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Authors: Kirol, Christopher P., Sutphin, Andrew L., Bond, Laura, Fuller, Mark R., and Maechtle, Thomas L.

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Mitigation effectiveness for improving nesting success of greater sage-grouse influenced by energy development

Christopher P. Kirol, Andrew L. Sutphin, Laura Bond, Mark R. Fuller and Thomas L. Maechtle

C. P. Kirol (chris@bighornec.com), A. L. Sutphin and T. L. Maechtle, Big Horn Environmental Consultants, 730 E. Burkitt, Sheridan, WY 82801, USA. – L. Bond, Biomolecular Research Center, Boise State Univ., 1910 University Drive, Boise, ID 83725, USA. – M. R. Fuller, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk Street, Boise, ID 83706, USA, and Boise State Univ. Raptor Research Center, Boise, ID 83725, USA

Sagebrush *Artemisia* spp. habitats being developed for oil and gas reserves are inhabited by sagebrush obligate species – including the greater sage-grouse *Centrocercus urophasianus* (sage-grouse) that is currently being considered for protection under the U.S. Endangered Species Act. Numerous studies suggest increasing oil and gas development may exacerbate species extinction risks. Therefore, there is a great need for effective on-site mitigation to reduce impacts to co-occurring wildlife such as sage-grouse. Nesting success is a primary factor in avian productivity and declines in nesting success are also thought to be an important contributor to population declines in sage-grouse. From 2008 to 2011 we monitored 296 nests of radio-marked female sage-grouse in a natural gas (NG) field in the Powder River Basin, Wyoming, USA, and compared nest survival in mitigated and non-mitigated development areas and relatively unaltered areas to determine if specific mitigation practices were enhancing nest survival. Nest survival was highest in relatively unaltered habitats followed by mitigated, and then non-mitigated NG areas. Reservoirs used for holding NG discharge water had the greatest support as having a direct relationship to nest survival. Within a 5-km^2 area surrounding a nest, the probability of nest failure increased by about 15% for every 1.5 km increase in reservoir water edge. Reducing reservoirs was a mitigation focus and sage-grouse nesting in mitigated areas were exposed to almost half of the amount of water edge compared to those in non-mitigated areas. Further, we found that an increase in sagebrush cover was positively related to nest survival. Consequently, mitigation efforts focused on reducing reservoir construction and reducing surface disturbance, especially when the surface disturbance results in sagebrush removal, are important to enhancing sage-grouse nesting success.

Increasing demand for energy is expected to result in more unaltered landscapes being used for the exploration and extraction of fossil fuels (Copeland et al. 2011). In western North America, an estimated 126 000 additional oil and gas wells will come into production over the next 20 years (Kiesecker et al. 2011). Energy development can result in direct, indirect and cumulative impacts to wildlife (Johnson and St-Laurent 2011). Because fossil fuel resources and associated development in western North America often occur in sagebrush *Artemisia* spp. ecosystems inhabited by sagebrush obligate species such as the greater sage-grouse *Centrocercus urophasianus* (sage-grouse), managers face complex challenges in balancing energy demands with species conservation.

In response to declines in sage-grouse numbers, which have been largely attributed to anthropogenic disturbance of sagebrush habitats, the US Fish and Wildlife Service (USFWS) determined that the sage-grouse was a candidate for protection under the US Endangered Species Act (USFWS 2010). The primary threats identified in the decision include habitat loss and a lack of regulatory mechanisms to prevent future impacts (USFWS 2010). Much of the oil and gas development in the West occurs on lands under the jurisdiction of the US Bureau of Land Management (BLM) that are guided by a multiple-use mandate, and BLM lands hold most of remaining sagebrush habitats in North America (Naugle et al. 2011). Thus there is a great need for effective mitigation strategies that reduce impacts of energy development on co-occurring wildlife, especially declining species.

Mitigation practices promoted by US regulatory agencies follow a hierarchy designed to avoid, minimize and restore biodiversity on-site while considering offset sites to address residual impacts (USFWS 1993, <www.fws.gov/policy/501fw2.html>). For oil and gas development, on-site mitigation (i.e. minimize impacts) generally involves redesigning operations and infrastructure, or infrastructure placement with a goal to abate impacts to wildlife. Previous research suggested that the on-site mitigation required by the BLM in sage-grouse habitat (BLM base requirements; US BLM 2003) were inadequate for maintaining stable sage-grouse populations (Walker et al. 2007a, Naugle et al. 2011). Our research covers a period from 2008 to 2011 during which 526 natural gas (NG) wells were developed

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in our study area and approximately 73% of these were developed following adaptive oil and gas development strategies (e.g. on-site mitigation beyond the BLM base requirements).

We assessed mitigation practices that included reducing vehicle traffic volume (Lyon and Anderson 2003, Holloran 2005) by using remote well monitoring (Naugle et al. 2011), transporting water in pipelines to treatment facilities or perennial drainages in lieu of constructing on-site water reservoirs (Walker et al. 2007b), minimizing sagebrush removal, especially from dense sagebrush stands (Doherty 2008), burying power lines (Connelly et al. 2000), reducing road and well pad construction and associated surface disturbance, and buffering industrial noise (Lyon and Anderson 2003, Holloran 2005). Remote well monitoring was expected to reduce direct sage-grouse adult and chick mortality from vehicle collisions and to reduce their avoidance of roads associated with human activity and associated noise (Lyon and Anderson 2003, Naugle et al. 2011). A reduction in overhead power lines was expected to reduce perching structures for predators of sage-grouse (adult, chick and nest) and minimize avoidance by sage-grouse (i.e. reduce functional habitat loss; Connelly et al. 2000). Reducing on-site reservoirs was expected to reduce direct habitat loss and to lessen sage-grouse deaths due to West Nile virus (WNv) being augmented by vector mosquitoes breeding in reservoir edge habitats (Walker et al. 2007b). Further, we hypothesized that reservoirs were facilitating the spread of novel predators into sagebrush habitats; such as the striped skunk *Mephitis mephitis* and common raccoon *Procyon lotor* that are generally associated with water and riparian areas (Larivière and Messier 1998, Armstrong 2008). Finally, reductions in road and well pad construction and reducing disturbance in dense sagebrush stands was expected to diminish direct loss of sage-grouse habitat (Holloran 2005, Doherty 2008) and, increase nest survival because sagebrush cover is associated with nest survival (Webb et al. 2012).

There has been extensive research of habitat use by sage-grouse in landscapes altered by energy development and to a lesser extent sage-grouse productivity and survival (Naugle et al. 2011). However, we found no research that tested outcomes of on-site mitigation effectiveness on sage-grouse productivity measures such as nesting success. Herein, we explore implications of on-site mitigation practices to sage-grouse nest survival.

Our primary objective was to determine if adaptive oil and gas development practices can mitigate negative effects of development on sage-grouse nesting success. Our second objective was to explore direct relationships between sage-grouse nest survival and the anthropogenic features of a NG field to determine if the on-site mitigation is targeting the infrastructure and development practices of greatest consequence to nest survival. More specifically, we designed this research to answer the questions: 1) does sage-grouse nest survival differ in mitigated, non-mitigated NG development habitats, and habitats not altered by NG development, and 2) what NG infrastructure features most influence observed differences in nest survival?

