Local and population-level responses of Greater Sage-Grouse to oil and gas and climatic variation in Wyoming

Rob R. Ramey II[1], Joseph L. Thorley[1], and Alexander S. Ivey[2]

[1]**Wildlife Science International Inc., Nederland, Colorado, USA**
[2]**Poisson Consulting Ltd., Nelson, British Columbia, Canada**
[3]**Terra Cognito GIS Services Inc., Eldora, Colorado, USA**

ABSTRACT

Background Relatively few conservation-based studies have explicitly quantified the extent to which population dynamics are consistent with local impacts. The Greater Sage-Grouse (*Centrocercus urophasianus*) is a large sexually dimorphic tetraonid that is endemic to the sagebrush habitat of western North America. The impacts of oil and gas development at individual leks has been well-documented. However, no previous studies have quantified the population-level response.
Methods Hierarchical models were used to estimate the effects of well pad density and climatic variation on individual lek counts and Greater Sage-Grouse management units over 32 years. The lek counts were analysed using General Linear Mixed Models while the management units were analysed using Gompertz State-Space Population Models. The models were fitted in a Maximum Likelihood framework. An information-theoretic approach was adopted.
Results Oil and gas was only an important predictor at individual leks. In contrast, regional climatic variation, as indexed by the Pacific Decadal Oscillation, was correlated with density changes at both the local and population-level.
Conclusions The results suggest that if inter-annual movement among working groups is negligible then the Sage-Grouse populations were able to largely compensate for the local impacts of oil and gas. Wildfile agencies should not base Sage-Grouse regulations solely on the results of local studies and need to account for the effects of regional climatic variation.

Keywords: Greater Sage-Grouse, Lek Counts, Population Dynamics, State-Space, Oil and Gas, Climate, Pacific Decadal Oscillation

INTRODUCTION

Effective conservation of a species requires an understanding of how human activities influence its distribution and abundance. Although much of science proceeds by experimental studies to understand the causal links between actions and responses, ethical and practical considerations typically prevent population-level experiments on species of concern. Consequently, many conservation-based ecological studies are forced to infer the population-level consequences of anthropogenic alterations from local gradients (Fukami and Wardle, 2005) in density (Gill et al., 2001), movement, habitat use, physiology, genetics, reproductive success or survival. However, relatively few studies explicitly quantify the extent to which the actual population-level responses may be consistent with the individual responses or local impacts (Fodrie et al., 2014).

The Greater Sage-Grouse (*Centrocercus urophasianus*, hereafter Sage-Grouse) is a large sexually dimorphic tetraonid that is endemic to the sagebrush (*Artemisia* spp.) habitat of western North America (Knick and Connelly, 2011). Each spring, adult males aggregate on open areas called leks where they display for females. Fertilized females then nest on the ground among the sagebrush. Initially, the chicks feed on insects before switching to forbs. The adults predominantly feed on sagebrush, especially in the winter. Most males begin lekking two years after hatching.

Based on historical observations, museum specimens and the presettlement distribution of Sage-Grouse habitat, it is estimated that habitat alteration and fragmentation has reduced the range of Sage-Grouse by approximately 44% (Schroeder et al., 2004). In addition, mean peak counts of males on leks, which are commonly used as a metric of relative population abundance (Connelly and Braun, 1997; Doherty et al., 2010; Fedy and Aldridge, 2011), have shown long-term declines in many remaining populations (Garton et al., 2011).

A multitude of studies have reported local negative effects of oil and gas (OAG) development on Sage-Grouse lek counts, movement, stress-levels and fitness components. The most frequently-reported phenomenon is the decline in lek counts with increasing densities of well pads (Walker et al., 2007; Doherty et al., 2010; Harju et al., 2010; Green et al., 2016). In addition, radio-tracking has been used to detect reductions in fitness components such as lower nest initiation rates (Lyon and Anderson, 2003) and lower annual survival of yearlings reared in areas where OAG infrastructure is present (Holloran et al., 2010). The development of Global Positioning System (GPS) telemetry methods has facilitated the fitting of more sophisticated and realistic spatially-explicit habitat use models which suggest that nest and brood failure is influenced by proximity to anthropogenic features (Dzialak et al., 2011). More recently, experimental studies have suggested that noise alone can reduce lek attendance (Blickley et al., 2012b) and increase stress hormones (Blickley et al., 2012a).

