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Research Article

# Greater Sage-Grouse Response to the Physical Footprint of Energy Development

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**ABSTRACT** Energy infrastructure and associated habitat loss can lead to reduced reproductive rates for a variety of species including the greater sage-grouse (*Centrocercus urophasianus*). Our goal was to refine our understanding of how the physical footprint of energy development relates to sage-grouse nest and brood survival. Our survival analyses were conditional upon the amount of surface disturbance female sage-grouse were exposed to during reproductive stages. We quantified levels of exposure and compared them to the surface disturbance levels of the surrounding area. From 2008–2014, we collected data in 6 study areas in Wyoming, USA, containing 4 primary types of renewable and nonrenewable energy development. Our research focused on press disturbance (i.e., disturbance sustained after initial disturbance and associated with existing energy infrastructure and human activity). Our results suggest exposure to press disturbance during nesting and brood-rearing was related to lower nest and brood survival, which manifested at different spatial scales. Our analysis of nest survival suggested that the likelihood of a successful nest was negatively associated with the amount of press disturbance within an 8-$km^2$ area. Broods exposed to any press disturbance within a 1-$km^2$ area were less likely to survive compared to broods not exposed to press disturbance. Female sage-grouse consistently used habitat with lower disturbance levels during reproductive periods. Greater than 90% of nest and brood-rearing locations were in habitat with <3% press disturbance within a 2.7-$km^2$ area. Our research links surface disturbance associated with press disturbance to reproductive costs incurred by sage-grouse exposed to diverse energy development. Our results demonstrate a pattern of female avoidance of areas where press disturbance was high during nesting and brood-rearing and survival of nests and broods were highest in areas that had the least amount of disturbance. Our findings underscore the importance of minimizing disturbance to maintain viable sage-grouse populations. © 2020 The Wildlife Society.

**KEY WORDS** brood survival, *Centrocercus urophasianus*, development, energy infrastructure, greater sage-grouse, nest survival, physical footprint, press disturbance.

Predicting species response to habitat alteration and fragmentation is one of the greatest challenges in wildlife conservation and management (With and King 1999). Recent estimates suggest that across 11 western and midwestern states in the United States, the area disturbed by oil and gas infrastructure built from 2000 to 2012 was about 3 million ha (Allred et al. 2015). The sagebrush (*Artemisia* spp.) biome is one of the most threatened in western North America, facing multiple stressors, including ongoing energy development and invasive plants (Noss et al. 1995, Knick et al. 2003, Copeland et al. 2009, Davies et al. 2011, Chambers et al. 2017). Energy infrastructure and associated habitat alteration cause displacement and reduced reproductive rates of a variety of sagebrush-occurring species including ungulates (Sawyer et al. 2006, Beckmann et al. 2012, Buchanan et al. 2014), sagebrush-obligate songbirds (Gilbert and Chalfoun 2011, Hethcoat and Chalfoun 2015), small mammals (Germaine et al. 2017), and greater sage-grouse (*Centrocercus urophasianus*, i.e., sage-grouse; Aldridge and Boyce 2007; Kirol et al. 2015*a*, *b*; Green et al. 2017; LeBeau et al. 2017). For example,

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Connelly et al. (2011) reported a range-wide sage-grouse nest survival rate that was 14% lower for nests located in habitat altered by anthropogenic development compared to nests in unaltered habitat.

Wyoming, USA, is important to the long-term conservation of the sagebrush biome and sage-grouse, containing approximately 25% of remaining sagebrush in North America and 37% of the world's sage-grouse population (Connelly et al. 2004; Doherty et al. 2010, 2016). Wyoming is also one of the largest producers of domestic energy and exports more energy to other states than any other state (U.S. Energy Information Administration 2016). Because of these demands, energy development in Wyoming often conflicts with conservation of wildlife populations and habitats (Copeland et al. 2011). Sage-grouse have become a surrogate for other species representing the plight of sagebrush ecosystems that face an expanding energy development footprint (Gamo et al. 2013, Hebblewhite 2017).

Conservation plans increasingly focus on the physical footprint of development, quantified as surface disturbance, as a regulatory mechanism to reduce effects on sage-grouse and other sagebrush-obligate species. The Wyoming Core Area policy represents an example of this type of conservation strategy. This policy was designed to maintain sage-grouse populations while allowing for limited energy development in sage-grouse habitat using surface disturbance caps as the primary regulatory mechanism (Doherty et al. 2011, Gamo and Beck 2017, State of Wyoming 2019). Specifically, the Core Area policy limits infrastructure development and removal of sagebrush within areas of high sage-grouse breeding population densities identified as Core Areas (Doherty et al. 2011, State of Wyoming 2019). Under the Wyoming Core Area policy, surface disturbance acts as an index to regulate all development, regardless of the type of disturbance (e.g., oil and gas development, transmission lines, or wildfire). The policy allows for a maximum of 5% surface disturbance when development projects occur within Core Areas (State of Wyoming 2019). The United States Bureau of Land Management (BLM) manages the majority of the remaining sagebrush ecosystems in the western United States and has adopted many aspects of the Wyoming Core Area policy, including a disturbance cap of 3% or 5% (Naugle et al. 2011; BLM 2015*a*, *b*).

The effectiveness of limiting surface disturbance to specific disturbance levels (e.g., 3% or 5%) to maintain sage-grouse populations has not been empirically tested. We focused on nest and brood survival because these reproductive parameters are critical to sage-grouse population persistence (Taylor et al. 2012). While acknowledging there is variability in sage-grouse population responses to different energy infrastructure (e.g., oil and gas, wind development; Kirol et al. 2015*a*, LeBeau et al. 2017), we assessed population-level effects of female sage-grouse exposure to different intensities of surface disturbance and nest and brood survival outcomes.

Consistent with previous studies, the physical footprint of energy development in our research was characterized by removal of natural vegetation for energy infrastructure (Smith et al. 2014, Hethcoat and Chalfoun 2015, Kirol et al. 2015*a*, Germaine et al. 2017). When surface disturbance was maintained after the initial perturbation and associated with existing infrastructure, we termed it press disturbance (i.e., disturbance sustained after initial disturbance and associated with existing energy infrastructure and human activity; Morrison et al. 2008). Pulse disturbance, in contrast, is disturbance that is not sustained after an initial perturbation (e.g., fire and mechanical or chemical sagebrush treatments; Smith and Beck 2018) and often originates from a natural process such as wildfire (Morrison et al. 2008). Many researchers have focused exclusively on pulse disturbances such as sagebrush treatments and fire. These researchers demonstrated that responses of sage-grouse to pulse disturbances in sagebrush ecosystems are often variable and can be different than documented responses to press disturbance (Dahlgren et al. 2006, Carlisle et al. 2018, Foster et al. 2018, Smith and Beck 2018).

