies for avoidance exist, but the essential piece is to place wind turbines and associated infrastructure outside of grouse habitat - and ideally far enough outside so as to avoid disturbing leks or other critical habitat features - in already disturbed areas, such as agricultural fields. Although reasonable to assume that this approach will largely avoid impacts to grouse (recognizing that uncertainty about adequate buffer distances exists), quantifying the value of this approach, especially in comparison to facilities constructed in suitable habitat, would prove useful. For a variety of reasons, we expect that impacts from facilities built in intact landscapes will be more significant than those of facilities in highly fragmented landscapes, even if both applied similar buffers to key features of habitat (e.g., leks). This suggests a particular importance of conducting studies at facilities constructed within core areas or other important strongholds of intact habitat, to the extent that such projects are proposed and permitted to move forward.

Current recommendations for minimizing the effects of new wind-energy facilities to prairie grouse do not have a strong evidentiary basis, as has been often noted (e.g., Manville 2004, Powell et al. 2017). Most recommendations focus on establishing setbacks from active leks and avoiding potential disturbance from construction noise and activity during the lekking and nesting period. Whether these measures, with a focus on leks in particular, are effective is unknown. Timing stipulations are relatively straightforward and do not require any additional research. Powell et al. (2017) provided useful guidance for design of studies that could inform setback distances, including: use of BAG designs, establishing gradients that are long enough to detect any diminishment in risk as a function of distance to wind-energy infrastructure, and adopting analytical approaches that allow for the possibility of thresholds in risk. As with all questions pertaining to prairie grouse, recognition of the potential for spatial heterogeneity in responses is key, meaning that these sorts of studies should be carried out in intact landscapes, in fragmented landscapes, and for as many different species as possible.

Several regional and state-specific compensation schemes exist with which developers can offset the effects of unavoidable impacts to prairie grouse. A variety of actions have also been identified by which developers could support offsite mitigation that would offset loss, degradation, and fragmentation that occurs as a result of constructing wind-energy facilities. However, these approaches rely on scientific studies to determine impact and calculate the required offset investment, which as we have noted is scarce for even the most well-studied

species. In many ways, the most pressing need in regard to compensatory mitigation is for better information about the magnitude and spatial extent of impacts.

Incorporate considerations of climate change

One of the challenges with map-based tools designed to help developers avoid impacts to prairie grouse and their habitats is that they are static and retrospective (i.e., they are based on past estimates of the distribution of habitat or individuals). With a rapidly changing climate, assumptions of stationarity are unlikely to be met. Areas to avoid today may well be unsuitable as habitat for prairie grouse within the next decade, whereas areas considered “safe” for new wind-energy infrastructure may occupy land that could otherwise be colonized as climate changes. Predicting changes in species distributions is difficult and prone to failure because we generally lack a mechanistic understanding of why species occur where they do, yet in a broad sense research that identifies where different species of prairie grouse are likely to occur over the next 50 years may help promote proactive siting decisions. Stakeholders might adopt a lower tolerance for risking adverse effects of development on future habitat strongholds, and corridors that provide access to them, and a higher tolerance for risk of adverse effects in areas likely to be rendered uninhabitable due to human-caused climate change.

There is often assumed to be a trade-off related to wind-energy development, in that it may have longer-term benefits to prairie grouse if it helps reduce consumption of fossil fuels and the consequent impacts of human-caused climate disruption. In addition, relative to fossil fuels, the impact of wind energy on habitat does not increase over time (excluding any delayed impacts), whereas coal mines and oil and gas wells eventually become unproductive and must be replaced with another mine or well, imposing an additional cost on the environment unless depleted sites are restored. However, these putative benefits of renewables have never been quantified, and thus it remains unclear whether, or to what extent, deleterious effects of constructing and operating wind-energy facilities are offset by the long-term benefits that may accrue in the form of lessened climate change. Although answering this question is unlikely to influence conservation policy or practice for prairie grouse in the short run, a full understanding of the costs and benefits to wildlife of transitioning to a low-carbon electricity sector may prove useful in informing broader conversations about wildlife conservation, climate change, and renewable energy, a conversation that to date has focused largely on describing potential costs of renewable energy build-out while assuming some quantifiable, yet unknown, benefit.