Copeland et al. (2009) estimated that future OAG development in the western United States (US) will cause a long-term 7 to 19% decline in Sage-Grouse numbers relative to 2007. While, Copeland et al. (2013) estimated that Sage-Grouse populations in Wyoming will decrease by 14 to 29%, but that a conservation strategy that includes the protection of core areas could reduce the loss to between 9 and 15%. As argued by Doherty et al. (2010), estimation of population-level impacts is important because it provides a biologically-based currency for quantifying the cost of OAG as well as the benefits of mitigation or conservation. However, to date no-one has examined whether Sage-Grouse population-level responses are consistent with the local studies.

Although it has received less attention than OAG, climatic variation has also been shown to influence Sage-Grouse lek counts, survival, clutch size and nesting success (Blomberg et al., 2012, 2014, 2017; Coates et al., 2016; Gibson et al., 2017). This is not surprising, as there is a long and ecologically important history of studies on the influence of climatic variation on the population dynamics of tetraonids (Moran, 1952, 1954; Ranta et al., 1995; Lindström et al., 1996; Cattadori et al., 2005; Ludwig et al., 2006; Kvasnes et al., 2010; Selås et al., 2011; Viterbi et al., 2015; Ross et al., 2016). Consequently, the current study also considers annual variation in regional climate as a potential predictor of Sage-Grouse population dynamics.

Previous studies of the effect of climatic variation on Sage-Grouse have used local temperature and precipitation data with mixed results (Blomberg et al., 2012; Green et al., 2016; Blomberg et al., 2014, 2017; Coates et al., 2016; Gibson et al., 2017; Green et al., 2016). However, large-scale climate indices often outperform local data in predicting population dynamics and ecological process (Stenseth et al., 2002; Hallett et al., 2004). The Pacific Decadal Oscillation (PDO), which is derived from the large-scale spatial pattern of sea surface temperature in the North Pacific Ocean (Mantua et al., 1997), is potentially the most important climatic process influencing the sagebrush biome (Neilson et al., 2005). Consequently, the PDO index was chosen as the climate indicator.

Wyoming was selected for the current study because it contains approximately 37% of the recent range-wide population of Sage-Grouse (Copeland et al., 2009; Fedy et al., 2012) and is home to substantial levels of OAG development dating to the late 1800s (Braun et al., 2002). The lek location and count data were also available for research.

METHODS

Data Preparation

Sage-Grouse Data The Sage-Grouse lek count and location data were provided by the State of Wyoming. To reduce potential biases, only the most reliable male lek counts were included in the analyses. In particular, only ground counts from leks that were checked for activity, and data that were collected between April 1st and May 7th as part of a survey or count were included (as per Wyoming Game and Fish guidelines). Lek counts for which the number of individuals of unknown sex were $\geq 5\%$ of the number of males (suggesting unreliable identification) were also excluded.

When there are multiple counts at the same lek in a single year, almost all authors take the maximum count (Holloran, 2005; Walker et al., 2007; Harju et al., 2010; Fedy and Aldridge, 2011; Fedy and Doherty, 2011; Garton et al., 2011; Blickley et al., 2012b; Blomberg et al., 2013; Davis et al., 2014; Garton et al., 2015; Coates et al., 2016; Fremgen et al., 2016; Monroe et al., 2016; Green et al., 2016). The justification for using the maximum count is articulated by (Garton et al., 2011, p. 296) who state that

> ...counts over the course of a single breeding season vary from a low at the beginning of the season, to peak in the middle, followed by a decline to the end, which necessitates using the maximum count from multiple counts across the entire season as the index.

However, as noted by Johnson and Rowland (2007), this results in a substantial upwards bias at leks with multiple counts. To understand why consider an unbiased die. The expectation with a single throw is 3.5. With two throws the expectation for the mean value is still 3.5 but the expectation for the maximum value is 4.47. To avoid this bias, several alternative approaches are available: exclude early and late counts and then either include the repeated counts in the model (Gregory and Beck, 2014) or take the mean of the repeated counts (as we did) and/or explicitly model the change in attendance through time (Walsh et al., 2004) as is done for spawning salmon (Hilborn et al., 1999).