Material and methods

Study site

This research occurred in the Powder River Basin (PRB), primarily in Johnson County with the northern portion extending into Sheridan County, Wyoming, USA (106°20′25.38″W, 44°18′35.431″N; Fig. 1). The study area encompassed 937-km^2 of which 61% was private land, 33% was public land administered by the BLM, and 6% was Wyoming state land. Cattle and sheep ranching were the primary agricultural uses and energy development, predominantly in the form of coal bed natural gas, was the primary energy extraction activity occurring in the study area. Seventy nine percent of the study area, including the majority of the private surface, held federally owned mineral rights under the jurisdiction of the BLM. At the end of the study period at total of 1499 wells were present within the study area. Well pads were generally developed at a density of 3.1 well pads per km^2 (80 acre spacing; US BLM 2003, Walker et al. 2007a). To the west, the study area was bordered by high quality nesting habitat (Doherty et al. 2010) that is part of a Wyoming sage-grouse conservation area (core area; <http://wgfd.wyo.gov/web2011/Departments/Wildlife/pdfs/SG_COREAREASV3_CONNECTIVITY0000657.pdf>; accessed 30 May 2014).

Sage-grouse nests in the PRB are exposed to native predators including the American badger *Taxidea taxus*, black-billed magpie *Pica hudsonia*, bobcat *Lynx rufus*, bullsnake *Pituophis catenifer sayi* and coyote *Canis latrans*. Additionally, exotic predators (Hagen 2011), including the striped skunk, red fox *Vulpes vulpes*, and common raccoon, inhabit the study area in association with anthropogenic habitat alteration (Hagen 2011).

The climate in the study area is semi-arid. Monthly average temperatures ranged from 21.6°C in the summer to –5.8°C in the winter. Annual precipitation averaged 33 cm to 43 cm and average annual snowfall ranged from 84 cm to 170 cm. The majority of the study area was shrub-steppe habitat dominated by Wyoming big sagebrush *A. tridentata wyomingensis*. Plains silver sagebrush *A. cana cana* was present but at much lower abundance and was limited to drainage corridors.

Field methods

We captured female sage-grouse in spring (mid-March through late April) 2008 through 2011 and in late summer (September) 2009 and 2010. In the spring, females were captured using a rocket-net (Giesen et al. 1982) and a CODA netlauncher on and near leks. In late summer, all females were captured with the CODA netlauncher. We adapted the CODA netlauncher to be a mobile unit, mounting it on a truck or all-terrain vehicle (ATV), that made it effective at capturing sage-grouse at or adjacent to lek locations (Sutphin and Maechtle unpubl.). We fitted VHF radio transmitters to female grouse. Transmitters weighed 22 g (~1.4% of mean female sage-grouse body mass), had a battery life expectancy of 789 d, and were equipped with mortality sensors. We classified sage-grouse as yearlings (first breeding season) or adults (second breeding season or older) based on

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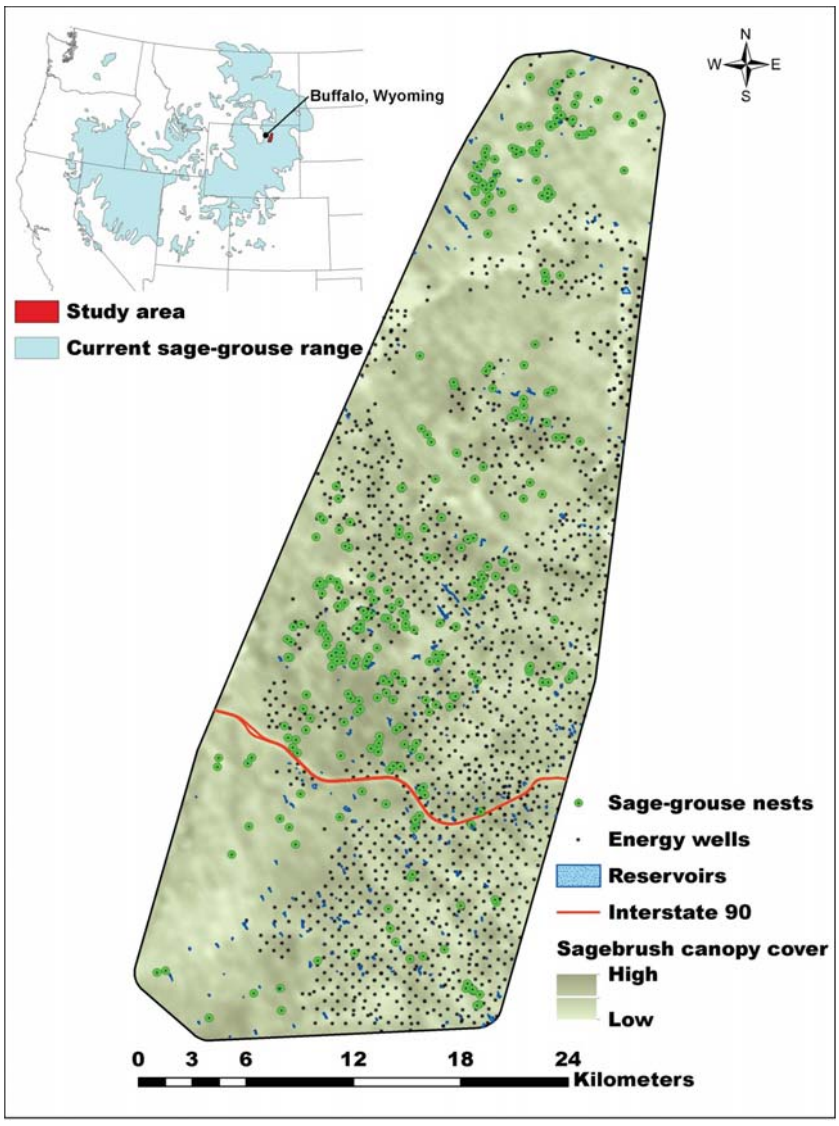


Figure 1. Study area and sage-grouse nest locations in northeast, Wyoming, USA, recorded in 2008–2011 and the current sage-grouse range.

the shape, condition and coloration of the outermost wing primaries (Eng 1955, Dalke et al. 1963). To obtain a representative and random sample of the sage-grouse population occupying the study area, we radio-marked females from 10 leks dispersed throughout the study area within and adjacent to NG development areas.