Our objectives were to describe the distribution of sage-grouse relative to different levels of press disturbance during the nesting and brood-rearing life stages, investigate different functional responses to increasing levels of press disturbance on nest and brood survival, and assess whether the effects of press disturbance on nest and brood survival were confounded by the presence of pulse disturbance. We tested the hypothesis that there is an average effect (i.e., a biological effect that represents a population-level estimate of that effect across local populations; Kéry and Royle 2016). A lack of support for an average effect across local sage-grouse populations would suggest that broadly applying surface disturbance caps to mitigate effects on sage-grouse may not be an effective conservation strategy.

## STUDY AREA

Our research focused on 6 study areas, which included a variety of landscapes and development types throughout Wyoming, ranging from coal bed natural gas in south-central and northeast Wyoming, conventional oil and gas development in southwest Wyoming, wind-generated electricity development in south-central Wyoming, and relatively unaltered areas from 2008–2014 (Fig. 1). Study areas included the Powder River Basin (PRB), Southwest Wyoming (SW), Atlantic Rim (AR), Seven Mile Hill (SMH), Jeffrey City (JC), and Stewart Creek (SC). Combined, our study areas encompassed 15,092 $km^2$ of land. Our study areas were characterized by flat to rough terrain with rolling hills, hogback ridges, knolls, and bisected by drainages. Long-term precipitation average across study areas ranged from 20.7 cm to 34.3 cm. Precipitation was fairly evenly distributed throughout the year but came as rain in the warmer summer months and snow in the colder winter months. In addition to sage-grouse, fauna in the study areas included sagebrush-associated mammals, birds, and reptiles, such as mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), American badger (*Taxidea taxus*), Brewer's sparrow (*Spizella breweri*), burrowing owl (*Athene cunicularia*), and greater short-horned lizard (*Sceloporus graciosus*; Gamo et al. 2013). Vegetation in all study areas was dominated by big sagebrush

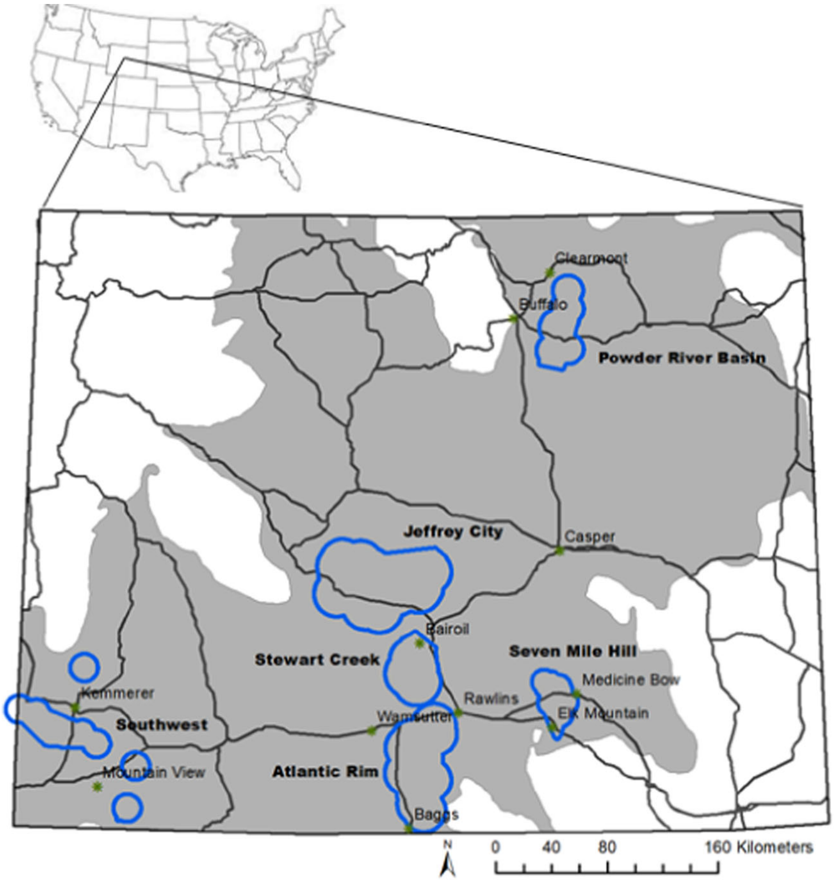


**Figure 1.** Study areas (blue polygons) with the current greater sage-grouse range in Wyoming, USA, shaded gray in the background, 2008–2014. Study areas composed approximately 10% of occupied sage-grouse habitat in Wyoming.

(*A. tridentata*), with Wyoming big sagebrush (*A. t. wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) the most common sagebrush species. Black sagebrush (*A. nova*) and low sagebrush (*A. arbuscula*) occurred on exposed ridges. Other common shrub species included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), and rabbitbrush (*Chrysothamnus* and *Ericameria* spp.). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) occurred within all study areas. Study area details are available online in Supporting Information.

# METHODS

## Field Methods

We captured female sage-grouse in 2008–2014 using a variety of capture methods including spot-light and hoopnet (Wakkinen et al. 1992), rocket-netting (Giesen et al. 1982), and a mobile CODA net launcher (Sutphin et al. 2018). We aged females as juveniles or adults based on the shape and condition of the outermost wing primaries, the outline of the primary tail feathers, and coloration of undertail coverts (Eng 1955, Dalke et al. 1963). We attached radio-transmitters (22-g and 17.5-g; Advanced Telemetry Systems, A4060, Isanti, MN, USA or Holohil Systems, RI-2D, Carp, ON, Canada) to females with a polyvinyl chloride (PVC)-covered wire necklace. In addition to radio-transmitters, in the JC study area we attached global positioning system (GPS)-transmitters (22-g Solar Argos/GPS platform transmitter terminal (PTT)-100, Microwave Telemetry, Columbia, MD, USA) with rump-mount harnesses to 28 females. We monitored radio-marked females weekly beginning mid-to-late April each year with hand-held receivers and 3-element Yagi antennas (R-1000, Communication Specialists, Orange, CA, USA). To be consistent with weekly monitoring intervals of the radio-marked individuals, we rarified location data from GPS-equipped females by randomly selecting 1 midday (i.e., 0900, 1200, or 1500 local time) location for each individual per week. We recorded use locations of females fitted with radio-transmitters with a hand-held GPS unit by circling a radio-marked female until the surveyor visually isolated the female's location.