To reduce the probability of population-level stochastic events influencing the results, the entire Upper Snake River, which has just 18 known leks was also excluded from the analyses. The final set of leks are mapped in Figure 1 and the associated lek counts are plotted in Figure 2.

The State of Wyoming recognizes eight Sage-Grouse working groups for population management and reporting (Fig. 1). For the purposes of the current study, we also treat them as if they are separate populations. The population densities (males per lek) were calculated by averaging the mean counts for individual leks for each working group in each year. The calculation assumes that a representative sample of leks were surveyed annually. Comparison with the preliminary analyses (see preprints from October 4, 2015 and June 7, 2017 at https://doi.org/10.1101/028274) indicate little difference between the current population densities and those estimated from a Generalized Linear Mixed Model (GLMM) that takes into account individual lek size. This suggests that the assumption of a representative sample of leks is reasonable. To minimize any other potential biases and ensure a similar error variance between years, population densities based on less than 24 leks were excluded from the analyses.

Oil and Gas Data Wyoming Oil and Gas Conservation Commission (WOGCC) conventional, coalbed and injection well pad location and production data were downloaded from the Wyoming Geospatial Hub (http://pathfinder.geospatialhub.org/datasets/). Well pads without a provided spud date were excluded as were well pads constructed before 1900 or after 2016. The included well pads are mapped in Figure 1.

The intensity of OAG development was quantified in terms of the well pad density (well pads/km^2) within a specific distance of the leks. Although the areal disturbance due to well pads or the areal disturbance due to well pads, pipelines and roads are arguably more relevant metrics, comparison with the preliminary analyses (https://doi.org/10.1101/028274) indicates a strong correlation between all three metrics. For simplicity we only consider well pad density. Following Green et al. (2016), we calculate well pad density at lek distances of 0.8, 1.6, 3.2, 6.4 and 12.8 km. The well pad densities for individual leks at 3.2 km are plotted in Figure 3.

Climatic Data The PDO index (Trenberth and Hurrell, 1994; Mantua et al., 1997) data were queried from the rpdo R package (Fig. 4).

Statistical Analysis

Local Models The individual lek counts were analysed using GLMMs (Bolker et al., 2009) with the standardized well pad density and PDO index as fixed effects and year and lek as random effects. The well pad density and PDO index were standardised to facilitate comparisons between variables. As preliminary analysis indicated that the lek counts were overdispersed, the GLMMs utilized a gamma-Poisson distribution (Ntzoufras, 2009).

More formally the full lek count model is described by the following equations

$$M_{i,y} \sim \mathrm{Poisson}(\mu_{i,y} \cdot \gamma_{i,y}) \tag{1}$$

$$\log(\mu_{i,y}) = \beta_0 + \beta_W \cdot \mathrm{Wells}_{i,y} + \beta_P \cdot \mathrm{PDO}_y + \alpha_{Li} + \alpha_{Y\,y} \tag{2}$$

$$\gamma_{i,y} \sim \mathrm{Gamma}(\sigma_\gamma^{-2}, \sigma_\gamma^{-2}) \tag{3}$$

$$\alpha_{Li} \sim \mathrm{Normal}(0, \sigma_L) \tag{4}$$

$$\alpha_{Y\,y} \sim \mathrm{Normal}(0, \sigma_Y) \tag{5}$$

where $M_{i,y}$ is the rounded mean count of males for the ith lek in the yth year, β_W and β_P are the fixed effects of the standardised well pad density ($\mathrm{Wells}_{i,y}$) and PDO index (PDO_y) on the expected count ($\mu_{i,y}$) and σ_γ, σ_L, σ_Y are the standard deviations of the random effects of overdispersion, lek and year. Key model parameters are also described in Table 1. The gamma distribution is parameterised in terms of its shape and rate.

To identify the most important spatial scale (distance from each lek when calculating the well pad density) and temporal lags, a total of 80 full models were fitted to the lek count data representing all combinations of the five lek distances (0.8, 1.6, 3.2, 6.4 and 12.8 km) and independent lags of one to four years in the well pad density (Walker et al., 2007; Doherty et al., 2010; Harju et al., 2010; Gregory and Beck, 2014) and PDO index. The relative importance of each spatial scale and temporal lag as a predictor of individual lek counts was assessed by calculating it's Akaike's weight (w_i) across all 80 full models (Burnham and Anderson, 2002).