We located radio-marked female sage-grouse on the ground using hand-held receivers and 3-element Yagi antennas during the nesting period (May–June). Nesting was confirmed by two consecutive visits that identified the radio-marked grouse using the same shrub or by visually observing the female on a nest with binoculars. After confirming a nest location, we monitored the status of the nest every 2–6 d until the conclusion of the nesting effort. To minimize disturbance to the female, we monitored the nests from a distance of ≥ 30 m using binoculars or by triangulating to the nest location using radio telemetry (Walker 2008). After recording or visiting a nest location, we retreated in a nonlinear and varying pattern each visit to prevent predators from following human scent to the nest. The fate of the nest (successful or unsuccessful) was determined by the condition of the eggshells and shell membranes (Wallestad and Pyrah 1974). A nest was considered successful if ≥ 1 egg hatched. We classified a nest as unsuccessful if it was depredated, naturally abandoned, or if the female died during incubation.

Predictor variables

Predictor variables used to explore our nest sample in the context of exposure to habitat conditions (e.g. mitigated and non-mitigated NG development) were compiled in a Geographic information system (GIS) framework and processed with ArcGIS 10.1 and Geospatial Modeling Environment (Beyer 2011). We developed environmental and anthropogenic variables at scales known to be biologically relevant to female sage-grouse during the reproductive period (Holloran and Anderson 2005, Aldridge and Boyce 2007, Doherty et al. 2010) but we limited these to four scales that were

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relevant to the scale of NG development and the accompanying mitigation strategies we were exploring (0.35 km^2, 1.0 km^2, 2.0 km^2 and 5.0 km^2; Table 1).

Reducing impacts of NG wells was a mitigation target because research has demonstrated that energy wells can have negative effects on nest productivity (Dzialak et al. 2011, Webb et al. 2012, Kirol et al. 2015). We obtained data about active, plugged, and abandoned wells from the Wyoming Oil and Gas Conservation Commission that included location, status date and spud date (initiation of drilling) updated to December 2011 (Table 1). Energy development was ongoing during the study; thus, to accurately characterize when infrastructure was established we time-stamped wells based on the spud date and batched them into year increments for

Table 1. Anthropogenic and environmental predictor variables and scales (i.e. analysis regions) considered in our daily nest survival modeling of greater sage-grouse nests (n = 296) in an energy-altered landscape in the Powder River Basin, Wyoming, 2008–2011.

Predictor variable	Variable structure	Description
Anthropogenic[ab]		
WellCnt[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	count of energy wells (primarily natural gas wells) within scale
WellPad[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	count of energy well pads (some pads contained > 1 energy well) within scale
NearWell	decay distance: 0.335, 0.564, 0.800, 1.260 (km)	distance to nearest energy well as decay per scale
NearRoad	decay distance: 0.335, 0.564, 0.800, 1.260 (km)	distance to the nearest class 1 = paved road (paved highway), class 2 = primary road (constructed and regularly maintained gravel road), or class 3 = resource road (short infrastructure access road) as decay per scale
NearClass1RD	decay distance: 0.335, 0.564, 0.800, 1.260 (km)	distance to the nearest class 2 road as decay per scale
NearClass2RD	decay distance: 0.335, 0.564, 0.800, 1.260 (km)	distance to the nearest class 2 road as decay per scale
NearClass3RD	decay distance: 0.335, 0.564, 0.800, 1.260 (km)	distance to the nearest class 3 road as decay per scale
AllRoad[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	total linear distance of all roads (class 1, class 2, and class 3 roads combined) within scale
Class1RD[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	total linear distance of class 1 roads within scale
Class2RD[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	total linear distance of class 2 roads within scale
Class3RD[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	total linear distance of class 3 roads within scale
NearPwrLine	decay distance: 0.335, 0.564, 0.800, 1.260 (km)	distance to nearest overhead power line as decay per scale
PwrLine[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	total linear distance of overhead power lines within scale
NearPersistWater	decay distance: 0.335, 0.564, 0.800, 1.260 (km)	distance to nearest water bodies that persist throughout the summer—energy and/or stock watering reservoirs, and perennial water drainages (Powder River and Crazy Woman Creek) as decay per scale
WaterEdge[c]	Scale: 0.35, 1.0, 2.0, 5.0 (km^2)	total linear distance of water edge in analysis region—energy and/or stock watering reservoirs, and perennial water drainages (Powder River and Crazy Woman Creek) within scale
SurfaceDistb[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	surface disturbance footprint (bare ground resulting from vegetation removal) as proportion of 10-m cells within scale—combination of anthropogenic features (energy infrastructure, all roads [class 1, 2, and 3 roads], man-made reservoirs, gravel pits, and dwellings)
Environmental[a]		
Sage[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	mean sagebrush *Artemisia* sp. cover (%; Homer et al. 2012) within scale
SageSD[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	standard deviation of sagebrush *Artemisia* sp. cover (%; Homer et al. 2012) within scale
ShrubHgt[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	mean shrub height (cm; Homer et al. 2012) within scale
ShrubHgtSD[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	standard deviation of shrub height (cm; Homer et al. 2012) within scale
TWI[c]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)	mean topographic wetness index (TWI; high values = increased soil moisture; Theobald 2007) within scale—processed using a 1/3-arc-second National Elevation Dataset (NED; 10-m DEM)
VRM[d]	scale: 0.35, 1.0, 2.0, 5.0 (km^2)[d]	mean topographic roughness (vector roughness measure [VRM; Sappington et al. 2007]) within scale calculated as a square analysis region—processed using a 1/3-arc-second National Elevation Dataset (NED; 10-m DEM)

[a]to ensure spatial accuracy, predictor variables were verified, corrected, or digitized using NAIP imagery (USDA national agriculture imagery program collected in 2006, 2009, and 2012) and ESRI world imagery (Environmental systems research institute world imagery web map that provides ≤ 1-m resolution satellite and aerial imagery).
[b]energy wells and associated infrastructure (roads, overhead power lines, man-made reservoirs), and surface disturbance footprint were time-stamped based on the corresponding well(s) spud date and as-built POD maps and batched into year increments to depict annual additions or deductions (i.e. wells that were plugged and abandoned during the study) in energy infrastructure during the study period.
[c]circular scales: 0.35 km^2 = 0.335-km radii, 1.0 km^2 = 0.564-km radii, 2.0 km^2 = 0.800-km radii, and 5.0 km^2 = 1.260-km radii.
[d]vector roughness measure (VRM) was calculated within a square scale.

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the entire study period (2008–2011). We confirmed active wells for each year (2008–2011) by checking the active well data against the plugged and abandoned well data.

One of the mitigation strategies was focused on reducing vehicle traffic and road construction. Because of inaccuracies in publically available roads layers (e.g. TIGER/Line 2010 public-domain road layers) in the PRB, we manually digitized roads (paved and gravel) using 1-m National Agriculture Imagery Program (NAIP) imagery at a ~1:3000 screen resolution. We classified our roads as: class 1 paved roads, class 2 primary roads (constructed and regularly maintained gravel roads), and class 3 resource roads (short infrastructure access roads; Finn and Knick 2011). For this research we were primarily concerned with roads that were used routinely to access wells and other human infrastructure; thus, our roads layer did not include primitive roads (i.e. 4×4 two-tracks) that are not maintained (Table 1).