We monitored radio-marked females at least once a week throughout the nesting season. To minimize human-induced nest depredation or nest abandonment, we subsequently monitored nests of radio-marked females with triangulation from a distance of ≥20 m. For GPS-equipped females, we visually inspected potential nests after the female left a location of clustered GPS points. We determined nest survival (i.e., nests with ≥1 hatched egg) by examining egg shells and other diagnostic signs after the female was no longer located at the nest site (Wallestad and Pyrah 1974).

We monitored females that hatched chicks at least once a week to record brood fate through mid-August each year. During each visit, we attempted to determine if the female was still with the brood by visually locating the chicks with binoculars or by observing brooding behavior by the female (e.g., distraction displays, feigning injury, clucking). We considered the brood the experimental unit, rather than individual chicks (Kirol et al. 2015*a*). We considered a brood to have survived if we observed ≥1 chick at 35–40 days post-hatch. We assessed brood survival at about 40 days post-hatch because the majority of chick mortality has already occurred by this age; consequently, chicks are more likely to survive to breeding age after this time (Gregg et al. 2007). We used night-time spotlight counts to verify brood fate between 35–40 days post-hatch (Walker et al. 2006, Dahlgren et al. 2010). Dahlgren et al. (2010) estimated 100% chick count accuracy using night-time spotlight counts. We did not conduct spotlight counts at SW in 2008–2011, AR in 2010–2011, or SC in 2010–2011; therefore, we did not include these years from those study areas in our brood survival analysis. Sage-grouse were captured, processed, and monitored in adherence with approved protocols (AR and SC studies: Wyoming Game and Fish Department [WGFD] Chapter 33 permits 572 and 699 and University of Wyoming Institutional Animal Care and Use Committee [UW IACUC] protocol 03032009; JC study: WGFD Chapter 33–801 permit and UW IACUC protocols 03132011 and 20140128JB0059; SW study: WGFD Chapter 33–657 and Utah State University IACUC protocol 33–357; SMH study: WGFD Chapter 33–572 issued to Western EcoSystems Technology; PRB study: WGFD Chapter 33–239 issued to Big Horn Environmental Consultants).

## Disturbance

We processed GIS data using ArcGIS Desktop version 10.3–10.7 (http://www.esri.com, accessed 20 May 2015), Geospatial Modeling Environment (http://www.spatialecology.com/gme, accessed 8 June 2015), and QGIS 2.8 (http://qgis.org/en/site/index.html, accessed 20 May 2015). We quantified surface disturbance following the process used by regulatory agencies in Wyoming (BLM 2015*a*, *b*; State of Wyoming 2019). We digitized surface disturbance following the Density and Disturbance Calculation Tool (DDCT) process (head's up digitizing at a min. 1:5000 scale; https://ddct.wygisc.org/ddct-cap-faqs.aspx, accessed 20 May 2015). After digitizing, we identified disturbances as a press or pulse disturbance. Press disturbance included areas that were stripped of native vegetation and were devegetated or vegetated with interim reclamation seed mixes (e.g., disturbed areas surrounding active well pads) and generally associated with infrastructure (Fig. 2). Examples of press disturbance in our study areas included improved roads (graveled and paved), energy infrastructure (e.g., oil and gas wells and facilities, wind turbines and facilities, coal mining infrastructure), railroads and associated infrastructure, human dwellings and associated development, man-made reservoirs (e.g., evaporation pits), and general electrical disturbance. Pulse disturbance was not associated with infrastructure features and may have had vegetation removed in the past, but the revegetated disturbed site was difficult to distinguish from surrounding non-disturbed vegetation when viewed with imagery. Examples of pulse disturbance included reclaimed energy development (e.g., reclaimed oil and gas pads, reclaimed mining disturbance), reclaimed pipelines, sagebrush reduction treatments (mechanical and chemical treatments, prescribed burns), and wildfire.

Because development was ongoing during our study, we time-stamped press and pulse disturbance layers per year. We used a variety of resources to accurately time-stamp disturbance. We obtained data about active, plugged, and abandoned wells from the Wyoming Oil and Gas Conservation Commission, which included locations, status dates, and spud dates (initiation of drilling) for the duration of our study. We time-stamped wells and associated infrastructure based on spud date. We also used as-built plan of development maps provided by the BLM to batch oil and gas infrastructure per year, when available. We used National Agriculture Imagery Program (NAIP) and Esri world imagery to inspect and visually time-stamp disturbance when other information was not available. We collected NAIP imagery for Wyoming between July and August on a 3-year rotation (2006, 2009, 2012, 2015; http://datagateway.nrcs.usda.gov, accessed 2 Sep 2016).

## Spatial Analysis

Landscape-scale environmental characteristics associated with sage-grouse nest and brood survival have been documented (Holloran et al. 2005; Aldridge and Boyce 2007; Guttery et al. 2013; Kirol et al. 2015*a*, *b*). We used previous studies to identify environmental predictor variables to include in nest and brood survival models. The purpose of these *a priori* environmental variables was to control for inherent differences in habitat across study areas prior to assessing the influence of press disturbance on nest and brood survival. The *a priori* environmental variables included sagebrush cover, shrub cover, bare ground, conifer tree density, compound topographic index (CTI), terrain roughness index (TRI), and total monthly precipitation. We used United States Geological Survey sagebrush layers to estimate sagebrush cover, shrub cover, and bare ground (Homer et al. 2012). Data derived from these layers were static and did not account for annual changes in vegetation after the imagery was obtained (Aug–Sep 2009). Therefore, we burned in the physical footprint of new disturbance each year after 2009 to produce dynamic raster layers for sagebrush cover, shrub cover, and bare ground to reflect ongoing vegetation removal. We used LANDFIRE version 1.3.0 to create a tree density layer (Ryan and Opperman 2013). We calculated CTI, TRI (Evans et al. 2014), and total monthly precipitation (PRISM Climate Group 2016). The CTI is a soil moisture index

