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Research Article

Investigating Impacts of Oil and Gas Development on Greater Sage-Grouse

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ABSTRACT The sagebrush (*Artemisia* spp.) ecosystem is one of the largest ecosystems in western North America providing habitat for species found nowhere else. Sagebrush habitats have experienced dramatic declines since the 1950s, mostly due to anthropogenic disturbances. The greater sage-grouse (*Centrocercus urophasianus*) is a sagebrush-obligate species that has experienced population declines over the last several decades, which are attributed to a variety of disturbances including the more recent threat of oil and gas development. We developed a hierarchical, Bayesian state-space model to investigate the impacts of 2 measures of oil and gas development, and environmental and habitat conditions, on sage-grouse populations in Wyoming, USA using male lek counts from 1984 to 2008. Lek attendance of male sage-grouse declined by approximately 2.5%/year and was negatively related to oil and gas well density. We found little support for the influence of sagebrush cover and precipitation on changes in lek counts. Our results support those of other studies reporting negative impacts of oil and gas development on sage-grouse populations and our modeling approach allowed us to make inference to a longer time scale and larger spatial extent than in previous studies. In addition to sage-grouse, development may also negatively affect other sagebrush-obligate species, and active management of sagebrush habitats may be necessary to maintain some species. © 2016 The Wildlife Society.

KEY WORDS Bayesian, *Centrocercus urophasianus*, greater sage-grouse, lek, oil and gas development, state-space model, Wyoming.

The sagebrush (*Artemisia* spp.) ecosystem is one of the largest ecosystems in western North America (Knick et al. 2003), and it provides habitat for species found nowhere else (e.g., sagebrush lizard [*Sceloporus graciosus*], sage thrasher [*Oreoscoptes montanus*], pygmy rabbit [*Brachylagus idahoensis*]; Rowland et al. 2011). Sagebrush habitats have decreased in size by 50% since the 1950s, and most of these declines are attributable to human disturbances (Griffin 2002, Bunting et al. 2003, Knick et al. 2011, Miller et al. 2011, Rowland and Leu 2011). Sagebrush habitats have been altered through the introduction of non-native grasses to provide forage for livestock (West 2000, Knick et al. 2011). Direct losses of sagebrush have also occurred through increasing agricultural and urban development and removal by prescribed fire and mechanical disturbance (Knick et al. 2011).

Development associated with oil and natural gas extraction is an increasing threat to sagebrush habitats as the number of wells associated with oil and natural gas extraction increase across the landscape. Construction of oil and gas wells results in the direct loss of sagebrush, but impacts have negative consequences at larger scales than the well pad and after drilling is complete, including alteration due to road and pipeline construction and changes in wildlife behavior (Northrup and Wittemyer 2012). Sawyer et al. (2006) reported that mule deer (*Odocoileus hemionus*) avoided well pads out to approximately 4 km and shifted their habitat use to less suitable areas in response to increased development. Other large mammals have changed home ranges, movement, and behavior in response to human activity (Dyer et al. 2002, Sawyer et al. 2009, Wasser et al. 2011, Northrup 2015). Disturbance from oil and gas development may also cause local declines in avian populations (Bayne et al. 2008, Gilbert and Chalfoun 2011, Jarnevich and Laubhan 2011), shifts in community structure (Bayne et al. 2008, Francis et al. 2012), and behavior modifications in response to increased noise pollution or other disturbance (Pitman et al. 2005, Francis et al. 2011). The cumulative effects of these impacts are not well studied but have potential negative consequences for ecosystem function (Francis et al. 2012).

The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a sagebrush-obligate species, has experienced population declines of 2%/year over the last several decades

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resulting in only 56% of its historical range currently being occupied (Connelly et al. 2004, Garton et al. 2011). These declines are partially attributed to negative impacts of oil and gas development on sage-grouse demographics and behavior. Oil and gas development negatively affects sage-grouse nest initiation rates and location (Lyon and Anderson 2003, Holloran et al. 2010, Fedy et al. 2014), chick survival (Aldridge and Boyce 2007), recruitment (Holloran et al. 2010), and adult survival (Holloran et al. 2010). Sage-grouse also avoid oil and gas wells and associated infrastructure when selecting wintering habitat (Doherty et al. 2008, Carpenter et al. 2010, Fedy et al. 2014).

Other studies have examined responses of sage-grouse populations to oil and gas development using lek counts, an often-used index of abundance (Harju et al. 2010, Taylor et al. 2013, Gregory and Beck 2014). All studies reported negative impacts of development on lek attendance or persistence (i.e., the presence of lekking males) across a variety of scales and using different measures of oil and gas development and response variables. Studies using lek persistence as a response variable (Harju et al. 2010, Hess and Beck 2012) provide insight into the factors influencing the presence of leks on the landscape but lose the ability to detect declining populations before they become inactive. Modeling lek attendance as a function of measures of oil and gas development addresses this issue, but some leks are inherently larger than others. A lek with a large number of attending males may be declining because of increasing development, but if counts remain relatively high, these declines might not be obvious. Additionally, many of these studies have been restricted to small spatial scales or short time periods because of inconsistent collection of lek count data prior to the late 1990s (Walker et al. 2007, Harju et al. 2010, Hess and Beck 2012, Taylor et al. 2013). Attempts have been made to address this shortcoming in the available data (Gregory and Beck 2014) and potential cycles in sage-grouse populations (Fedy and Aldridge 2011) by interpolating and smoothing lek counts across 20 years. However, these studies did not incorporate the uncertainty associated with the interpolation into their analyses and potentially underestimated the uncertainty associated with estimated effects of factors that may affect lek attendance.

We investigated the impacts of oil and gas development and environmental and habitat conditions on changes in male sage-grouse lek attendance in Wyoming, USA, from 1984 to 2008 using a well-established hierarchical, Bayesian state-space modeling framework (Kéry et al. 2009, Kéry and Schaub 2012). Unlike previous analyses of lek data, a Bayesian framework allowed us to use data over a longer time period, including lek counts prior to the rapid increase in oil and gas development in Wyoming in the mid-1990s. It also interpolated unobserved lek counts and the uncertainty associated with them, avoiding the need to truncate the data set to only leks with complete observations or aggregating lek observations across a larger temporal period. This approach allowed us to borrow information from well-sampled leks to make inference at larger spatial and temporal scales where data were sparse. Using a state-space model, we were able to estimate the relationships between covariates and the proportional changes in lek attendance and account for variation in counts due to population cycles and observer error, though we are unable to separate these sources of uncertainty without repeated counts. Lek counts may not accurately represent populations because of low and inconsistent attendance within a day and across the breeding season and the inability of observers to detect all individuals present (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004). Our model incorporated this uncertainty in lek counts when estimating the effects of covariates, such that the precision of covariate effect sizes accurately represented all sources of uncertainty in the ecological and observation processes. Our objectives were to evaluate the impact of oil and gas development on changes in lek attendance over large spatial extents and long temporal scales, while accounting for habitat and environmental covariates and provide estimates of local and statewide trends in lek attendance.