Minimizing overhead power lines was a mitigation focus. Overhead power line location data, updated to 2012, was obtained from Powder River Energy Corporation. Overhead power lines were checked for spatial accuracy using ESRI world imagery that provides ≤ 1-m resolution satellite and aerial imagery (<http://services.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer>, accessed 1 April 2013). Individual power poles are visible with this imagery (Table 1).

Coal bed natural gas extraction requires the dewatering of wells which results in large amounts of produced water that is often stored in reservoirs. Reservoir construction causes direct habitat loss and has been linked to sage-grouse deaths from WNv infections related to increases in mosquito habitat (Walker et al. 2007b). The variable persistent water was defined as surface water that was maintained throughout the summer and included reservoirs and ponds and two perennial drainages – Powder River and Crazy Woman Creek (Table 1). Reservoirs and ponds in our study area were man-made and constructed for NG water storage or livestock watering. Surface water edge was manually digitized using NAIP imagery. Because NAIP imagery is collected between July–August in Wyoming this reflected persistence of surface water throughout the summer.

A mitigation focus was to reduce surface disturbance associated with NG development that results in direct habitat loss and habitat fragmentation that can lead to increased predation (Hagen 2011). We calculated the footprint of surface disturbance – bare ground devoid of vegetation – by creating a disturbance layer. In developing this layer, with the exception of roads, we manually digitized surface disturbance using NAIP imagery at a ~1:3000 screen resolution across the study area. The disturbance area of class 1, 2 and 3 roads were generated by buffering each road class by an average disturbance width measured in the field and confirmed using imagery. The average disturbance width in our study area was 8 m, 10 m and 30 m for class 1, 2 and 3 roads, respectively. Our surface disturbance data consisted of all anthropogenic disturbance including well pads, compressor sites, transfer stations, paved and gravel roads, man-made reservoirs, human dwellings and gravel pits (Table 1).

We found that the unprocessed infrastructure data had many inaccuracies, such as incorrect well locations. Using available imagery we found that the well points were often not accurate to the actual pad location, with no spatial pattern to this inconsistency, or a well structure would be visible but lack a well point in the database. Further, we determined that publically available roads layers were not sufficient to use at the finer scales assessed here because the roads in these layers often did not track the actual road footprint and frequently did not have a road denoted when a road was present. Therefore, we used NAIP and ESRI world imagery to inspect the analysis area and validate, digitize or correct infrastructure locations. The NAIP imagery used was collected for Wyoming, USA between July–August on a 3-year rotation (2006, 2009, 2012; <http://datagateway.nrcs.usda.gov>, accessed 1 July 2013).

We used the time-stamped wells and as-built plan of development (POD) maps, provided by the BLM-Buffalo Field Office, to batch all NG variables (e.g. roads, reservoirs, power lines, surface disturbance) into year increments to depict annual additions or deductions (i.e. wells that were plugged and abandoned during the study). Wells and corresponding infrastructure that were drilled (spud date) by 1 May in the sample year were included in that year. The POD maps reflect individual NG development areas with all associated infrastructure (roads, wells, reservoirs, utility corridors, etc.). PODs are specific to individual producers and POD maps are dated based on construction completion.

We modeled nest distance from feature variables using exponential distance decay functions (Table 1; Fedy and Martin 2011) to account for decreasing magnitude of influence with increasing distance from anthropogenic features (e.g. distance to nearest road or to overhead power line) on nest survival. The calculated decay value using the form $e^{(-d/\alpha)}$ where d was the distance in kilometers from the nest to the feature, and α was set to correspond with each window size radius – 0.335-km, 0.564-km, 0.800-km and 1.260-km. This transformation scaled each variable between 0 and 1, with the highest values close to the feature of interest and 0 at the farthest distances.

Relationships between environmental characteristics (i.e. vegetation and terrain features) and sage-grouse nest survival have been well documented in previous research (Holloran 2005, Aldridge and Boyce 2007, Dzialak et al. 2011, Webb et al. 2012, Kirol et al. 2015). We included environmental variables in our modeling effort to facilitate interpretation of anthropogenic effects and mitigation by controlling for habitat variability related to environmental differences in our nest sample. The environmental variables compiled included four vegetation variables: shrub height (variable includes all shrub species), standard deviation in shrub height, sagebrush *Artemisia* sp. canopy cover, and the standard deviation in sagebrush canopy cover all processed from Wyoming sagebrush products (Homer et al. 2012); and two terrain variables: topographic wetness index (TWI; Theobald 2007), and vector roughness measure (VRM; Sappington et al. 2007; Table 1). TWI is a form of compound topographic index (CTI) that predicts surface water accumulation on the basis of landscape concavity and hydrology (Theobald 2007). VRM represents terrain ruggedness with low VRM values indicating flatter areas (low slope), moderate values indicating high slope but relatively even terrain (low ruggedness), and high values indicating high slope and broken terrain (high ruggedness; Sappington et al. 2007). We visually

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checked the accuracy of environmental variables with ESRI world imagery.

Exposure-type factor variable

The on-site mitigation practices were implemented by Anadarko Petroleum Corporation [APC] in cooperation with the BLM. These practices were implemented for NG development that started in 2008. We separated our well data into two strata of wells, either mitigated or non-mitigated. Mitigated wells were those that were constructed by APC and were established in 2008 or after – reflecting when mitigation was implemented by APC. Non-mitigated NG wells were wells that were drilled by other producers, that were not implementing mitigation beyond the BLM base requirements (US BLM 2003), and wells that were drilled by APC prior to 2008 before the mitigation strategies were implemented. Wells and supporting infrastructure (roads, power lines and reservoirs) were generally developed concurrently within a POD (in our study area PODs contained from 1 to 98 wells). Consequently, mitigated and non-mitigated wells and associated infrastructure were spatially clustered. Therefore, as-built POD maps further informed our mitigated and non-mitigated well groupings.

In concurrence with our research objective to test effects of mitigation and because on-site mitigation is not necessarily localized to an individual well but more broadly applied to a POD (e.g. reduced surface disturbance, buried power lines, and remote well monitoring), nests were grouped by an exposure-type variable into four levels based on development and mitigation exposure. Relative to each scale (0.335-km radii, 0.564-km radii, 0.800-km radii and 1.260-km radii), the nest sample was categorized as within mitigated development (level 2: mitigated nests), within non-mitigated development (level 3: non-mitigated nests), on the periphery of development (level 4), or in relatively unaltered habitats outside of development (level 1: unaltered nests). Exposure-type level 1 indicated that no energy development (e.g. wells and associated infrastructure) or energy related development (e.g. access roads and overhead power lines) was within scale. However, non-energy related anthropogenic features may have been in scale (e.g. livestock watering reservoirs). Level 2 indicated that the majority ($>50\%$) of the energy development within the scale was mitigated. Level 3 indicated that less than 50% of the energy development within the scale was mitigated. Nests classified as level 4 were those that had energy related access roads or overhead power lines within scale but no energy wells or PODs within scale. For example, nests classified as level 4 may have had a class 2 access road within scale that was used to access energy development. Most nests within development were conclusively in mitigated or non-mitigated PODs (level 2 or 3) and no nests in our sample were exposed to an even split of mitigated and non-mitigated NG development.