Putting it all together: an agenda for actionable research

Uncertainty abounds in regard to the costs and benefits of wind energy for prairie grouse, yet development of new facilities will proceed regardless. The challenge for science-based decision-making, then, is how to proceed in the absence of complete information. Within our collective expertise, we have identified what we think are the most pressing questions and problems to address. We suggest doing so via the following course of action.

First, identify range-wide, hierarchical clusters of populations to inform multi-scale sampling efforts. Doing so will help studies at individual wind-energy facilities determine suitable control sites (e.g., leks within the same sub-population) and/or suitable gradient length for BAG designs. It will also help prioritize pre-construction data collection when paired with wind-energy development potential and set the stage for future studies of cumulative impacts.

Second, where possible, resample prairie-grouse populations at operating wind facilities that have been the focus of previous study. Use these re-visits to test the hypothesis that long-term effects of wind-energy development may result from 1) unstudied population processes during the initial research period, 2) cumulative effects on a variety of population responses, and 3) indirect effects to broader community processes that may take a long time to manifest (e.g. numerical or functional responses of relatively long-lived predators).

Third, initiate new research across multiple study sites using a standardized study design and sampling protocols, keeping in mind the importance of obtaining pre-construction data. To date, existing data do not allow for contextual assessments of impacts (e.g., potential mediating habitat conditions) because of differences in designs among studies. Opportunities to study multiple species at a single site (e.g., Greater Sage-Grouse and Columbian Sharp-tailed Grouse) should be capitalized upon, as should opportunities to work with understudied species. Use BAG designs and test the efficacy of the setback distances proposed here and by other authors. When publishing results, include a description of any mitigation measures adopted (e.g., timing restrictions on construction operations, burying power lines, setbacks from leks or other critical elements of habitat) so as to facilitate future retrospective analyses.

Fourth, using the populations identified in step 1, undertake analyses to address the cumulative effects of wind-energy development, for example by estimating the association between population trends (or indices of these trends, like lek counts) and density of wind-energy infrastructure while controlling for confounding factors such as land-cover change due to other anthropogenic activities. If possible, to speed learning, undertake these analyses with existing data through collaborations with state agencies, consultants, industry, and NGOs that maintain monitoring programs.

Fifth, continue to refine predicted changes in distribution of prairie grouse in response to climate change and use these to develop risk-tolerance maps to help refine existing site-screening tools. Different stakeholders will tolerate different levels of risk, so this question cannot be answered by the research community alone. For these tools to prove useful they will likely require extensive input and co-development by stakeholders.

Conclusions

Protecting existing habitat, restoring degraded habitat, and re-connecting isolated patches of habitat are cornerstones of wildlife conservation. Given the threat that unmitigated climate change poses to habitat for all species, including North American prairie grouse, substituting

energy derived from fossil fuels with energy from low-carbon sources like wind is an important part of a long-term strategy to conserve grouse populations. The challenge is how to do so without inadvertently increasing the risk of extinction from the direct and indirect effects of wind-energy infrastructure. The few studies conducted to date indicate that construction and operation of wind-energy facilities can affect habitat use by prairie grouse but reveal no consistent effects on demographic rates nor evidence of extensive functional habitat loss, at least over the relatively short timescales considered thus far. These qualitative conclusions are consistent with a quantitative meta-analysis of the effects of proximity to a wind turbine on survival, habitat use, and lek attendance among prairie grouse (LeBeau et al. 2020a).