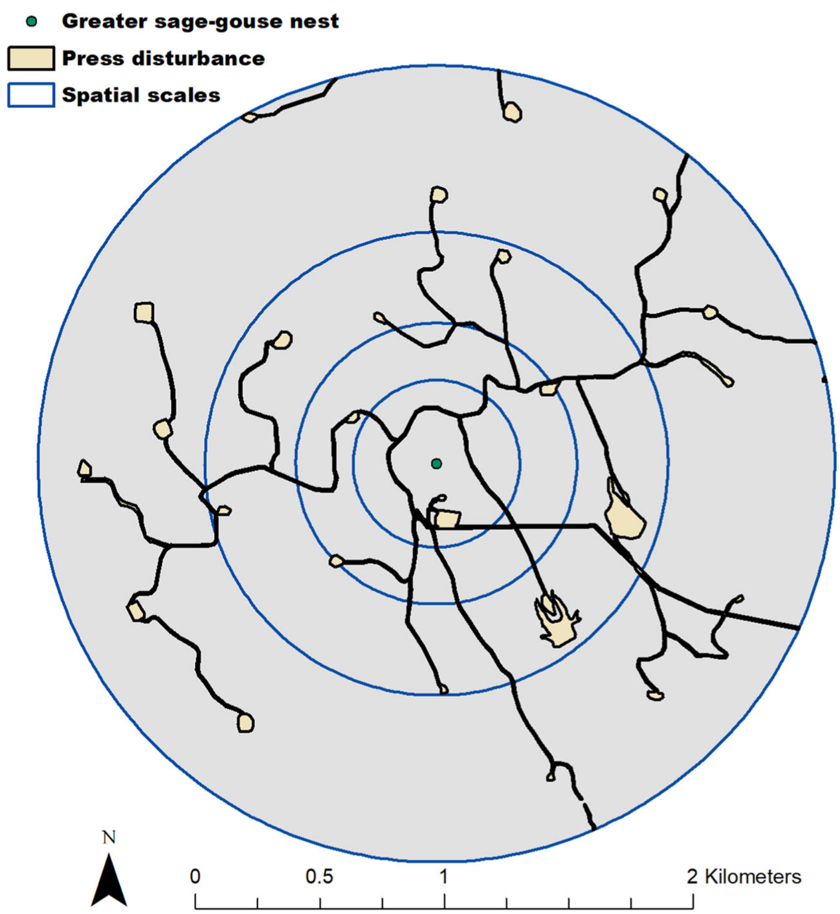


**Figure 2.** An example of a greater sage-grouse nest exposed to press disturbance (i.e., disturbance sustained after initial disturbance and associated with existing energy infrastructure and human activity) from natural gas development, Powder River Basin, Wyoming, USA, 2008. The blue circles represent the 4 scales we assessed in our nest and brood survival analyses. From the nest outward, the first blue circle is the 0.35-km$^2$ (0.335-km radii) scale, followed by the 1-km$^2$ (0.564-km radii), 2.7-km$^2$ (0.93-km radii), and the 8-km$^2$ (1.6-km radii) scale. This nest was exposed to 6% press disturbance at the 0.35-km$^2$ scale and 1.8% press disturbance at the 8-km$^2$ scale.

that estimates surface water accumulation on the basis of landscape concavity and hydrology to predict mesic and riparian areas (Theobald 2007).

On the basis of sage-grouse biology and previous research, we evaluated the influence of predictor variables on nest and brood survival at 4 spatial scales: 1) 0.335-km radii (0.35 km$^2$), 2) 0.564-km radii (1 km$^2$), 3) 0.93-km radii (2.7 km$^2$), and 4) 1.6-km radii (8 km$^2$; Holloran and Anderson 2005, Aldridge and Boyce 2007, Fedy et al. 2014, Kirol et al. 2015*a*). Certain scales we assessed were similar to federal and state sage-grouse policy guidelines, including a 1-km no surface occupancy buffer and a 2.6-km$^2$ infrastructure density limitation (BLM 2015*a*, *b*; State of Wyoming 2019). We calculated summary statistics for the spatial predictor variables at each scale (Fig. 2).

## Exposure at Nest, Brood, and Available Locations

We used data from nesting and brood-rearing female sage-grouse exposed to various types of energy infrastructure and press disturbance levels. Because our survival analyses were conditional upon the levels of disturbance exposure during nesting and brood-rearing, we quantified the percent of press and pulse disturbance that nests and broods were exposed to at the 2.7-km$^2$ scale and compared this to the disturbance levels of surrounding areas (i.e., available habitat). We described disturbance levels at the 2.7-km$^2$ scale because it is a commonly used management scale and relates directly to the DDCT process (State of Wyoming 2019). To identify the extent of available habitat for comparison, we used sage-grouse movements as a biologically meaningful method to quantify habitat availability (Johnson 1980). For each study area, we calculated distances from lek-of-capture (presumed lek of breeding) to nest and brood-rearing locations of marked females to establish study area boundaries to define the available habitat extent. We buffered the capture leks by a radius distance that contained 95% of the lek-of-capture to female nest distances and female with brood movement distances for each study area. If the analysis extent did not contain all nesting and brood-rearing locations for the study area, we merged the analysis extent with a minimum convex polygon (MCP) to form the final analysis extent that included 100% of the locations. Ninety-five percent movement distances for all study areas ranged from 8.5 km in SMH to 17.0 km in SC. Movement distances were comparable to those summarized in a Wyoming statewide sage-grouse movement analysis (Fedy et al. 2012). To describe disturbance levels of available habitat, we generated random locations (i.e., pseudo-absence points) at a ratio of about 5 times the number of used (nest and brood-rearing) locations within each defined study area extent (Buskirk and Millspaugh 2003). We batched random locations with corresponding nest or brood-rearing locations by year to account for temporal changes in disturbance because of ongoing development during the study.

**Nest and Brood Survival**

To assess relationships between surface disturbance and nest and brood survival, we used the Cox mixed effects model (package coxme) allowing for the inclusion of random effects in R (R version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria; Therneau 2015). Random effects provide increased precision and reduced uncertainty when interest is focused on population-level estimates derived from spatially distinct subpopulations (Kéry and Royle 2016). Because our data were from different years and study areas (e.g., random variation across space and time), we nested study area within year as a random effect (Bolker et al. 2009). The nested random effect accounted for the temporal and spatial clustering of our data and allowed us to share information among different populations and years (Bolker et al. 2009, Kéry and Royle 2016). All models in the subsequent steps included study area nested within year as a random effect.

Because females with broods were moving through the environment, variable exposure changed through time (time-dependent) and intervals were discontinuous; therefore, we analyzed brood survival using the Andersen-Gill formulation of the Cox model (Anderson and Gill 1982). For broods, we assigned variable information across intervals centered at the observation time to the midway point of the next observation time. We assessed brood survival risk as average cumulative exposure over the brood survival period because it was more appropriate to assess risk based on varying exposure to habitat features over time rather than solely on the last location where a female was no longer with a brood (Kirol et al. 2015*a*). For example, individual chicks may die throughout the exposure period, not necessarily simultaneously.

Exposure periods ($t$) for our survival analyses were $t=27$ days and $t=40$ days for nest and brood survival, respectively. We applied a 27-day nest survival period because high interval GPS data collected in the JC study area supported a 27-day incubation period (Smith et al. 2018). We assigned nest fate date (i.e., event) as the midpoint between the last monitoring interval. We right-censored nests and broods that survived the entire period, or those with unknown fates (Hosmer and Lemeshow 2008). We located the majority of nests during early incubation, which allowed us to estimate a nest initiation date (Shaffer 2004). For nests that did not have a pre-nesting female observation, we assigned nest initiation by standardizing the first day of the nest exposure period to the first nest initiation recorded that year for each study area (Dinsmore et al. 2002). We used ordinal date as a predictor in our models because research on sage-grouse and other birds suggests that nests initiated later in the season (i.e., a later ordinal date) may have increased survival risk (Nur et al. 2004, Webb et al. 2012). Nests from second or third attempts following failed nesting (i.e., renests) may not be independent of first nests; therefore, we excluded renests from the survival analysis. We did not include nests and females with broods that had incomplete observation histories in survival analyses.