Given the number of studies showing negative impacts of oil and gas development on sage-grouse fecundity (Lyon and Anderson 2003, Holloran et al. 2010, Fedy et al. 2014), recruitment (Holloran et al. 2010), survival (Aldridge and Boyce 2007, Holloran et al. 2010), and lek attendance (Doherty et al. 2010*a*, Harju et al. 2010, Hess and Beck 2012, Taylor et al. 2013, Gregory and Beck 2014), we hypothesized that sage-grouse would respond negatively to oil and gas development. We also investigated the influence of precipitation and the amount of sagebrush vegetation surrounding a lek on changes in lek attendance. Sage-grouse are strongly dependent on sagebrush throughout their life-cycle (Connelly et al. 2000, 2011*b*; Fedy et al. 2014), and sage-grouse survival (Swenson 1986, Barnett and Crawford 1994, Johnson and Braun 1999) and recruitment (Connelly et al. 1991, Gregg et al. 1994, Holloran et al. 2005, Doherty et al. 2010*b*) are positively influenced by the amount and height of sagebrush. Likewise, studies have reported positive influences of precipitation on nest success, clutch size (Holloran et al. 2005, Blomberg et al. 2014*a*), and chick and juvenile survival (Aldridge and Boyce 2007, Blomberg et al. 2014*b*). Because of the positive response of sage-grouse survival and recruitment to precipitation and sagebrush, we expected lek attendance to respond positively to both variables.

Sage-grouse use large areas and selection of habitats takes place at multiple spatial scales (Aldridge and Boyce 2008; Doherty et al. 2008, 2010*b*; Aldridge et al. 2012; Fedy et al. 2014), so we examined whether the influence of each of the covariates described varied across multiple spatial scales. Because the majority of sage-grouse nests are located within 7.5 km of a lek (Wakkinen et al. 1992, Holloran and Anderson 2005) and we expected the covariates to influence recruitment, we expected larger scales to exhibit stronger influences on lek attendance. We also explored whether lek attendance exhibited delayed responses to the time-varying covariates. We expected support for longer lag effects because lek attendance would respond to the influence of covariates from prior years on recruitment because males mature and join the breeding population at 2–3 years old.

STUDY AREA

We conducted our study across Wyoming, USA, which covers approximately 253,500 km^2; current sage-grouse distribution covers approximately 69% of the state (Fig. 1). Sagebrush ecosystems account for approximately 37% of Wyoming's land cover followed by mixed-grass prairie (17.5%) and lodgepole pine (*Pinus contorta*) forest (6.5%; Driese et al. 1997). Sagebrush and mixed-grass prairie ecosystems also occur in large, relatively unbroken tracts. Approximately 44% of land in Wyoming is privately owned and the Bureau of Land Management (BLM) and the United States Forest Service are the largest public landowners at 28% and 14%, respectively. Most oil and gas development in Wyoming has occurred in the southwestern and northeastern corners of the state (Fig. 2). Average precipitation was lowest in central Wyoming, greater in the mixed-grass prairies of the eastern portion of the state, and the greatest at high elevations (PRISM Climate Group 2008).

METHODS

Sage-Grouse Lek Data

As part of a statewide monitoring effort of sage-grouse populations, the Wyoming Game and Fish Department (WGFD) and partnering agencies collected lek count data from across Wyoming using procedures approved by WGFD (Christiansen 2012). We used this survey data from 1980 to 2008 collected by WGFD, other natural resource agency personnel, or volunteers following WGFD protocols to model the impacts of environmental and anthropogenic factors on lek attendance. We also fit random intercept effects for each of the BLM field offices in Wyoming (Fig. 1). By doing this, we attempted to account for potential autocorrelation between lek counts within and among years due to environmental factors or management practices that may vary regionally and that we did not include as covariates in our analyses. Leks are designated based on the observation of ≥ 2 male sage-grouse engaged in courtship displays (Christiansen 2012). A satellite lek is defined as a relatively small lek (<15 males) within 500 m of a larger lek and is assumed to be part of the same breeding population. Within the sage-grouse database, WGFD combines the counts from a satellite lek with those from the main lek with which it is associated. We restricted our analyses to active leks with count data ($n = 614$).

Lek counts have been criticized for their inability to accurately reflect abundance and sex ratios of sage-grouse (Beck and Braun 1980, Walsh et al. 2004, Johnson and Rowland 2007). This is due to low attendance rates across sexes and ages (Jenni and Hartzler 1978, Walsh et al. 2004), inconsistent use throughout the breeding season or within a day (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004), and imperfect detection of individuals that are present on leks during counts (Walsh et al. 2004). However, several studies have shown that standardizing survey protocols by performing counts around sunrise, repeating counts throughout the breeding season, and training observers can reduce the sampling variation in counts (Jenni and Hartzler 1978, Emmons and Braun 1984,