Statistical analysis

We explored potential relationships between predictor variables and daily nest survival (DNS) using logistic exposure (LE) described by Shaffer (2004) and Rotella et al. (2004). Estimates of nest survival (i.e. ≥ 1 egg hatched) were based on a 28 day incubation period. Early assessments indicated that year was best included as fixed effect, and that it was not necessary to model covariance with respect to re-nests or nesting attempts by the same female over multiple years. Predictor variables, other than decay distances, were standardized (subtracting the overall mean value from each observation and dividing by the overall standard deviation) resulting in a value range of approximately –5.0 to 5.0. This step allowed for higher numerical efficiency (Fox 2008) and prevented observations that naturally occurred as larger values to overly influence parameter estimates. Pearson correlation was calculated between all pairs of variables and we did not allow variables displaying high correlation ($\geq |0.7|$) to be included in the same model at any stage in our modeling effort.

Because our primary goal was to evaluate relative changes in nest survival in the presence of NG development and mitigation, we identified the most appropriate scales for the environmental variables by assessing AIC_c scores (Hurvich and Tsai 1989, Burnham and Anderson 2009). Once these scales were identified, we left the environmental variables and study year in the model to select the mitigation scale and anthropogenic variables. The environmental variables did not compete with anthropogenic variables; their presence was needed to account for variation in observed nest survival and to facilitate interpretation of the anthropogenic variables as statistical control variables (Hosmer and Lemeshow 2008).

In combination with our multi-scale environmental model and study year we fit all four scales of exposure-type to assess the most informative scale. We selected the exposure-type variable-scale with the lowest AIC_c score. The model with the selected exposure-type variable, the environmental variables and study year formed our base model that was used in subsequential modeling steps.

We next considered each anthropogenic variable, at each scale, with the base model (study year, environmental variables and exposure-type). We selected the best supported variable-scale for each anthropogenic predictor, based on either AIC_c or, when there was near parity in AIC_c scores, support by the degree of 85% confidence interval (CI) overlap of the individual predictor variables (i.e. the variables with the least amount of overlap of zero; Hosmer and Lemeshow 2008, Arnold 2010). We fit all possible combinations of these 10 selected anthropogenic variables, as well as interaction terms between anthropogenic variables and habitat (environmental variables) that made biological sense as multiplicative effects or had literature support. The interaction terms we explored included: sagebrush cover (Sage) $\times$ well density (WellCnt; Walker et al. 2007a), sagebrush cover $\times$ road density (AllRoad; Pitman et. al. 2005), sagebrush $\times$ disturbance (SurfaceDistb; Holloran et al. 2005), and shrub height (ShrubHgt) $\times$ distance to power line (NearPwrLine), sagebrush cover $\times$ power line density (PwrLine), and sagebrush cover $\times$ water edge (WaterEdge). The variables in the interaction terms were also explored at all scales and scale combinations.

Throughout the modeling steps we assessed model adequacy by examining residual plots for trends with included and unincluded predictor variables (Tutz 2012). This allowed an additional review of the scales chosen as well as an

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indication of whether additional variables should be considered. We followed Arnold (2010) to identify variables as uninformative by variable weights and parameter estimates that had 85% CIs that overlapped zero.

We used variance decomposition to assess how much variation in sage-grouse nest survival is explained by habitat (i.e. environmental variables), study year, exposure-type and anthropogenic features in our study area. Variance decomposition is a statistical approach to partition the explained variation or the relative influence of different variables or variable sets in a full model (Whittaker 1984, Lawler and Edwards 2006). It uses the maximum likelihood function to separate the total model variation into shared and pure variation. Shared variation is jointly explained by different variables or variable sets and pure variation is the variation that is independently explained by a single variable or variable set. We defined our full model for variance decomposition as the total set of the variables in the top and competitive ($\Delta AIC_c \leq 2.0$) model(s). The model types for this assessment were groups of predictors that explain anthropogenic features (type 1), habitat characteristics (type 2), study year (type 3) and exposure-type (type 4).

All computations were conducted using SAS ver. 9.3. Model-derived results (e.g. coefficients and nest survival predictions) are presented with 85% CIs for compatibility with the AIC_c variable selection process (Arnold 2010).

Results

We monitored 301 nests (n = 68 in 2008, n = 76 in 2009, n = 84 in 2010 and n = 68 in 2011) from 2008–2011 of which 156 were unsuccessful. Five of these nests were unsuccessful due to abandonment and the remainder of the unsuccessful nests (n = 151 or 96.7%) were lost to predators. We did not use the five abandoned nests in our LE estimates and modeling because abandonment could have been observer-induced. We recorded 7, 9, 10 and 5 second nest attempts in 2008, 2009, 2010 and 2011, respectively and 1 third nest attempt in 2008 and 2009. The raw LE nest survival estimate for the entire analysis sample (n = 296) was 54% (95% CI: 48–60%). We found a significant ($\propto = 0.05$) difference in nest survival among years ($\chi^2_3 = 9.1$, $p = 0.028$) but not between adults and yearlings ($\chi^2_1 = 1.81$, $p = 0.179$) or first and second nests ($\chi^2_1 = 2.80$, $p = 0.094$).

The environmental model containing study year (Year) and Sage_0.35, SageSD_2.0, ShrubHgtSD_5.0, TWI_2.0, and VRM_0.35 had the lowest AIC_c of the 1025 environmental combinations considered (Supplementary material Appendix 1 Table A1). The exposure-type variable was best supported at the 2.0 km² scale (ExposureType_2.0) in our modeling effort. Therefore, the variables Sage_0.35, SageSD_2.0, ShrubHgtSD_5.0, TWI_2.0, VRM_0.35, ExposureType_2.0 and Year formed our base model (Table 2). Four of the five environmental variables in the base model were significant at the $\propto = 0.15$ level (Table 2).

The best supported anthropogenic variable-scales included Class2RD_1.0, Class3RD_2.0, PwrLine_5.0, NearPersistWater_5.0, NearPwrLine_2.0, NearRoad_5.0, NearWell_0.35, SurfaceDistb_0.35, WaterEdge_5.0 and WellPad_5.0. With all combinations of the base model and anthropogenic predictors, we compared 1024 models. The top model was highly competitive ($\Delta AIC_c \leq 2$) with 24 other models in the set, including the base model alone (Supplementary material Appendix 1 Table A2). The top model, base model + WaterEdge_5.0, was the only model with greater AIC_c support (0.3 ΔAIC_c) than the base model (the second best model in the set). We dealt with model selection uncertainty by further examining each of the anthropogenic predictors' association with DNS in conjunction with our top model (model containing the base variables and WaterEdge_5.0). Again these anthropogenic variables proved to be unsupported (parameter estimate 85% CI overlapped 0) as predictors of nest survival (Table 3).