We calculated Pearson correlation coefficients between all variables and did not allow variables displaying high correlation ($|r| \geq 0.6$) to be included in the same model at any stage of modeling. We checked for stability and consistency of regression coefficient estimates, ensuring that inclusion of moderately correlated variables ($0.3 \leq |r| \leq 0.6$) did not result in coefficient sign switching.

We identified the most parsimonious environmental model by comparing models with Akaike's Information Criterion (AIC; Burnham and Anderson 2002). When AIC scores were nearly equivalent (within 2 AIC [$\Delta$AIC]), we evaluated support by the degree of 85% confidence interval overlap of the individual predictor variables (i.e., the variables with the least amount of overlap of zero; Burnham and Anderson 2002, Arnold 2010). First, we identified the best supported scales for each environmental predictor variable that were identified *a priori*, based on AIC and 85% overlap, using simple models that contained the predictor variable and random effects. Then we included all possible combinations of uncorrelated predictor variables and selected the model that had the lowest AIC score. The top-ranked environmental model formed the base model (Webb et al. 2012, Kirol et al. 2015*b*). The purpose of the base model was to account for environmental variation in our survival models (i.e., as statistical control variables; Hosmer and Lemeshow 2008) and to facilitate interpretation of the disturbance predictor variables.

In combination with our base model, we examined functional relationships, in the form of linear, quadratic, or cubic (Burnham and Anderson 2002), of press disturbance exposure (% exposure) at each scale. We identified the most informative representation of press disturbance based on AIC and the degree of 85% confidence interval overlap of zero. We considered press disturbance variables to have no statistical support if the AIC score was nearly equivalent to the base model ($\leq 2$ $\Delta$AIC) and the coverage of the 85% confidence interval overlapped zero (Hosmer and Lemeshow 2008, Arnold 2010). If we did not detect statistical support for a functional relationship, we evaluated a categorical relationship between press disturbance exposure ($0=$ no exposure to press disturbance at scale, $1=$ exposure to press disturbance at scale) and survival. Finally, after identifying the best-supported relationship between press disturbance exposure and nest or brood survival, we combined pulse disturbance as an additive term to the nest and brood survival models (base-model variables + press disturbance + pulse disturbance) to investigate if the presence of pulse disturbance acted as an effect modifier of press disturbance on nest and brood survival. We assessed the degree of effect modification as the percent change in the coefficient estimate of press disturbance (Hosmer and Lemeshow 2008). We examined plotted Schoenfeld residuals, to check that the proportional hazards assumption for all variables in our final models was not violated (Hosmer and Lemeshow 2008).

# RESULTS

## Nest and Brood Exposure

We collected data across 7 years (2008–2014) at 6 spatially distinct study areas that included 1,049 nest locations, 2,810 brood-rearing locations, and 19,320 random locations representing available habitat (Table 1). The median exposure of all nests to press disturbance was 0.3% (range = 0–20%) at the 2.7-$km^2$ scale. Across all study areas and development types, 70% of nests were located in habitat with 0–1% press disturbance and 91% of nests were in areas with <3% press disturbance. In areas with <1% press disturbance, the frequency of nest locations was greater than randomly distributed available locations (i.e., available habitat). But when press disturbance exposure reached 1–2%, the frequency of available habitat exceeded the frequency of nest locations (Fig. 3). Brood-rearing locations exhibited the same trend with the frequency of available habitat surpassing the frequency of brood-rearing locations when press disturbance exposure reached 1–2% (Fig. 3). The median exposure of all brood-rearing locations to press disturbance was also 0.3% (range = 0–20%). Habitat with 0–1% disturbance contained 69% of brood-rearing locations and 91% of all brood-rearing locations were in habitat with <3% press disturbance at the 2.7-$km^2$ scale. The general pattern of nest and brood-rearing locations occurring in higher frequency in habitat with lower disturbance levels (0–3% press disturbance), was consistent across study areas and development types (Table S1; Figs. S1–S7, available online in Supporting Information).

With the randomly distributed available locations and at the same scale (2.7 $km^2$), we quantified the overall average disturbance across each study area, which, as per the DDCT process, included both press and pulse disturbance. The average press and pulse disturbance was 5% (median = 1%, range = 0–99.9%) for all study areas combined. Of the average disturbance captured by the DDCT process, 2% (median = 0.5%, range = 0–83%) was press disturbance and 3% (median = 0%, range = 0–99.9%) was pulse disturbance. The range of pulse disturbance approached 100% because some available locations fell within a large wildfire scar (captured per the DDCT process) in the SW study area.

## Nest Survival

Of the 1,049 nests monitored, we did not include 37 abandoned nests in our survival analysis because we did not know the cause of abandonment and did not include 4 nests because their fates were unknown. We also did not include renests ($n = 77$) in our nest survival analysis. Nest survival across study areas ($n = 931$) was 51% (85% CI = 49–54%). Nest survival estimates for each study area were AR = 48% (85% CI = 42–55%), JC = 52% (85% CI = 47–56%), PRB = 59% (85% CI = 55–63%), SC = 57% (85% CI = 48–69%), SMH = 36% (85% CI = 30–44%), and SW = 48% (85% CI = 43–53%).

The top-ranked AIC base model for daily nest survival included 2 of the 8 environmental predictor variables we assessed. The base model included ordinal date and CTI. Ordinal date indicated that nests initiated later in the nesting season had a higher risk of failure. Nest survival was also negatively correlated with CTI within 0.930 km of a nest (2.7-$km^2$ area), suggesting greater risk of nest failure in more mesic areas (i.e., areas with higher potential moisture accumulation).

Of the disturbance scales and functional relationships assessed, press disturbance as a linear relationship at the largest scale (8.0 $km^2$) had the greatest statistical support; however, the direction of the effect was the same across all of the 4 scales assessed (Table 2). At the most supported scale, the 85% confidence intervals for the press disturbance slightly overlapped 0 (Table 2). The relationship suggested that as press disturbance increased within 1.6 km of a nest (8.0-$km^2$ area), the risk of nest failure gradually increased (Fig. 4). At this scale, our nest survival model predicted that likelihood of nest failure would increase by approximately 3% with a 5% increase in press disturbance (Fig. 4). About 91% of nests were exposed to <3% press disturbance. Consequently, predictions beyond 3% press disturbance were informed by about 9% of the sample, which is reflected by widening confidence intervals as press disturbance exposure increased (Figs. 3 and 4). We found no support for nonlinear (quadratic or cubic) functional relationships between nest survival and press disturbance at any scale. We also did not find support for pulse disturbances as an effect modifier of press disturbance on nest survival. We found no evidence of non-proportional hazards of any predictor variables included in our final nest survival model.