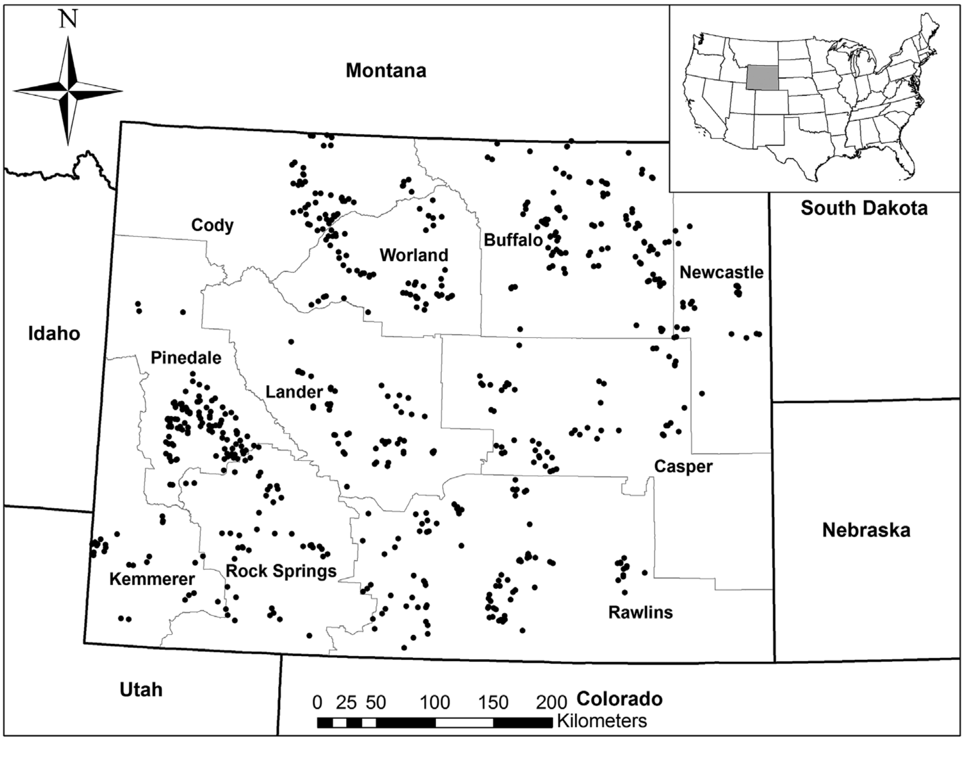

Figure 1. Location of 614 greater sage-grouse leks and 10 Bureau of Land Management field offices (bold name labels) in Wyoming, USA, used for state-space analysis, 1984–2008.

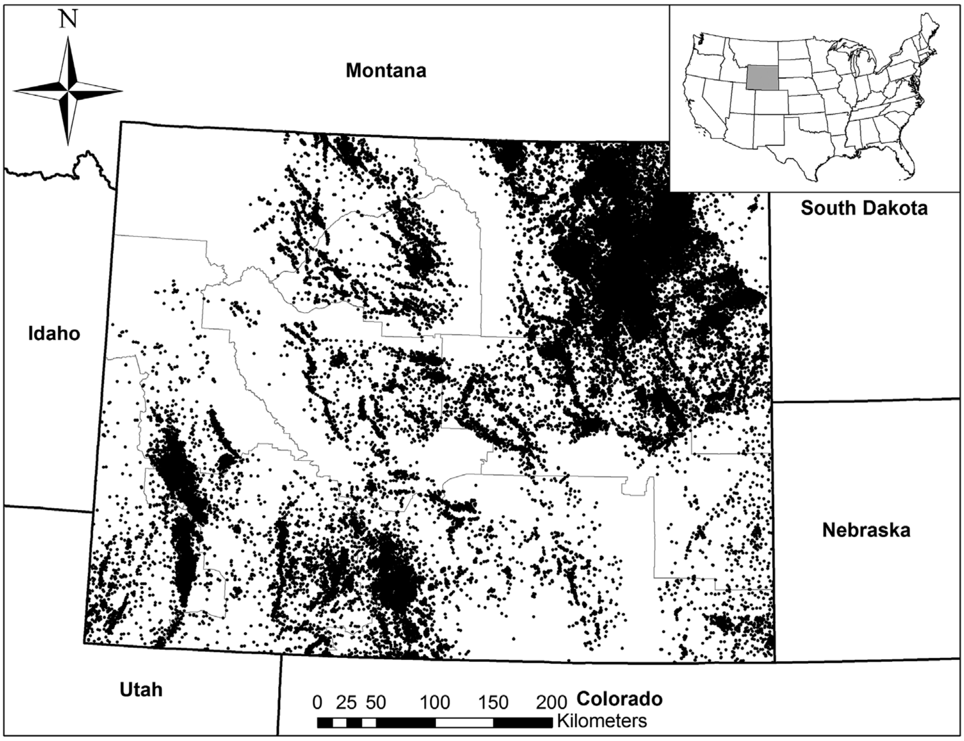

Figure 2. Location of 91,262 oil and gas wells in Wyoming, USA, used to calculate oil and gas metrics used in state-space analysis of greater sage-grouse, 1980–2008. Light grey lines represent Bureau of Land Management field office boundaries.

Walsh et al. 2004, Johnson and Rowland 2007) and provide a reasonable index with which to estimate population trends (Blomberg et al. 2013). Leks were sampled by WGFD from early March to early May to coincide with the peak of the breeding season based on latitude, elevation, and weather (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004, Christiansen 2012). We used only counts that occurred between 30 minutes pre-sunrise to 90 minutes post-sunrise, the most active lekking period of the day (Jenni and Hartzler 1978), which increases the likelihood that counts represent the maximum number of sage-grouse present on a given day. The WGFD recommends that counts occur between 30 minutes pre-sunrise to 60 minutes post-sunrise. Simulations have shown little difference in estimates or loss of precision in extending counts to 90 minutes post-sunrise (Monroe et al. 2016), so we included these counts to increase sample sizes. Because male sage-grouse have higher and more regular lek attendance than females (Emmons and Braun 1984, Walsh et al. 2004), we used the maximum male count within a year at a lek. Additionally, we restricted our analysis to leks with ≥ 2 counts over the study period, because our parameter of interest was the change in lek attendance across years rather than the counts themselves. These restrictions resulted in a data set consisting of 3,382 lek-year counts at 614 leks from 1984–2008 (Fig. 1).

Oil and Gas Data

We obtained information on oil and gas well characteristics and locations from the Wyoming Oil and Gas Conservation Commission (WOGCC; WOGCC 2011) for 1980–2008. We included pre-production wells with permits to drill, non-mechanical and mechanical producing wells, wells with a notice of intent to abandon, and active non-producing wells (Table S1, available online in Supporting Information). Within this original data set, 91.6% were producing wells. We calculated metrics for each year using non-abandoned wells with spud dates (i.e., date of ground penetration) or completion dates less than or equal to the year of interest. This resulted in the inclusion of 91,262 wells in our analyses (Fig. 2) for annual estimates of activity on the landscape.

We hypothesized that sage-grouse may respond differently to oil and gas disturbance depending on dispersion of wells surrounding a lek. If well pads are located near each other, they may have a smaller impact on sage-grouse populations than the same number of wells spread across the landscape because the infrastructure associated with the well pads will increase as the dispersion of wells increases. The well pad footprints may overlap, reducing the direct loss of sagebrush habitat, and any indirect disturbances (e.g., noise, lights, vehicular traffic) may also be reduced. Therefore, we included 2 measures of oil and gas development in our analysis calculated for each year of the study: well density (wells/km^2) and disturbance area of well pads (km^2). We calculated disturbance area in ArcGIS Desktop 10.0 (Environmental Systems Research Institute, Redlands, CA, USA) by creating a 60-m buffer around each well corresponding to the approximate size of a well pad, dissolving the resulting polygons to ensure areas were not accounted for more than once, and summing the area of the resulting polygons within a specified buffer around each lek.