Once the model with the most important spatial scale and temporal lags had been identified, the relative importance of β_W and β_P was quantified by calculating their Akaike's weights across the selected full model and the three reduced variants representing all combinations of the two parameters (Burnham and Anderson, 2002). The local effect sizes (Bradford et al., 2005) of OAG development and the PDO index were then plotted in terms of a) the predicted percent change in the lek count with a increase of 1 standard deviation with 95% confidence intervals (CIs) and b) the predicted percent change in the lek count across the observed range of values. Both sets of predictions were averaged across all four models (Burnham and Anderson, 2002).

Population Models The annual population densities (mean males per lek) in each working group were analysed using Gompertz State-Space Population Models (Dennis et al., 2006; Garton et al., 2011; Knape and de Valpine, 2012) with the standardized well pad density and standardized PDO index as fixed effects and year and group as random effects. Gompertz State-Space Population Models (GSSPMs) were used because they incorporate density-dependence (Dennis et al., 2006; Knape and de Valpine, 2012) and process error (Dennis et al., 2006; Auger-Méthé et al., 2016); have well-known statistical properties (Dennis et al., 2006; Knape, 2008); and because Gompertz models have have performed well in explaining rates of change for Sage-Grouse in general and Wyoming Sage-Grouse in particular (Garton et al., 2011).

The full population model is described by the following equations

$$\log(M_{g,y}) \sim \mathrm{Normal}(\log(\mu_{g,y}), \sigma_\varepsilon) \tag{6}$$

$$\log(\mu_{g,y}) = \beta_0 + (\beta_D + 1 + \alpha_{G\,g}) \cdot \log(\mu_{g,y-1}) + \beta_W \cdot \mathrm{Wells}_{g,y} + \beta_P \cdot \mathrm{PDO}_y + \alpha_{Y\,y} + \alpha_{\eta\,g,y} \tag{7}$$

$$\log(\mu_{g,0}) \sim \mathrm{Normal}(\beta_I, \sigma_I) \tag{8}$$

$$\alpha_{G\,g} \sim \mathrm{Normal}(0, \sigma_G) \tag{9}$$

$$\alpha_{Y\,y} \sim \mathrm{Normal}(0, \sigma_Y) \tag{10}$$

$$\alpha_{\eta\,g,y} \sim \mathrm{Normal}(0, \sigma_\eta) \tag{11}$$

where $M_{g,y}$ is the density at the gth group in the yth year, $\mu_{g,y}$ and $\mu_{g,0}$ are the expected densities at the gth group in the yth and initial year, respectively, β_D is the typical density-dependence and $\alpha_{G\,g}$ is the group-level random effect on the density-dependence, σ_ε and $\alpha_{\eta\,g,y}$ are observer and process error (Dennis et al., 2006) and the other terms are approximately equivalent to those in the lek count model. The equivalence is only approximate as the terms in the population model act on the change in density (as opposed to density).

The purpose of the study was to compare local predictions with those at the population level. Consequently, the average well pad density in each working group was calculated at the spatial scale that was most important in the local analyses. Nonetheless, as the timing of effects could differ between the local count models and the population dynamic models, the relative importance of each lag of one to four years in the well pad density and the PDO index was assessed by calculating its w_i across the 16 full models representing all combinations of the lags.

Once the model with the most important temporal lags had been identified, the relative importance of β_W and β_P was once again quantified by calculating their Akaike's weights across the four models representing all combinations of the two parameters.

To further facilitate comparison with the local models, the population-level effect sizes of OAG development and the PDO index were plotted in terms of a) the predicted percent change in the population growth rate with a increase of 1 standard deviation with 95% CIs and b) the predicted percent change in the carrying capacity (N_∞) across the observed range of values. Both sets of predictions were averaged across all four models.

The carrying capacity, which represents the long-term expected density around which a population fluctuates (Dennis et al., 2006), is given by

$$\log(N_\infty) = \frac{-(\beta_0 + \beta_W \cdot \mathrm{Wells}_{g,y} + \beta_P \cdot \mathrm{PDO}_y)}{\beta_D + \alpha_{Gg}}. \qquad (12)$$

Model Fitting and Adequacy

The models were fit using Maximum Likelihood (Millar, 2011). As the random effects were the same in each set of models, the Akaike's weights were based on the marginal Akaike's Information Criterion (Burnham and Anderson, 2002) corrected for small sample size (Burnham and Anderson, 2002; Vaida and Blanchard, 2005; Greven and Kneib, 2010). Model adequacy was assessed by plotting and analysis of the standardized residuals from the full model (Burnham and Anderson, 2002) with the most important spatial scale and lags.