## Brood Survival

Brood survival data consisted of 336 brood-rearing females ($n = 2,236$ locations) that had complete observation

**Table 1.** Sample sizes of greater sage-grouse nest and brood-rearing locations. We generated random locations for each study area and compared them to the exposure of nests and broods to disturbance (%) within 2.7 $km^2$, Wyoming, USA, 2008–2014.

| Study area | Years | Nest locations | Brood-rearing locations | Random locations |
|---|---|---|---|---|
| Powder River Basin | 2008–2011 | 308 | 945 | 6,220 |
| Southwest Wyoming | 2008–2011 | 194 | 270 | 2,320 |
| Atlantic Rim | 2008–2011 | 127 | 329 | 2,300 |
| Stewart Creek | 2008–2011 | 53 | 251 | 1,520 |
| Seven Mile Hill | 2009–2010 | 95 | 362 | 2,270 |
| Jeffrey City | 2011–2014 | 272 | 670 | 4,690 |
| All study areas | 2008–2014 | 1,049 | 2,827 | 19,320 |

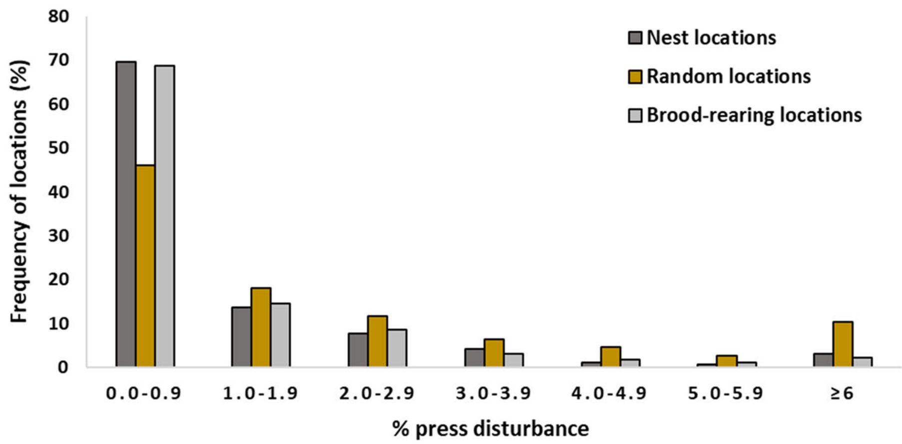


**Figure 3.** Percent press disturbance (i.e., disturbance sustained after initial disturbance and associated with existing energy infrastructure and human activity) exposure at the 2.7-$km^2$ scale comparing greater sage-grouse nest ($n = 1,049$), brood-rearing ($n = 2,827$), and randomly distributed available locations (i.e., pseudo-absence points) from all study areas, Wyoming, USA, 2008–2014.

histories. Brood survival to 40 days post-hatch for the entire sample was 73% (85% CI = 69–77%). Brood survival estimates for individual study areas were AR = 68% (85% CI = 57–80%), JC = 69% (85% CI = 63–76%), PRB = 77% (85% CI = 71–83%), SC = 96% (85% CI = 89–100%), and SMH = 60% (85% CI = 48–78%). We did not include brood data from the SW study area or SC in years 2010 and 2011 in our brood survival models because monitoring was infrequent and brood fates were not verified at 40 days.

Environmental and surface disturbance variables included in brood survival models represented cumulative exposure over the period preceding a mortality event or over the entire brood period if broods survived (~40 days post-hatch). Based on AIC support, the top-ranked base model for daily brood survival included ordinal date, precipitation, and CTI (Table 3). Ordinal date indicated that broods hatching later in the season had a higher risk of mortality. Increased average monthly precipitation was associated with reduced brood survival. Brood survival was also negatively associated with average CTI across consecutive locations at the 1-$km^2$ scale. The significance of the CTI predictor variable suggests that broods occupying wetter areas experience greater mortality risk.

We found no statistical support for a functional relationship, linear or nonlinear, between a unit change (1%) in press disturbance and daily brood survival at any scale, based on AIC and the degree of 85% confidence interval overlap. Similar to nests, the majority of brood-rearing areas were located in habitat with <3% press disturbance; thus, information on broods exposed to increasing levels of disturbance was sparse (Fig. 3). When we modeled press disturbance as a factor-level variable, statistical support increased and this relationship had the most support at the 1-$km^2$ scale (Table 3). At this scale, broods exposed to any press disturbance across consecutive locations were less likely to survive than broods not exposed to press disturbance. Survival estimates to 40 days post-hatch for broods exposed to press disturbance were approximately 10% lower than broods that were not exposed to press disturbance.

When we tested the inclusion of pulse disturbance, also as a factor-level variable, we found that pulse disturbance acted as an effect modifier of press disturbance on brood survival. The pulse disturbance factor had the greatest effect on the press disturbance coefficient as an additive term in the model at the 2.7-$km^2$ scale (Table 3). Pulse disturbance moderately confounded the effect of the press disturbance coefficient with a percent coefficient change of 8.9% (Hosmer and Lemeshow 2008). Survival estimates to

**Table 2.** Top Cox proportional hazard model assessing relationships between press disturbance and greater sage-grouse nest survival. We used the base model to assess the best-supported press disturbance relationship and scale: 0.35 $km^2$, 1 $km^2$, 2.7 $km^2$, and 8 $km^2$. Nests were located in 6 study areas throughout Wyoming, USA, 2008–2014.

| Predictor variable (spatial scale) | Coefficient | 85% CI | | Risk ratio |
|---|---|---|---|---|
| | | Lower | Upper | |
| Base model with study area nested within year as a random effect | | | | |
| Ordinal date | 0.013 | 0.007 | 0.018 | 1.01 |
| Compound topographic index (2.7 $km^2$) | 0.182 | 0.115 | 0.257 | 1.20 |
| Base model + disturbance predictor variable | | | | |
| Press disturbance (8 $km^2$)[a] | 0.024 | −0.003 | 0.051 | 1.03 |
| Press disturbance (2.7 $km^2$) | 0.017 | −0.012 | 0.047 | 1.02 |
| Press disturbance (1 $km^2$) | 0.016 | −0.013 | 0.045 | 1.02 |
| Press disturbance (0.35 $km^2$) | 0.017 | −0.011 | 0.044 | 1.02 |

[a] Press disturbance (i.e., disturbance sustained after initial disturbance and associated with existing energy infrastructure and human activity) had the most statistical support at the 8-$km^2$ scale with 85% confidence intervals only slightly overlapping zero.