Accounting for the overlap approximates the well pad size when ≥1 well locations occur on a single well pad. The disturbance area measures the footprint area associated with the well pads within a given distance of a lek.

Habitat and Environmental Conditions

We used remotely sensed geographic information system (GIS) vegetation products (Homer et al. 2008, 2012) that measured the percent vegetation composition within a 30-m pixel across the state of Wyoming. Homer et al. (2012) used a hierarchical classification of remotely sensed imagery and ground sampling to estimate the percent cover of bare ground, litter, herbaceous plants (i.e., forbs, grasses), and shrubs within 30-m pixels for 2006–2007 ground conditions. We used the percent cover of all sagebrush in our analyses to account for variation in lek count attendance due to the influence of sagebrush cover on demographic parameters (e.g., survival, fecundity). We used Geospatial Modelling Environment 0.7.3.0 (GME; http://www.spatialecology.com/gme, accessed 30 May 2016) and ArcGIS Desktop 10.2.2 to calculate the mean percent sagebrush cover for each lek at each spatial extent.

We examined the influence of precipitation during 2 time periods in the year prior to sage-grouse breeding that have positive relationships with nesting success (Holloran et al. 2005): winter-spring (Jan–Jun) and spring (Apr–May). We hypothesized that higher precipitation amounts would result in taller herbaceous vegetation in that year and, subsequently, taller residual cover in the next year to conceal nests (Skinner et al. 2002, Holloran et al. 2005). We obtained monthly, 4-km-resolution Parameter-Elevation Regressions on Independent Slopes Model (PRISM) precipitation data for 1980–2008 (PRISM Climate Group 2008). For each year, we summed the total precipitation for each 4-km pixel across winter-spring (Jan–Jun) and spring (Apr–May). We then used GME to calculate the mean precipitation for each of those periods at each lek for each spatial extent.

Spatial and Temporal Scales

Because sage-grouse select habitats at multiple spatial scales (Aldridge and Boyce 2008; Doherty et al. 2008, 2010*b*; Aldridge et al. 2012; Fedy et al. 2014), we investigated how changes in lek attendance responded to each of these covariates at 5 spatial scales: 800 m, 1,600 m, 3,200 m, 5,000 m, and 6,400 m around a lek. Oil and gas wells may have effects at smaller scales, such as reducing lek attendance because of the direct avoidance of wells by males (Walker et al. 2007). Oil and gas development, along with precipitation and sagebrush cover, may also have impacts at larger scales by influencing nest location and initiation attempts (Wakkinen et al. 1992, Lyon and Anderson 2003, Holloran et al. 2005, Doherty et al. 2010*b*) or affecting chick survival (Aldridge and Boyce 2007).

The influence of covariates on lek attendance may not be immediate. Female sage-grouse are highly philopatric to nesting sites (Schroeder et al. 1999, Holloran 2005, Holloran and Anderson 2005) and adult males are philopatric to leks (Holloran 2005). However, yearling females avoid oil and gas infrastructure more than adult females and yearling males avoid leks near infrastructure (Holloran 2005). Therefore, it may take several years for the impacts of development to become apparent in lek attendance because birds alive before development die and new generations move farther from disturbed areas. This hypothesis is supported by several studies (Walker et al. 2007, Holloran et al. 2010, Taylor et al. 2013, Gregory and Beck 2014) so we included time lags of 1–4 years on all of the time-varying covariates in analyses.

Statistical Analysis

We used a Bayesian, hierarchical state-space model to estimate changes in lek attendance. State-space models typically allow the separation of process and observation error in time-series with unobserved processes or data, but they can still be useful when this separation in sources of variation are not possible (de Valpine and Hastings 2002, Buckland et al. 2004, Clark and Bjørnstad 2004, Kéry and Schaub 2012). We could not explicitly separate the 2 sources of error because of the inclusion of time-varying covariates and the lack of repeated counts.

We modeled the number of males at lek i in year $t = 1, N_{i,1}$, as

$$\log(N_{i,1}) \sim Norm\left(\mu_{N_1}, \sigma^2_{N_1}\right)$$

where μ_{N_1} and $\sigma^2_{N_1}$ are the mean and variance, respectively, of counts across all leks in year 1. We modeled attendance at $t > 1$ as a function of the previous year's attendance and the intrinsic growth rate, $r_{i,t}$:

$$\log(N_{i,t+1}) = \log(N_{i,t}) + r_{i,t}$$

Growth rates were sampled from a normal distribution,

$$r_{i,t} \sim Norm\left(\mu_{r_{i,t}}, \sigma^2_r\right)$$

where $\mu_{r_{i,t}}$ is the mean growth rate, given the covariates measured at lek i in year t, and σ^2_r is the process error for growth rates at all leks. We modeled $\mu_{r_{i,t}}$ as a function of the covariates described in the previous section, such that

$$\mu_{r_{i,t}} = \beta_{FO_i} + x'_{i,t}\beta$$

where β_{FO_i} is the intercept for the field office in which lek i is located, $x'_{i,t}$ is a covariate vector, and β is a regression coefficient vector. We assumed the field office-specific intercepts came from a normal distribution

$$\beta_{FO} \sim Norm\left(\mu_{\beta_{FO}}, \sigma^2_{\beta_{FO}}\right)$$

where $\mu_{\beta_{FO}}$ and $\sigma^2_{\beta_{FO}}$ are hyperparameters representing the state-level mean intercept in regional growth rates and its variance, respectively. This hyperdistribution represents the state-wide intercept, yet allows us to account for regional differences in lek attendance. We also calculated the finite rate of increase, $\lambda = \exp(r)$, as the percent change per year in lek attendance. We estimated changes in lek attendance for all lek/year combinations even when data were sparse, and the uncertainties in growth rates for infrequently surveyed leks were accounted for when estimating covariate relationships. We standardized all covariates so that they had a mean of 0 and standard deviation of 1. To model the observation process, we assumed that the maximum male counts came from a Poisson distribution,

$$y_{i,t} \sim Pois(N_{i,t})$$

We took a Bayesian approach to estimate model parameters using Markov chain Monte Carlo (MCMC) simulation implemented in JAGS 3.4.0 (Plummer 2003, 2013) using the package R2jags in the R statistical computing environment (R Core Team 2013). We used vague prior distributions for all estimated parameters:

$$\sigma_r \sim Unif(0, 20)$$

$$\mu_{\beta_{FO}} \sim Norm(0, 100)$$

$$\sigma_{\beta_{FO}} \sim Unif(0, 20)$$

and

$$\beta \sim Norm(0, 100)$$

We converted all standard deviations to precision ($1/\text{SD}^2$) for implementation in JAGS.