Table 2. The coefficients (β) and the 85% confidence interval (CI) for the predictor variables forming our base model explaining greater sage-grouse nest survival (n = 296) in an energy-altered landscape in the Powder River Basin, Wyoming, 2008–2011.

Predictor variable	Scale	β	Lower CI	Upper CI
Intercept		3.659	3.244	4.075
Sage	0.35 km²	0.262	0.087	0.436
SageSD	2.00 km²	−0.128	−0.314	0.058
ShrubHgtSD	5.00 km²	0.230	0.087	0.374
TWI	2.00 km²	0.157	0.002	0.312
VRM	0.35 km²	0.253	0.063	0.442
Year 1 (2008)		−0.017	−0.430	0.395
Year 2 (2009)		−0.309	−0.696	0.078
Year 3 (2010)		−0.653	−1.020	−0.285
Year 4 (2011)		Reference		
Exposure-type (level 1)	2.00 km²	0.724	0.287	1.161
Exposure-type (level 2)	2.00 km²	0.548	0.171	0.924
Exposure-type (level 3)	2.00 km²	0.385	−0.054	0.824
Exposure-type (level 4)	2.00 km²	Reference		

Interaction terms between anthropogenic features and habitat (sagebrush cover and shrub height) had little model support. Of the 104 multiplicative models explored, the interaction term in this set with the lowest AIC_c score had less support than the base model alone (1.4 ΔAIC_c; Supplementary material Appendix 1 Table A2).

WaterEdge_5.0 was the only anthropogenic predictor that had a parameter estimate 85% CI that did not overlap 0 and had the greatest support as assessed by relative importance (Table 3). Based on relative importance weights WaterEdge_5.0 was a 1.7 times more plausible predictor of DNS when compared to NearRoad_5.0, the anthropogenic predictor with the second highest importance weight. Water edge within 1.260 km of a nest (5.0 km² scale) was negatively related to sage-grouse nest survival. At this scale, nest exposure to water edge ranged from 0.0–8.4 km. With approximately a 1.5 km increase in water edge the odds of nest failure increased by 15% (1–30%). The predictor variable water edge incorporated all water edge including the only two natural water features, Powder River and Crazy Woman Creek (Table 1). Of our nest sample, only 1% (n = 4) of nests were within 1.260 km (5.0 km² scale) of these natural water features and the closest nest was 0.790 km from Crazy Woman Creek. Therefore, the detected association between DNS and water edge was primarily driven by man-made reservoirs.

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Table 3. Summary of anthropogenic variable importance in logistic exposure models that are represented in the competitive model set ($\Delta AIC_c \leq 2$) of greater sage-grouse nest survival (n = 296) in an energy-altered landscape in the Powder River Basin, Wyoming, 2008–2011. The table presents the variable weights based on the top and competing models (24 models) and the number of models that contain each predictor (models present). The base model (Sage_0.35 + SageSD_2.0 + ShrubHgtSD_5.0 + TWI_2.0 + VRM_0.35 + Year + ExposureType_2.0) was fixed in all models. The coefficients (β) and 85% confidence interval (CI) for WaterEdge are from our top model (base model + WaterEdge_5.0). The β and the 85% CI for the remainder of the anthropogenic variables are from our top model fitted with the variable of interest (e.g. base model + WaterEdge_5.0 + NearRoad_5.0). The β and corresponding CI for that predictor variable are highlighted in gray if the 85% CI that does not overlap zero. Results are from standardized variables.

Predictor variable	Scale	Decay distance	Variable weight	Models present (no.)	β	Lower CI	Upper CI
WaterEdge	5.00 km²		0.507	13	−0.155	−0.301	−0.010
					Variable + top model[a]		
NearRoad		1.260 km	0.287	8	−0.712	−1.693	0.268
WellPad	5.00 km²		0.161	4	0.151	−0.061	0.362
NearPwrLine		0.800 km	0.142	4	0.384	−0.184	0.953
NearWell		0.335 km	0.142	4	0.524	−0.399	1.447
Class2RD	1.00 km²		0.068	2	0.073	−0.085	0.231
PwrLine	5.00 km²		0.061	2	0.054	−0.097	0.205
SurfaceDistb	0.35 km²		0.060	2	−0.061	−0.219	0.097
Class3RD	2.00 km²		0.055	2	0.022	−0.165	0.209
NearPersistWater		1.260 km	0.030	1	0.260	−0.555	1.086

[a]hereafter variables β and corresponding CI are from the variable of interest fitted with our top model. The top model contains eight terms (Sage_0.35 + SageSD_2.0 + ShrubHgtSD_5.0 + TWI_2.0 + VRM_0.35 + Year + ExposureType_2.0 [base model] + WaterEdge_5.0).

Prior to adjusting for nest exposure to different environmental conditions (e.g. environmental and terrain predictor variables), the LE nest survival estimates for non-mitigated nests (level 3) were 14% lower than mitigated nests (level 2). When the model was adjusted for different environmental conditions (i.e. base model), the LE nest survival predictions narrowed but level 3 was still 5% lower than level 2. Yet, the 85% CI for level 2 nests overlapped unaltered nests (level 1) and level 3 nests (Fig. 2). For all LE nest survival models, before and after adjusting for environmental and anthropogenic factors, the pattern in nest survival remained the same with nest survival being the highest outside development, second highest in mitigated areas, and lower in non-mitigated NG development areas (Table 4).

The average amount of WaterEdge_5.0 exposure differed among the four exposure-type nests defined at the 2.0 km² scale. Nests in level 1, level 2, level 3 and level 4 on average were exposed to 1.696 ± 0.215 km, 1.208 ± 0.140 km, 2.313 ± 0.289 km and 1.321 ± 0.225 km of persistent water edge, respectively. Nests in non-mitigated development were exposed to the greatest amount of water edge. Surface disturbance exposure also diverged among levels. Surface disturbance exposure within a 2.0 km² area, the best supported scale in which the nests were categorized into the exposure-type variable, was: level 1 = 0.16 ± 0.03%, level 2 = 1.99 ± 0.11%, level 3 = 2.79 ± 0.22% and level 4 = 1.42 ± 0.17%. At a more localized scale (0.35 km²), the scale in which greater sagebrush cover had the most support as a predictor of DNS, the average percent of surface disturbance exposure per exposure-type was: level 1 = 0.12 ± 0.04%, level 2 = 1.85 ± 0.13%, level 3 = 2.58 ± 0.36% and level 4 = 1.22 ± 0.23%. Nests in non-mitigated NG development were exposed to the greatest amount of surface disturbance and, as expected, nests outside of development were exposed to the least amount of surface disturbance.