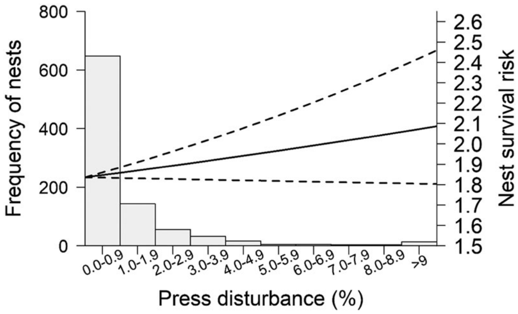


**Figure 4.** Relative risk (risk ratio) of daily greater sage-grouse nest failure related to the percent press disturbance (i.e., disturbance sustained after initial disturbance and associated with existing energy infrastructure and human activity) exposure at the 8-km$^2$ scale. The histogram in the background represents the disturbance exposure of the nests ($n = 931$) assessed at this scale, Wyoming, USA, 2008–2014.

40 days post-hatch for broods exposed to press disturbance and pulse disturbance were approximately 1% lower than those only exposed to press disturbance and 11% lower than broods that were not exposed to any disturbance. We found no evidence of non-proportional hazards for any of the predictor variables included in the top model.

## DISCUSSION

Our research accounts for regional variability in biological effects of sage-grouse exposure to the physical footprint of energy development by incorporating several spatially distinct study areas across Wyoming. We found support for average negative effects of disturbance on 2 critical sage-grouse reproductive rates. The exposure of our sample of sage-grouse to several types of development and infrastructure allowed us to identify population-level effects of the disturbance footprint associated with development. Our findings suggest that as press disturbance increased in sage-grouse nesting habitat, nests exposed to increasing disturbance experienced a gradually increasing risk of failure. Therefore, a surface disturbance cap of 3% or 5% would not eliminate negative effects of press disturbance on nest survival, but lower disturbance intensities would be expected to reduce effects on nest survival when compared to higher disturbance intensities. Our brood survival results suggest that any press disturbance in brood-rearing habitat increased risk for broods and the relationship we detected was irrelevant to the intensity of disturbance. The distribution of nesting and brood-rearing locations relative to press disturbance in our study supports other research that has repeatedly demonstrated that sage-grouse and other wildlife may avoid otherwise suitable habitat as the intensity of energy development increases (Sawyer et al. 2006, Naugle et al. 2011, Germaine et al. 2017). This avoidance behavior highlights the difficulty of detecting demographic consequences of increasing development when higher density development areas are being avoided by wildlife species.

There is much previous research that has focused on the response of sage-grouse to specific development types or infrastructure features, including wind turbines, conventional oil wells, natural gas wells, or transmission lines (Aldridge and Boyce 2007, Dinkins et al. 2014, Rice et al. 2016, Lebeau et al. 2017, Gibson et al. 2018). Because this was not the intent of our research, we did not isolate potential effects from exposure to specific infrastructure features. For instance, at the spatial scales we assessed, the sample of nesting and brood-rearing sage-grouse in the SMH study area were exposed primarily to wind energy infrastructure but also to a major highway and surface coal mining, all of which were quantified as press or pulse disturbance in our analyses.

We documented a gradual reduction in nest survival as press disturbance exposure increased within the largest scale (8-km$^2$ area). Compared to the smaller scales, there was more statistical support at the largest scale. Yet, the effect direction, demonstrating a negative association between press disturbance and nest survival, was consistent across all of the scales we assessed. The greater support at the larger scale suggests that nests within the interior of an energy development field, nests that are surrounded by a network of press disturbance, are more likely to fail than nests that are exposed to more localized and less widely distributed press disturbance. For example, sage-grouse nesting in habitat patches within an oil and gas field may be at greater risk of nest failure than those on the periphery of the field. A similar effect of energy disturbance on nest survival of sagebrush-obligate songbirds nesting within oil and gas

**Table 3.** Top Cox proportional hazard model assessing relationships between press disturbance and greater sage-grouse brood survival. We used the base model to assess the best-supported press disturbance (i.e., disturbance sustained after initial disturbance and associated with existing energy infrastructure and human activity) relationship and scale: 0.35 km$^2$, 1 km$^2$, 2.7 km$^2$, and 8 km$^2$. The pulse disturbance variable as an additive term confounded the effect of press disturbance on brood survival. Brood survival data were from 5 study areas throughout Wyoming, USA, 2008–2014.

| Predictor variable (spatial scale) | Coefficient | 85% CI | | Risk ratio |
|---|---|---|---|---|
| | | Lower | Upper | |
| Base model with study area nested within year as a random effect | | | | |
| Ordinal date | 0.016 | 0.002 | 0.029 | 1.02 |
| Precipitation | 0.009 | 0.002 | 0.017 | 1.01 |
| Compound topographic index (1 km$^2$) | 0.263 | 0.083 | 0.443 | 1.30 |
| Base model + press disturbance predictor variable | | | | |
| Press disturbance (factor variable, 1 km$^2$) | 0.431 | 0.040 | 0.822 | 1.54 |
| Base model + press disturbance predictor variable + confounding predictor variable | | | | |
| Press disturbance (factor variable, 1 km$^2$) | 0.471 | 0.069 | 0.873 | 1.60 |
| Pulse disturbance (factor variable, 2.7 km$^2$)[a] | −0.165 | −0.517 | 0.186 | 0.85 |

[a] Pulse disturbance was not statistically supported as a predictor variable alone but acted as an effect modifier of press disturbance.

fields was detected by Hethcoat and Chalfoun (2015). They suggest that habitat patches within oil and gas fields appear to act as population sinks for breeding sagebrush songbirds (Hethcoat and Chalfoun 2015).

We did not detect an average functional response between increasing press disturbance exposure and daily brood survival. During the brood-rearing period, exposure to any press disturbance reduced brood survival compared to broods not exposed to press disturbance within a 1-$km^2$ area (>0.564 km from development). At this same scale, negative associations between surface disturbance and reproductive rates have been documented in other sagebrush-obligate birds (Hethcoat and Chalfoun 2015). Brewer's sparrow, sagebrush sparrow (*Artemisiospiza nevadensis*), and sage thrasher (*Oreoscoptes montanus*), experienced reduced nest survival as the physical footprint of oil and gas development increased within a 1-$km^2$ area (Hethcoat and Chalfoun 2015). Holloran et al. (2010) reported that annual survival of yearling female sage-grouse reared within 1.65 km (8.6 $km^2$) of infrastructure was 64.9% compared to 100% survival for yearling females reared outside of development (>1.65 km).