Because of the large number of possible combinations of covariates and the high correlation between covariates within a group of covariates (i.e., oil and gas, sagebrush cover, precipitation), we used a sequential approach to model building. We fit all univariable models and chose the best predictive model (see next paragraph) from each covariate group to include in the next step of model building. We then fit models for all additive and 2-way interactive combinations of the top covariates from each covariate group. We also included a null model to represent the overall lek trend across time and a quadratic term for the top oil and gas covariate in our final model set to test for thresholds, where lek attendance may not be affected by low levels of development (Doherty et al. 2010*a*). We obtained 20,000 MCMC samples and used a burn-in period of 10,000 iterations for models in the final model set from which we made inferences regarding the factors influencing sage-grouse lek attendance.

We used 10-fold cross-validation to measure the performance of the models in our model sets (Hooten and Hobbs 2015). Cross-validation consists of grouping the data into K approximately even groups, fitting a model to the data excluding that in group k, y_{-k}, and comparing predictions for the left out data, y_k. We repeated the process for each group of data and calculated a metric for each iteration and summed across all iterations to produce a cross-validation score for the entire data set. We calculated our cross-validation score (*CVS*) as

$$CVS = -2\sum_{k=1}^{K} \log\left(\frac{\sum_{t=1}^{T}[y_k|y_{-k}, \theta^{(t)}]}{T}\right)$$

where $[y_k|y_{-k}, \theta^{(t)}]$ is the likelihood of y_k, given y_{-k} and $\theta^{(t)}$, the t^{th} MCMC sample (out of T total MCMC samples) of the model parameters. Unlike more widely used model selection criteria (e.g., Akaike's Information Criterion), there is no general rule of thumb regarding the amount of evidence provided by cross-validation scores within a model set (Hooten and Hobbs 2015); it is merely a measure of the predictive ability of a model. We considered the model with the smallest *CVS* to be the best model.

We used 3 chains and computed the Gelman-Rubin convergence statistic ($\hat{R}$), which was <1.1 for all model parameters (Gelman and Rubin 1992, Brooks and Gelman 1998) to determine when the algorithms converged. We assessed the fit of the models using a Bayesian *P*-value based on the mean squared error (Kéry and Schaub 2012),

$$P = \frac{\sum_{t=1}^{T}\text{MSE}_t}{T}$$

where

$$\text{MSE}_t\begin{cases} 1, \text{if } \Sigma\dfrac{(\tilde{y}-\hat{y})^2}{k} > & \Sigma\dfrac{(y-\hat{y})^2}{k} \\ 0, \text{if } \Sigma\dfrac{(\tilde{y}-\hat{y})^2}{k} \leq & \Sigma\dfrac{(y-\hat{y})^2}{k} \end{cases}$$

and y is the observed data, $\hat{y}$ is the predicted data, $\tilde{y}$ is simulated data based on MCMC samples at iteration T, and k is the sample size. A *P*-value >0.05 suggests sufficient fit of the model to the data (Hooten and Hobbs 2015).

RESULTS

As expected, most oil and gas covariates were correlated across space and time. Seventy-five percent of the 780 combinations of oil and gas metrics, including spatial scales and lag, had Pearson's correlation coefficients $r > 0.70$, with a minimum of $r = 0.56$. Percent sagebrush at the 3 scales was correlated, with all $r \geq 0.940$. Winter-spring and spring precipitation were correlated across scales for a given lag (all $r > 0.65$) but were uncorrelated across lags (range: 0.05–0.45).

Lek attendance decreased by 2.5% ($\lambda = 0.975$, 95% credible interval [CrI]: 0.962, 0.988) per year across the state from 1984 to 2008, based on the null model. Three hundred twenty-seven leks (53.3%) showed declines over the study period, with 45.6% of those (24.3% of leks overall) resulting in significant declines (Fig. 3). Significant declines ranged from 2.1% (95% CrI: [0.9%, 3.1%]; max. count: 48 M) to 42.4% (95% CrI: [33.9%, 50.0%]; max. count: 46 M) per year. Likewise, 46.7% of leks showed increasing lek attendance over the study period, with 56.1% of those leks showing significant gains (26.2% of leks overall). Overall, the magnitudes of annual gains were smaller than the losses for declining leks; significant increases ranged from 1.4% (95% CrI: [0.4%, 1.4%]; max. count: 155 M) to 55.4% (95% CrI: [38.1%, 76.3%]; max. count: 77 M) per year.

Cross-validation scores across all oil and gas metrics used to explain variation in changes in lek attendance were similar (Tables 1 and S2). This was likely due to high correlation between covariates. Models including well density within