Software

The data preparation, analysis and plotting were performed using R version 3.4.1 (R Core Team, 2017) and the R package TMB (Kristensen et al., 2016). The analysis R scripts and publicly available data are archived at https://doi.org/10.5281/zenodo.837866. The Sage-Grouse data are available from the Wyoming Department of Fish and Game.

RESULTS

Local Models

The Akaike weights for the spatial scales indicate that 3.2 km is strongly supported (w_i = 0.95) as the most important lek distance for predicting individual lek counts (Table 2). The Akaike weights for the lags in the well pad density also provided very strong support for a single candidate with the lag of one year receiving a weight of 0.92 (Table 3). The situation with the PDO index lags was less clear-cut (Table 4), although a lag of two years received the majority of the support (w_i = 0.77). Consequently, the full local model with a lek distance of 3.2 km and lags of one and two years years in the well pad density and the PDO index, respectively, was selected as the final model. The standardized residuals, with the exception of a negligible number of high outliers, were approximately normally distributed and displayed homogeneity of variance.

The Akaike weights for β_W and β_P (Table 1) across the final full model and the three reduced models indicate that both are very strongly supported ($w_i \geq 0.99$) as predictors of individual lek counts (Table 5). The model averaged predictions indicate that an increase of one standard deviation in the density of well pads (0.89) is associated with a decrease in the lek count of almost 20% while the equivalent change in the PDO index (0.82) is associated with an increase of almost 20% (Fig. 5). The predictions across the range of observed values indicate that a density of 2.5 well pads/km^2 is associated with a decline of 50% (Fig. 6) while an change in the PDO index from zero to one is associated with a 25% increase (Fig. 7).

Population Models

Based on the results of the local models, a lek distance of 3.2 km was selected. At this spatial scale there is substantial variation within and among working groups in the levels of OAG development (Fig. 8). The Akaike weights for the lag in the well pad density (Table 6) were completely indifferent (w_i = 0.25 for all candidates) while the Akaike weights for the PDO index (Table 7) clearly supported a lag of one year (w_i = 0.83). The residuals were approximately normally distributed with homogeneity of variance.

The Akaike weights for β_W and β_P (Table 1) across the final full model and the three reduced models indicate that while the PDO index is well supported (w_i = 0.91) as a predictor of population changes, there is little support ($w_i = 0.24$) for well pad density (Table 8). The model-averaged estimates indicate a close fit to the data (Fig. 9), which is to be expected given that the population model includes process error (Dennis et al., 2006). The model-averaged predictions, indicate that an increase of one standard deviation in the density of well pads (0.32) is associated with no change in the expected population density the following year while the equivalent change in the PDO index (0.87) is associated with an increase of just under 10% (Fig. 10). The predictions across the range of observed values indicate no relationship between OAG and the carry capacity (Fig. 11) and an increase of 50% in the carry capacity with a change in the PDO index from zero to one (Fig. 12).

DISCUSSION

Oil and Gas

The results suggest that while the density of well pads within 3.2 km has impacted the counts of male Sage-Grouse at individual leks over the past 32 years, it was not an important explanatory variable at the population-level. There are three potential explanations for discrepancies between local impacts and population-level responses (Fodrie et al., 2014). The first is that the local impacts have been overestimated. The second is that population models lack the statistical power to detect the response; and the third, is that the populations were able to compensate for the local impacts of oil and gas. Distinguishing between these alternatives is critical for understanding the effects of human activities on a species of concern. We discuss each in turn below.

Local Impacts Multiple studies (Walker et al., 2007; Doherty et al., 2010; Harju et al., 2010; Green et al., 2016), including the current one, have all detected a strong negative association between OAG and local lek counts. It is therefore highly likely that OAG development has a substantial local impact on counts at individual leks.