Variance decomposition suggested that environmental predictor variables explained the largest amount of variation

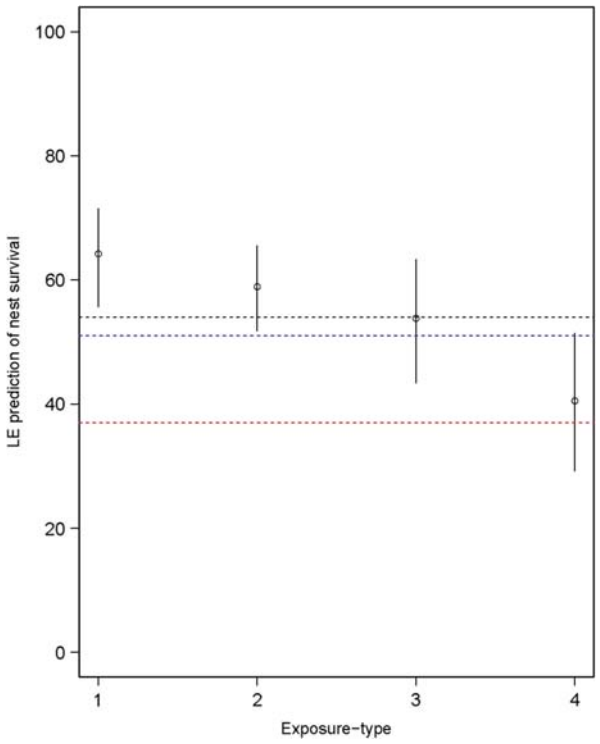


Figure 2. Model-based logistic exposure (LE) nest survival predictions and 85% confidence intervals for of sage-grouse nests distributed into four levels (i.e. subsamples) based on different exposure to energy development and on-site mitigation (factor variable ExposureType_2.0; Table 1) in the Powder River Basin, Wyoming, 2008–2011. The LE predictions are derived from our base model (Sage_0.35 + SageSD_2.0 + ShrubHgtSD_5.0 + TWI_2.0 + VRM_0.35 + Year + Exposure-type_2.0) that controls for confounding factors such as study year and habitat characteristics. The black dashed line is the LE nest success estimate (54%) for our entire nest sample. The blue and red dashed lines are range-wide average sage-grouse nest success estimates from non-altered (51%) and altered (37%) habitats, respectively (Connelly et al. 2011).

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Table 4. Greater sage-grouse nest survival estimates (non-adjusted model) and nest survival model predictions (base model and top model) for nests with different exposure to energy development and mitigation (Exposure-type) in the Powder River Basin, Wyoming, 2008–2011. Estimates and predictions include 85% confidence intervals. The nest sample (n = 296) is distributed per level as follows: level 1 = 87 nests, level 2 = 114 nests, level 3 = 51 nests and level 4 = 44 nests.

	Logistic exposure nest survival estimates/predictions		
Exposure-type	Non-adjusted model	Base model (environmental + year)	Top model (environment + year + water edge)
Level 1 (unaltered habitat)	61% (53–68%)	64% (56–72%)	65% (56–72%)
Level 2 (mitigated development)	58% (51–65%)	59% (52–66%)	58% (51–65%)
Level 3 (non-mitigated development)	44% (34–53%)	54% (43–63%)	57% (46–66%)
Level 4 (periphery of development)	44% (33–54%)	41% (29–51%)	39% (28–50%)

in DNS (33.2%). Anthropogenic variables explained 22.1%, exposure-type explained 3.8%, and study year explained 25.4%. We detected very little variance explained by shared components. The only shared component of any magnitude was shared variation of 13.8% between the anthropogenic and exposure-type components; all other shared components explained less than 5%.

Discussion

We found that nest survival estimates from mitigated development areas, both before and after model-adjusting (58% to 59%), were relatively high when compared to other sage-grouse research in altered and unaltered habitats. Previous on-site mitigation for oil and gas development in sage-grouse habitat has been deemed unsuccessful for maintaining sage-grouse populations (Walker et al. 2007a, Naugle et al. 2011). Our results from an enhanced on-site mitigation strategy suggest a measurable improvement in nest survival when these mitigation strategies are implemented. The PRB has undergone extensive gas development during the last 15 years and persistence of this sage-grouse population has been uncertain (USFWS 2010), so increased nest survival associated with these mitigation strategies may improve the likelihood of persistence.

Poor nest survival rates can dramatically limit population growth in sage-grouse (Schroeder et al. 1999, Taylor et al. 2012). As with many avian species (Liebezeit et al. 2009), sage-grouse nest survival is generally lower in human-altered habitats, regardless of the type of development, when compared to unaltered habitats (Connelly et al 2011, LeBeau et al. 2014). Lower nest survival in human-altered habitats is likely a consequence of diminished habitat quality and predator subsidization in these altered habitats (Chalfoun et al. 2002, Hagen 2011). Our results support the conclusion that undisturbed habitats yield the highest nest survival estimates when compared to altered habitats. Connelly et al. (2011) reported an average range-wide nest survival rate of 37% for sage-grouse nests located in altered habitats compared to 51% nest survival in unaltered habitats (Connelly et al. 2011) and Webb et al. (2012) reported a 28.9% nest survival rate in energy-altered habitats in Wind River Basin, Wyoming. Our findings suggest that reduced construction of reservoirs for holding NG discharge water was the on-site mitigation measure that had the greatest positive benefit to nest survival of sage-grouse in NG development areas. Additionally, our findings suggest that mitigation focused on reducing sagebrush removal was also important to bolstering nest survival.

Our nest survival models consistently revealed that nests in mitigated development had the second highest survival, followed by nests in non-mitigated development. When we account for habitat differences between areas (model-adjusted with environmental predictor variables) we found that nest survival in mitigated development areas was 5% lower than nest survival in unaltered areas but 5% higher than nests in non-mitigated development; however, the 85% CI for these predictions overlap (Fig. 2). After adjusting for all the predictors in our top model, environmental factors plus water edge, there was little difference between nest survival predictions (1%) for nests in mitigated development and non-mitigated development. This suggests that the predictors comprising our top model are accounting for the majority of difference in nest survival between these areas; thus, giving us greater confidence in our top model as well as the importance of water edge (e.g. man-made reservoirs). The pattern in nest survival for the different exposure-types, both before and after adjusting for environmental differences, provide evidence that on-site mitigation resulted in a moderate increase in sage-grouse nest survival when compared to NG development without these mitigation practices in place.

We detected a significant and negative association between nest survival and water edge within 1.3 km of a nest site. This suggests that mitigation focused on managing produced water by transporting it in pipelines to treatment facilities or perennial drainages rather than constructing on-site reservoirs was an important component of the implemented mitigation on sage-grouse nest survival. The relationship between water reservoirs and reduced sage-grouse nest survival in oil and gas development areas support previous findings indicating sage-grouse nest survival was lower in habitats closer to water features and energy development in two study sites in Wyoming (Dzialak et al. 2011, Webb et al. 2012). However, we did not find that proximity to water edge was driving nest failures; rather, nests with a greater amount of water edge within the habitat surrounding the nest were less likely to be successful. We speculate that this negative association with water edge is because predators concentrate foraging activities in areas with more water edge resulting in an increased chance that a nest will be discovered. Further, predators that are generally associated with water and are proficient predators of avian nests, such as the striped skunk (Larivière and Messier 1998, Hagen 2011), may be contributing to decreased nest survival in these areas. Thus, we theorize that anthropogenic water edge may be

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subsidizing nest predators, including those that would not use the area regularly if greater water edge and other anthropogenic features were not present. Novel nest predators including the striped skunk (Larivière and Messier 1998) appear to be moving into sagebrush habitats in the PRB.