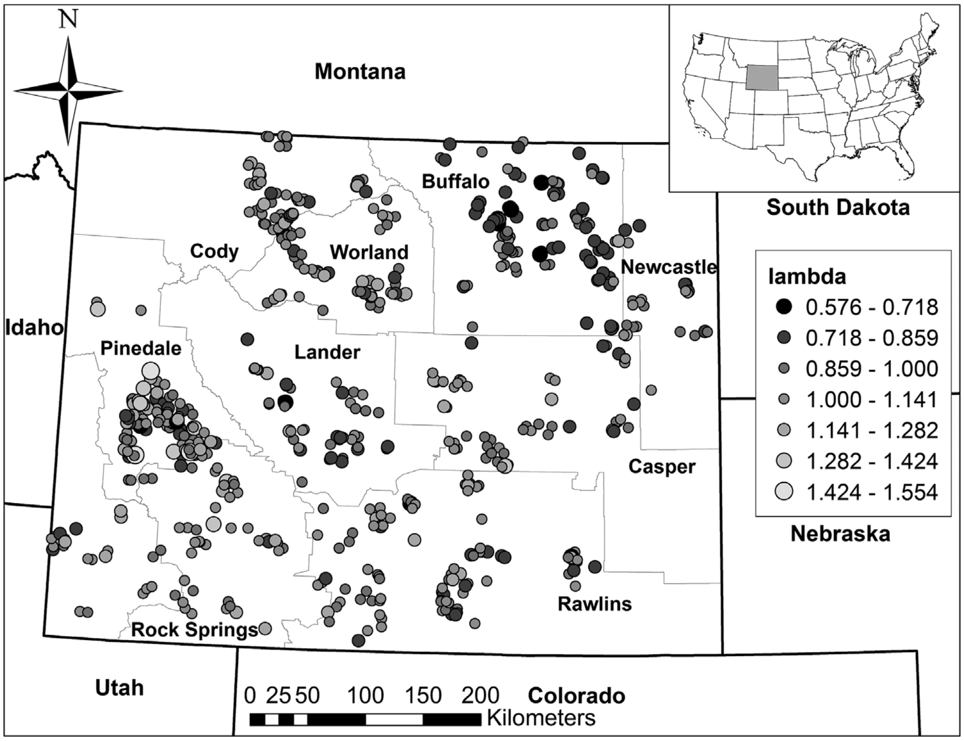

Figure 3. Location and trends of male lek attendance (lambda; λ) of 614 greater sage-grouse leks in Wyoming, USA, 1984–2008. Shades of gray correspond to trend direction, with λ = 1 indicating stable attendance, and point sizes correspond to the magnitude of the trend, with larger points representing larger declines or increases. Bureau of Land Management field offices are labeled.

6,400 m at various time lags performed the best in each model set for all 4 time lags and a 4-year lag on well density was the best model for 4 of the 5 spatial scales. Effect sizes of oil and gas metrics did not vary much across time lags and by metric (i.e., well density or disturbance area), but effects decreased as spatial scale decreased, approaching zero at 800 m. The model that included a 4-year lag of well density within 6,400 m of a lek (well density, hereafter) had the best predictive ability for changes in lek attendance of any of the oil and gas metrics and showed a negative effect of well density on changes in lek attendance ($\beta = -0.020$, [−0.034, −0.006]).

The model including percent sagebrush cover within 3,200 m of a lek (sagebrush cover, hereafter) performed the best among the model set for sagebrush covariates. As with the oil and gas metrics, cross-validation scores were similar for all 3 models (1,600 m: −50.41597; 3,200 m: −50.39557; 6,400 m: −50.38167). Changes in lek attendance relative to sagebrush cover were effectively zero ($\beta = 0.001$, [−0.015, 0.017]).

The model including a 1-year lag on winter-spring precipitation at 6,400 m (spring precipitation, hereafter) was the best performing model overall (Tables 2 and S3), but effects were not significant ($\beta = 0.009$, [−0.011, 0.029]).

Table 1. Cross-validation scores (*CVS*) and model ranks for the top 5 univariable models including covariates of oil and gas development to estimate changes in male greater sage-grouse lek attendance in Wyoming, USA, 1984–2008. A smaller *CVS* suggests better predictive abilities of the model. All oil and gas metrics presented were measured within 6,400 m of a lek at lags of 1–4 years.

Metric[a]	Lag[b]	*CVS*	Rank
Well density	4	−50.46247	1
Well density	3	−50.44397	2
Disturbance area	2	−50.44195	3
Disturbance area	1	−50.42960	4
Well density	2	−50.42844	5

[a] Well density is the number of wells/km^2. Disturbance area is the surface disturbance of oil and gas well pads (km^2).
[b] A 1-year lag suggests that changes in lek attendance from t to t+1 are influenced by the metric as calculated in t−1.

Table 2. Cross-validation scores (*CVS*) and model ranks for the top 5 univariable models including covariates of precipitation to estimate changes in male greater sage-grouse lek attendance in Wyoming, USA, 1984–2008. A smaller *CVS* suggests better predictive abilities of the model, and we considered the top model to be the one with the smallest *CVS*. We calculated the mean spring (Apr–May) or winter-spring (Jan–Jun) precipitation within a given radial distance (m) of a lek, as determined by the scale column, at lags of 1–4 years, using Parameter-Elevation Regressions on Independent Slopes Model (PRISM) precipitation data.

Metric	Scale	Lag[a]	*CVS*	Rank
Winter-spring	6,400	1	−50.43018	1
Spring	3,200	3	−50.42932	2
Spring	3,200	2	−50.42345	3
Spring	1,600	4	−50.41817	4
Spring	6,400	3	−50.41615	5

[a] A 1-year lag suggests that changes in lek attendance from t to t+1 are influenced by the metric as calculated in t−1.

There were no obvious patterns in models including precipitation covariates across time lags or spatial scales.

Models including well density performed the best within our final model set, with 10 of the top 11 models including well density. The top model included well density and an interactive term between sagebrush cover and winter-spring precipitation (Table 3). However, *CVS*s were the same to 2 decimal places for the 2 best models. We used the second best model (well density only) to make inferences because of the small differences in *CVS*s and because the sagebrush cover and precipitation main effects and their interaction were small and their 95% credible intervals included zero. The model that included a quadratic term on well density did not perform well and the null model performed the second worst in our final model set (Table 3). The Bayesian *P*-value for the best overall model (Bayesian $P = 0.46$) suggested an adequate fit of the model to the data.

Lek attendance in the average field office, given the average statewide well density, decreased over the study period, though not significantly (Table 4). Only the Buffalo field office showed a significant change in lek attendance, given the average statewide well density. When no wells were present within 6,400 m of a lek, attendance for the average field office was stable over the study period (Fig. 4). Lek attendance decreased more rapidly as well density increased and reached declines of 17.0%/year at 5.24 wells/km^2, the highest observed well densities at a 4-year lag. Declines became significant when well density reached approximately 4 wells/km^2 ($\lambda = 0.862$, 95% CrI: [0.748, 0.999]).

DISCUSSION

Several studies have investigated the impacts of oil and gas development on sage-grouse lek attendance, though many were conducted over short time periods, small spatial scales, or did not account for all sources of uncertainty in the ecological and observational processes (Harju et al. 2010, Taylor et al. 2013, Gregory and Beck 2014). We present an approach using a hierarchical, Bayesian state-space model (Kéry et al. 2009, Kéry and Schaub 2012) that addresses some of the shortcomings in these studies. The lack of repeated counts in our data did not allow us to separate the contribution of process and observation error to uncertainties

Table 3. Cross-validation scores (*CVS*) and model ranks for multivariable models including main effects and interactions between the top covariates of oil and gas development, sagebrush cover, and precipitation to estimate changes in male greater sage-grouse lek attendance in Wyoming, USA, 1984–2008. The top univariable models, a model including a quadratic term on well density, and the null model are also included in the model set. Well represents a 4-year lag on well density within 6,400 m of a lek, sagebrush represents the percent sagebrush cover within 3,200 m of a lek, and precip represents a 1-year lag on the mean winter-spring (Jan–Jun) precipitation within 6,400 m of a lek. A smaller *CVS* suggests better predictive abilities of the model, and we considered the top model to be the one with the smallest *CVS*.