Much interest lies in identifying biological thresholds, or points of abrupt change in ecological condition, in which wildlife populations may persist in landscapes being modified by anthropogenic development (Huggett 2005, Johnson and St-Laurent 2011, Doherty et. al 2016). Our nest and brood survival results did not provide support for a threshold type response to disturbance (e.g., average effect) that was consistent across regions. We think this difference in the functional response reiterates that effects of energy development identified locally may diverge across regions and energy types. For instance, Kirol et al. (2015*a*) identified a biological threshold in survival for sage-grouse broods, where the likelihood of survival decreased markedly when surface disturbance reached 4–5%. This study occurred in a single region, however, and only included natural gas development (Kirol et al. 2015*a*).

Our results provide some evidence that the addition of pulse disturbance, as defined here, within a larger area (2.7 $km^2$) confounded the effect of press disturbance on brood survival. Thus, pulse disturbances, such as sagebrush reduction treatments, may have an additive negative effect on brood survival in areas already affected by press disturbance.

Survival modeling is largely dependent on the number of events (e.g., nest failure or brood loss) and, consequently, the statistical confidence for functional relationships between survival and the explanatory variable of interest (e.g., press disturbance) is dependent on the distribution of events relative to a change in the explanatory variable (Hosmer and Lemeshow 2008). Therefore, it is likely that the skewed distribution of nest and brood-rearing locations in areas with less disturbance contributed to reduced statistical confidence in our survival modeling, especially as model predictions extended to the higher press disturbance levels present in available habitat (Fig. 3). Smith et al. (2014) encountered a similar issue when studying habitat use and female sage-grouse survival related to exposure to oil and gas development during winter. These authors suggested that avoidance behavior exhibited by female sage-grouse in winter may have masked their ability to detect functional responses between adult survival and exposure to increasing densities of oil and gas development.

Our findings showed a consistent pattern across regions in which nesting and brood-rearing locations were heavily skewed toward habitat with lower press disturbance levels relative to available habitat. There is much research that provides support for avoidance behavior in sage-grouse; therefore, this behavior is likely influencing this skewed distribution (Naugle et al. 2011, Hovick et al. 2014). For example, approximately 70%, 84%, and 91% of nesting and brood-rearing locations were located in areas with <1%, <2%, and <3% press disturbance, respectively. Other sage-grouse studies that have assessed surface disturbance as an index of energy development and sagebrush loss, point to similar levels of surface disturbance where avoidance behavior results in population declines. Research covering the western portion of the sage-grouse range, using peak male sage-grouse lek counts as a population index, demonstrated that surface disturbance >3% led to local sage-grouse population declines (Knick et al. 2013). Aldridge et al. (2012) reported that Gunnison sage-grouse (*C. minimus*) use of nesting habitat declined dramatically when ≥10% of the area within 1.5 km was devoid of sagebrush cover. Populations of other sagebrush-obligate species are negatively affected at similar disturbance levels. For instance, the presence and abundance of the pygmy rabbit (*Brachylagus idahoensis*) declined sharply once oil and gas surface disturbance reached 2% within a 3-$km^2$ area (1-km radii; Germaine et al. 2017).

The Wyoming Core Area policy represents an example of a strategy that regulates the physical footprint of anthropogenic development as a way to mitigate effects on sage-grouse populations. The DDCT process used to quantify surface disturbance in Wyoming identifies press and pulse disturbances and both of these different disturbances contribute to the 5% disturbance cap. This policy does not limit disturbance to 5% within entire Core Areas *per se* but limits disturbance within development project areas occurring in Core Areas (State of Wyoming 2019). We found that the DDCT process identified more pulse disturbance (3%) than press disturbance (2%) in our study areas. Therefore, when the DDCT process was applied to our study areas as a whole, it limited press disturbance allowances closer to 2%, on average, because the other nearly 3% of allowances were absorbed by pulse disturbances. As described previously, a 2% press disturbance level would encompass the majority of female sage-grouse nesting and brood-rearing locations in our study areas. If no pulse disturbance was identified in a development area, however, the DDCT process would allow for 5% press disturbance. Allowances for a 5% level of only press disturbance, within a 2.7-$km^2$ area, would exclude approximately 96% of the nest and brood-rearing locations across all of our study areas.

Our research represented management-oriented science relating the conservation of sage-grouse and the complexities of balancing species conservation with energy development demands. Sage-grouse nest and brood survival exhibited a consistent relationship with press disturbance, suggesting that the physical footprint of energy development is a valid proxy for management designed to reduce effects on sage-grouse populations in habitat undergoing development. Our results support an average response across regions and different energy development types for both nest and brood survival and negative effects on nest survival increased proportionate to increasing levels of exposure to press disturbance. Nest and brood survival results, however, did not indicate thresholds, a specific level of press disturbance, at which these reproductive rates change abruptly. The predictive ability of our survival models were likely hindered by a clear pattern of use by nesting and brood-rearing female sage-grouse where nesting and brood-rearing locations were disproportionately located in areas with lower levels of press disturbance (0–3%). In all of our study areas, which combined covered nearly 10% of the sage-grouse range in Wyoming, habitat with lower levels of disturbance was available to nesting and brood-rearing females, usually on the periphery of development areas. Therefore, more research is needed to understand how these reproductive rates may be influenced by disturbance in development areas where habitat with lower levels of disturbance are no longer available to sage-grouse populations (i.e., areas in which females cannot avoid nesting and brood-rearing in habitats with >3% press disturbance). Our results provide a clearer understanding of the reproductive costs incurred by sage-grouse in regions that have experienced diverse energy development pressures.

## MANAGEMENT IMPLICATIONS

Managers should avoid or minimize press disturbance in sage-grouse nesting and brood-rearing habitat that has been identified as having a high probability of use during these reproductive stages. If press disturbance is unavoidable in these areas, managers should expect and plan for lower reproductive success for nesting and brood-rearing female sage-grouse even when press disturbance levels are <5% within a project area. Minimizing the spatial extent of disturbance by clustering development is a potentially useful management tool because clustered development, while localizing the disturbance footprint, minimizes the breadth of press disturbance in adjacent sage-grouse habitat within a project area. Placement decisions should consider sage-grouse habitat suitability when clustering development and efforts should be made to cluster that development outside (≥1.6 km) of nesting and brood-rearing habitats. In addition, our results provide evidence that applying pulse disturbances, such as sagebrush reduction treatments, in sage-grouse habitat that already contains press disturbance is not beneficial to sage-grouse and may act to further reduce brood survival rates.

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