NG related water features are of particular importance in the PRB because these features aid in the spread of WNv into sage-grouse habitat (Zou et al. 2006). The combination of West Nile virus and energy development has been a major threat to sage-grouse population persistence in the PRB (Walker et al. 2007b, Walker and Naugle 2011). Sage-grouse adults and chicks are extremely susceptible to WNv infection and infection almost always results in death (Walker et al. 2007b, Walker and Naugle 2011). Therefore, adding water features to energy development landscape in the PRB and in other areas where WNv is present can result in double jeopardy for sage-grouse populations as these water features are associated with increased mortalities and depressed nest survival.

At the end of our study (2011), 191 NG related reservoirs had been constructed in our study area. However, sage-grouse nests in mitigated development areas, on average, were exposed to almost half the amount of water edge compared to those located in non-mitigated development areas (5.0 km^2 scale). The differences in water edge provides further evidence that the divergence in nest survival between mitigated and non-mitigated development areas was largely being driven by the reduction in NG reservoir construction.

The importance of sagebrush cover to sage-grouse nest survival is well known (Schroeder et al. 1999). Consistent with other research (Webb et al. 2012, Kirol et al. 2015), nests in our study that were centered in areas with greater sagebrush cover at a localized scale (within 0.34 km of a nest) were more likely to be successful than nests surrounded by less sagebrush cover. Yet, surface disturbance was not statistically supported as having a direct effect on sage-grouse nest survival although the effect direction was the same (e.g. increased surface disturbance had a negative association with nest survival). This relationship is logical because surface disturbance did not always result in sagebrush removal because not all of the development occurred in sagebrush stands. These findings considered together suggest that mitigation efforts focused on reduced surface disturbance, especially in the form of sagebrush removal, are also consequential to sage-grouse nest survival.

We did not detect a direct association between nest survival and NG wells (distance to a well or well density). This finding contrasts with studies in which nests closer to energy wells were more likely to fail (Dzialak et al. 2011, Webb et al. 2012), but corroborated by others that did not detect a direct association between energy wells and nest survival (Aldridge and Boyce 2007, Dinkins 2013, Kirol et al. 2015). Predation is a regular factor affecting sage-grouse nesting success and anthropogenic changes to the environment can affect predation (Hagen 2011). Therefore, we suspect that the variety of relationships that have been found during different studies on sage-grouse nesting success in human-altered landscapes results in part from differences among study areas in relation to the shifts in predator community structure, abundance, and behavior (Chalfoun et al. 2002, Hagen 2011). Predator shifts likely respond differently to varying types and extents of development, including such factors as vegetation change, infrastructure, and many other factors that accompany the "human footprint" (Leu et al. 2008).

Common ravens *Corvus corax* are effective sage-grouse nest predators (Bui et al. 2010, Coates and Delehanty 2010, Hagen 2011), but, as of 2011, not a single common raven nest was recorded in our study area (<www.blm.gov/wy/st/en/field_offices/Buffalo/wildlife/data.html>, accessed 1 February 2012). Therefore, we theorize that the sparseness of common ravens provides a partial explanation for the relatively high sage-grouse nest survival in our study. Also, abundance of common ravens may help explain some inconsistencies in identified associations between sage-grouse nest survival and specific infrastructure features among different studies (e.g. distance to a well, Dzialak et al. 2011) because certain infrastructure, such as wells and power poles, provide perching and nesting structures used by ravens (Bui et al. 2010). Thus, sage-grouse nests closer to these features would be more likely to be predated by ravens.

Sage-grouse research using presence–absence data has consistently revealed disproportionately low use of habitat associated with energy infrastructure (Aldridge and Boyce 2007, Naugle et al. 2011, Hess and Beck 2012, Smith et al. 2014). Therefore, it is important to consider our findings in the context of female sage-grouse choices for nest placement. That is, in some cases avoidance behavior could have prevented us from detecting effects of infrastructure on sage-grouse nest fate because of little or no nesting occurring near that feature. For instance, we did not find a direct relationship between nest survival and the density or distance to overhead power lines. However, similar to other prairie grouse species (Pitman et al. 2005), sage-grouse in our study rarely nested proximate to overhead power lines or in areas with higher power line densities. Only 13% of our nest sample was located within 0.34 km of an overhead power line and 78% of our nests were located in habitats with a power line densities less than 17 km per 5.0 km^2; even though there was approximately 296 km of overhead power lines in our study area and densities exceeded 51 km per 5 km^2 in some areas.

Unexpectedly, our lowest nest survival estimates of 40% came from level 4, which were nests outside of primary development areas but still within 0.8-km of energy related infrastructure (e.g. access roads, overhead power lines). Level 4 contained our lowest sample of nests (n = 44) compared to the other levels. We found that these nests were mainly clustered along a major energy access road (used to access several PODs) and the interstate. Although our results do not explain the lower survival estimate for level 4, we suspect that the proximity of these nests to the interstate and a heavily used access road might have negatively affected nest survival.

Variance decomposition revealed that environmental variables specific to vegetation characteristics explained the largest amount of variation in nest survival in our study area. In addition, nest survival differences among years explained a significant portion of the variability in nest survival. The exposure-type factor variable, explaining development and mitigation, only explained 4% of the variation in nest survival when considered alone. Yet, exposure-type shared 14% of the variation in nest survival with anthropogenic variables that, when considered alone, explained 21% of the variation.

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The shared variation between anthropogenic and exposure-type components provides additional evidence that differences in distribution and density of anthropogenic features within the four exposure-types is related to nest survival.

Our work is the first to quantify and evaluate the benefits of a research informed on-site mitigation strategy for sage-grouse and demonstrate that adaptive oil and gas development practices can have measurable benefits to a critical sage-grouse fitness parameter. Our findings are especially important for sage-grouse conservation because the majority of sagebrush habitats are managed by agencies with multiple-use mandates (USFWS 2010) and empirically testing the consequences of changes in development practices (i.e. on-site mitigation) is an important component of adaptive management (Boyce 2011). After dissecting the components of a NG field, we found that minimizing NG reservoir construction was the most consequential mitigation practice in relation to nest survival. Therefore, limiting reservoir construction may reduce impacts to sage-grouse populations in oil and gas fields and be an added conservation benefit to the Wyoming sage-grouse core area initiative (State of Wyoming Executive Order 2011-2). We were able to quantify the effects of mitigation on sage-grouse productivity compared to non-mitigated energy development. Our results further support the need for studies of the specific mechanisms, such as predator–prey ecology (Hagen 2011), that are critical to understanding sage-grouse productivity and better informed mitigation in landscapes undergoing energy development.

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Supplementary material (available online as Appendix wlb.00002 at <www.wildlifebiology.org/readers/appendix>). Appendix 1.

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