Model	*CVS*	Rank
Well + sagebrush + precip + sagebrush × precip	−50.46320	1
Well	−50.46247	2
Well + precip	−50.45359	3
Well + sagebrush + precip	−50.45126	4
Well + sagebrush	−50.44669	5
Well + sagebrush + precip + well × sagebrush	−50.44571	6
Well + precip + well × precip	−50.44324	7
Well + sagebrush + precip + well × precip	−50.43915	8
Well + sagebrush + well × sagebrush	−50.43368	9
Precip	−50.43018	10
Well + well^2	−50.42801	11
Sagebrush + precip + sagebrush × precip	−50.41598	12
Sagebrush	−50.41597	13
Null	−50.40264	14
Sagebrush + precip	−50.39870	15

Table 4. Means and 95% credible intervals (CrI) from posterior distributions for the top model from the multivariable analysis of changes in male greater sage-grouse lek attendance in Wyoming, USA, 1984–2008. The model included a 4-year time lag on well density within 6,400 m of a lek (β_{WD}). Each Bureau of Land Management field office (β_{FO_i}) had a random intercept that came from a hyperdistribution with mean $\mu_{\beta_{FO}}$ and standard deviation $\sigma_{\beta_{FO}}$. The field offices included 1) Buffalo, 2) Casper, 3) Cody, 4) Kemmerer, 5) Lander, 6) Newcastle, 7) Pinedale, 8) Rawlins, 9) Rock Springs, and 10) Worland. The process error is represented by σ_r. Parameters with significant parameter estimates (i.e., 95% credible intervals do not include 0) are indicated with an asterisk.

Parameter	$\bar{x}$	95% CrI
$\beta_{WD}{}^*$	−0.020	(−0.034, −0.006)
$\beta_{FO_1}{}^*$	−0.096	(−0.128, −0.066)
β_{FO_2}	0.003	(−0.033, 0.039)
β_{FO_3}	0.000	(−0.036, 0.037)
β_{FO_4}	0.012	(−0.035, 0.061)
β_{FO_5}	−0.018	(−0.055, 0.019)
β_{FO_6}	−0.029	(−0.078, 0.019)
β_{FO_7}	0.008	(−0.019, 0.036)
β_{FO_8}	−0.002	(−0.030, 0.027)
β_{FO_9}	0.018	(−0.018, 0.054)
$\beta_{FO_{10}}$	−0.007	(−0.042, 0.028)
$\mu_{\beta_{FO}}$	−0.011	(−0.046, 0.025)
$\sigma_{\beta_{FO}}$	0.003	(0.001, 0.010)
σ_r	0.534	(0.514, 0.555)

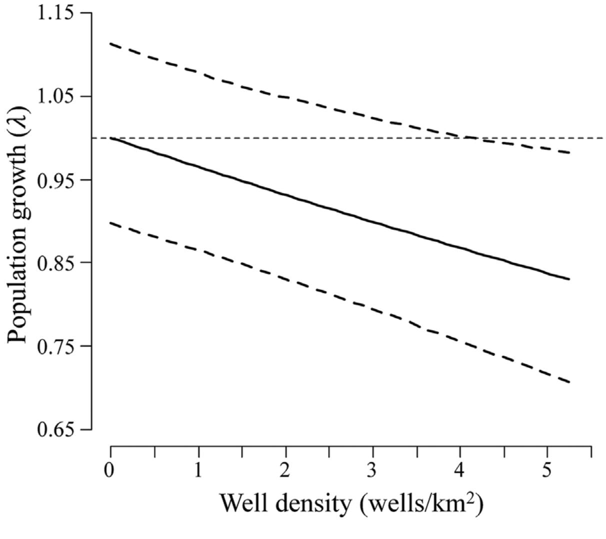

Figure 4. Mean (solid line) and 95% credible intervals (dashed lines) change in male greater sage-grouse lek attendance (λ) in response to a 4-year lag of well density within 6,400 m of a lek in Wyoming, USA. We randomly drew values for the intercept using the posterior distribution for hyperparameters representing average Bureau of Land Management field office intercepts across Wyoming. The dashed horizontal line at $\lambda = 1$ represents a stable population.

in the response of lek attendance to covariates. However, this approach allowed us to make inference to a larger number of leks and over longer time periods by borrowing information from well-sampled leks to predict counts at poorly sampled leks. Uncertainties in the relationships between attendance at poorly sampled leks and oil and gas disturbance are accounted for in coefficient estimates, and, despite these uncertainties, we were still able to confirm the general findings of previous studies.

We estimated statewide annual declines in lek attendance of 2.5% based on our null model, which is similar to trends estimated in other studies for various Wyoming sage-grouse populations (Walker et al. 2007, Garton et al. 2011, Gregory and Beck 2014). However, as with other studies, we saw a large range of growth rates across our study area (Fig. 3) and declines were associated with higher well densities. Oil and gas development correlates well with sage-grouse population declines from 1984 to 2008 in Wyoming, which is supported by other findings (Doherty et al. 2010*b*, Harju et al. 2010, Hess and Beck 2012, Taylor et al. 2013, Gregory and Beck 2014). As with other studies, we also found support for 4-year lag effects of oil and gas development on lek attendance (Walker et al. 2007, Doherty et al. 2010*a*, Harju et al. 2010, Gregory and Beck 2014). This result suggests that development likely affects recruitment into the breeding population rather than avoidance of wells by adult males or adult survival. Adult sage-grouse are highly philopatric to lek sites (Dalke et al. 1963, Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985, Connelly et al. 2011*a*), and males typically recruit to the breeding population in 2–3 years. We would expect a delayed response in lek attendance if development affects recruitment, either by reducing fecundity or avoidance of disturbance by nesting females, as adult males die and are not replaced by young males.

On average, lek attendance was stable when no oil and gas development was present within 6,400 m (Fig. 4). However, attendance declined as development increased. Declines did not become significant until well density reached approximately 4 wells/km^2; at this well density, we predict mean declines of nearly 14%/year ($\lambda = 0.862$, 95% CrI: [0.748, 0.999]). In 2008, Wyoming implemented measures to protect core areas of the sage-grouse population under the Sage-Grouse Executive Order (State of Wyoming 2008, 2015). The intent of this executive order was to maintain habitat for a large portion of Wyoming's sage-grouse population through fire suppression, habitat management, and limiting oil and gas development. The density of active wells near a lek within a core area is limited to 0.39 well pads/km^2 (State of Wyoming 2015), which may contain up to 64 wells/pad. The linear relationships we found between well density and lek attendance may not hold at such high densities, but even 1 well/pad at this pad density would correspond to a decline of approximately 1.4%/year ($\lambda = 0.986$, 95% CrI: [0.885, 1.100]) within core areas, based on our results (Fig. 4). These predicted declines are not significant because of the uncertainty associated with lek counts and sparse data but suggest that declines in sage-grouse populations may continue within core areas at these development levels.