Important uncertainties remain, however, some of which we have identified: we need longer-term studies to rule out the possibility that negative effects are time-lagged (or, alternatively, we need to revisit previously studied populations), we need replication at additional facilities in different landscapes to quantify the range of variation in responses across species and across sites, and we need to be cautious about predicting long-term outcomes of wind-energy build-out from studies at single facilities. We assume that reducing uncertainty in these areas will improve conservation outcomes for prairie grouse while allowing for a more rapid transition away from fossil fuels, but we acknowledge the potential value of conducting a formal analysis of the costs and benefits of collecting additional data (i.e., estimating the value of information and of reducing uncertainty; Bolam et al. 2019). For example, if the benefit of reducing epistemic uncertainty as to the appropriate buffer distance is low, then limited resources might better be invested in other research or directly in conservation actions that benefit prairie grouse. Finally, we need to quantify the potential benefits of wind energy in reducing the impacts of climate change on prairie grouse in order to better understand how we can optimize the balance between minimizing extinction risk for prairie grouse and hastening the transition to a low-carbon energy sector.

Several design elements should underpin future work at wind-energy facilities. In particular, we recommend a coordinated program of research that focuses on using geographically extensive, replicated studies of empirically defined populations; that incorporate best practices of impact analysis, including the collection of pre-construction data, the use of suitable control sites for comparison, and designs that can estimate impact thresholds and refine our understanding of what constitutes a useful setback distance; and that moves away from a focus on measuring individual rates in local sub-populations and towards an approach that allows insight into changes in population growth rate, which is the parameter of most interest from a conservation standpoint. If comprising a series of thoughtfully designed studies, this proposed program of research will help answer many of the most pressing questions that we face. Finally, however, even the most well-designed research program may fail to produce actionable knowledge if it is not constructed, carried out, and disseminated with the full participation of all stakeholders (Cash et al. 2003, Karl et al. 2007, Cook et al. 2013, Mauser et al. 2013), including industry, state and Federal agencies, environmental NGOs, and scientists.

For the foreseeable future, decisions about permits and conservation measures still will be made in the absence of complete information. The research needed to fill key gaps in our

knowledge will require at least 5 years to conduct, and in the meantime it is likely that at least some new facilities will be built or permitted in areas occupied by one or more species of prairie grouse. Based on the limited evidence on hand, we recommend the following approaches. First evaluate the context of each project in relation to identified habitats, leks, telemetry data, and existing levels of disturbance while using the best available information on the effects of wind-energy facilities on prairie grouse. Some impacts can be avoided by placing new infrastructure in already disturbed areas. Minimize impacts with standard measures: avoid construction activities during lekking periods, bury transmission lines, and minimize the density of new roads. Direct tests of the efficacy of these measures are lacking, but given evidence that noise disrupts breeding by sage grouse, that avian predators of prairie grouse will use power lines as perches from which to hunt, and that roads are one of the largest sources of land-cover change in a wind-energy facility, they represent a useful starting point. Limited data also suggest that buffering leks by 1.5 - 3 km will help minimize effects of wind-energy infrastructure constructed within suitable habitat. The buffers, as noted, are empirically derived but should be tested and not simply assumed to be sufficient.

In some areas and for some species compensatory mitigation is also an option. Given broad uncertainty as the effects of wind energy on prairie grouse, however, the adequacy of existing compensation schemes is also uncertain. The potential for compensatory mitigation may best be informed by analyses at the population level, using empirically defined populations as we have outlined, that allow for the possibility of cumulative effects. Any additive effect of the density of wind-energy infrastructure on growth rates could be estimated and used as a cost function for determining what level of compensation is appropriate.

We recognize that this is an ambitious agenda and it must be implemented in relatively short order. Because both time and resources are limited, it is likely that the agenda we have proposed will require further narrowing to focus on elements deemed most essential by the broader stakeholder community. With the emerging consensus regarding the need to substantially reduce greenhouse-gas emissions over the next decade (IPCC 2019), pressure to increase the deployment of renewable energy sources like wind will only become more intense. To do so while conserving populations of prairie grouse will require a coordinated effort to link research, monitoring, and management that treats every new wind-energy development as an opportunity to test hypotheses and refine mitigation approaches.

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