Though several studies have examined the impacts of oil and gas development on sage-grouse lek attendance, we provide the first comparison of 2 measures of disturbance due to development. Other studies have typically used well or well pad density at various spatial scales and time lags as a measure of oil and gas development (Doherty et al. 2010*a*, Harju et al. 2010, Hess and Beck 2012, Taylor et al. 2013, Gregory and Beck 2014). However, the distribution of wells around a lek may play an important role in the magnitude of the impacts (Walker et al. 2007), so we fit models including disturbance area to account for these differences. If wells are located close to other wells, disturbance due to light and noise will be concentrated in a smaller area, leaving a larger proportion of the landscape undisturbed. Additionally, fewer roads and pipelines may be necessary, resulting in reduced infrastructure and less habitat fragmentation and disturbance from vehicular traffic. We were unable to find differences between the models that included well density and those that included disturbance area because of high correlation between these covariates, suggesting that a simple measure of well density may be suitable to capture correlative effects of energy development on sage-grouse population trends across broad geographic extents. This does not dismiss that more local impacts on survival may be occurring in response to how development takes place (Holloran et al. 2005, Aldridge and Boyce 2007).

There was only one BLM field office that showed significant declines over the study period (Buffalo; Table S4). However, the largest mean growth for any field office was only 2.1%/year ($\lambda = 1.021$, [0.990, 1.052]), suggesting that future development may result in declines in these currently stable regions. We acknowledge that BLM field offices may be too large and arbitrary to represent natural groupings of leks that respond to local habitat and weather conditions, but all models including random intercepts for field office performed better than the best fixed-intercept model we fit in preliminary analyses. This suggests that some autocorrelation in changes in lek attendance occurs at this scale and it may provide a useful way to group leks to account for this correlation and improve the precision of estimates.

We found little evidence that the amount of sagebrush surrounding a lek influenced changes in lek attendance. However, numerous studies have described the importance of sagebrush to sage-grouse throughout their life cycle (Remington and Braun 1985, Gregg et al. 1994, Holloran et al. 2005, Doherty et al. 2010*b*, Fedy et al. 2014). Therefore, we think that the effects of sagebrush in our models were small and imprecise (coefficient of variation, $\sigma/\mu = 7.76$) because we were only able to obtain estimates of sagebrush cover from 2006 to 2007. Changes in sagebrush cover are negatively correlated with changes in well density because oil and gas development often occurs in areas of high sagebrush cover (Knick et al. 2003, Connelly et al. 2011*b*, Finn and Knick 2011) and removes sagebrush habitat. Though time-varying estimates of sagebrush cover would better represent changes in available habitat throughout the study period, we expected the single estimate to represent sagebrush abundance. In addition, having an estimate from near the end of our study period allows us to evaluate the cumulative impacts of sagebrush loss at leks and it corresponds to the years with the highest data coverage. More frequent measures of sagebrush cover for southwestern Wyoming are being estimated (C. G. Homer, United States Geological Survey, unpublished data), and future studies should investigate the impacts of changes in sagebrush cover over time on sage-grouse population trends (lek attendance).

Precipitation can have a positive influence on nesting success, clutch size, and chick and juvenile survival (Holloran et al. 2005, Blomberg et al. 2014*a*,*b*), potentially resulting in impacts on male lek attendance as males enter the breeding population. We found little evidence for the effect of precipitation on lek attendance and responses to lags were not differentiated. The lack of evidence for strong impacts of precipitation is possibly due to the scale of the PRISM data used in our analyses (i.e., 4-km). This extent may be too coarse spatially and temporally to capture the mechanisms influencing sage-grouse recruitment or the error associated with estimation of these metrics may be too large, overwhelming any potential effects. However, other studies on sage-grouse in the Great Basin used similar measures and found positive responses of recruitment and population growth to increasing precipitation (Blomberg et al. 2012, Coates et al. 2015). The Great Basin has lower annual precipitation and drier and warmer soils than Wyoming (Coates et al. 2015), and its sage-grouse populations may be more sensitive to precipitation. Finally, the timing of precipitation may play an important role in how sage-grouse populations respond. We included time periods shown to affect recruitment in Wyoming (Holloran et al. 2005). However, precipitation during other times may influence other demographic parameters, such as adult survival, to which populations may be more sensitive. Future studies should investigate the importance of precipitation timing on various demographic vital rates and population growth.

We acknowledge that lek counts are not an ideal direct measure of sage-grouse populations. Attendance rates of sage-grouse vary throughout the day, breeding season, and across sexes and age classes (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004, Johnson and Rowland 2007). However, survey protocols are standardized within Wyoming to ensure that maximum male counts provide a reasonable index to abundance (Fedy and Aldridge 2011, Christiansen 2012, Blomberg et al. 2013). The assumption that detection rates of sage-grouse are constant across surveys and observers poses an additional problem (Walsh et al. 2004). Even if the number of males present at a lek is constant across surveys, counts will provide a biased index of abundance if detection probabilities are not constant (Anderson 2001). Standardization of protocols and training of observers likely reduces the variation in detection probabilities so that changes in lek counts more accurately reflect changes in abundance rather than detection (Walsh et al. 2004). Additionally, our model included an error term to account for some of the variation in counts due to process error and assumed counts were a random variable, accounting for observation error. Because we could not assume closure of the lek-attending sage-grouse population between surveys, we were able to use only 1 count from each lek in a given year. Having additional counts, possibly from a second observer counting at the same time, could provide replication to estimate detection probabilities (Nichols et al. 2000, Forcey et al. 2006) and tease apart variation due to process and observation error. However, this requires financial and personnel resources, and tradeoffs between replication and the number of leks sampled should be assessed based on the information desired by management agencies (Fedy and Aldridge 2011).

MANAGEMENT IMPLICATIONS

Our findings contribute to the growing number of studies suggesting oil and gas development has negative impacts on sage-grouse populations and suggest that current regulations may only be sufficient for limiting population declines but not for reversing these trends. Additionally, areas not protected under the executive order are not subject to core-area regulations and may experience larger increases in oil and gas development and, therefore, larger declines in sage-grouse populations.

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