Statistical Power The second possible explanation for the mismatch between the local impact of OAG and the apparent absence of a population-level response is that the population models lack statistical power. Although many studies perform post-experimental analyses to determine the statistical power, this is unnecessary. As Hoenig and Heisey (2001) state

> Once we have constructed a confidence interval, power calculations yield no additional insights. It is pointless to perform power calculations for hypotheses outside of the confidence interval because the data have already told us that these are unlikely values.

In the case of the current study, the effect size estimates (Fig. 10) indicate that, if the assumptions of the GSSPMs all hold (Greenland et al., 2016), then the model has sufficient power to rule out a population-level effect of any biologically meaningful size.

This key finding leaves us with two possibilites. The first possibility, which we discuss below, is that the estimates from the GSSPMs are unreliable and the second, which we discuss in the next section, is that the Sage-Grouse populations were able to compensate for the local impacts of OAG.

Population Models It is well-known that if observational error is large compared to the process error, then GSSPMs may suffer from estimation problems (Dennis et al., 2006; Auger-Méthé et al., 2016). However, examination of the parameter estimates and their associated CIs indicate that the observational and process errors are a similar magnitude and that both are relatively well defined (Table 8). Furthermore, the preliminary analyses which used a three-stage population model without process error also ruled out a biologically meaningful population-level effect of OAG.

A second possibility is that the GSSPMs' estimates are unreliable because the average number of males per lek is a poor indicator of the actual population density. For example, the probability of male Sage-Grouse attending a lek has been reported to vary annually between 0.56 and 0.87 (Blomberg et al., 2013). However, as the current models include 32 years of data and incorporate annual variation they are well-suited for assessing population growth (Blomberg et al., 2013).

A third possibility is that the mean density of well pads within 3.2 km of the leks is a poor indicator of the potential population-level impact. In particular, such a metric does not account for the fact that well pads close to a large lek are likely to have a greater population-level impact than those close to a small lek. However, the annual working group OAG metrics from the preliminary analyses, which incorporated lek size, are very similar to those from the current study.

Alternatively, the estimates may be unreliable due to movement among the working groups. This is a potential concern because the resultant source-sink dynamics (Kirol et al., 2015a) would diminish the estimated population-level effects of OAG. Although some individuals can move 50 km between life-stages (Fedy et al., 2012), analysis of genetic and lek count data suggests that movement among 10 clusters which roughly approximate the working groups is less than 1.1% per year (Row et al., 2016).

Ecological Compensation The third, and final, explanation for the mismatch between the local impacts of OAG and the negligible population-level response is that the birds were able compensate for the local losses. Such compensation could have occurred due to density-dependent processes, movement of birds (behavioral response to disturbance) and/or changes in industrial practices and regulations (in effect, a societal response of humans to Sage-Grouse). For example, as well as the GSSPM parameter estimates, which indicate that the population growth rate increases at lower densities, it has been shown that Sage-Grouse can compensate for hunting harvest (Sedinger et al., 2010); that nest initiation is influenced by density dependence (Blomberg et al., 2017); and that there is spatial heterogeneity in the patterns of population regulation (LaMontagne et al., 2002). Alternatively, Sage-Grouse may have behaviorally compensated for the local impacts by moving to less disturbed leks (Gill et al., 2001; Fedy et al., 2012, 2015). Finally it is worth noting that since 1996, OAG companies have increasingly been required to adopt various mitigation (Kirol et al., 2015b) and conservation measures. It is therefore possible that any apparent compensation was partly due to more ecological practices.

Climatic Variation

The current study indicates that the PDO index is a statistically and biologically important predictor of changes in Sage-Grouse number at both the lek and population level. This is perhaps not surprising given the fact that the PDO has previously been used, in combination with the Atlantic Multi-Decadal Oscillation and El Nino Southern Oscillation, to predict drought, drought-related fire frequency, and precipitation trends in the western USA and Rocky Mountains (Schoennagel et al., 2007; Kitchen, 2015; Heyerdahl et al., 2008).

Although the current study does not identify the causal pathways through which sea surface temperatures in the North Pacific influences the Sage-Grouse population growth rate we note that in Wyoming, a positive PDO correlates with cooler, wetter weather, while a negative phase tends to produce warmer, drier conditions (McCabe et al., 2004). We also note that given the relatively poor performance of local precipitation and temperature metrics (Blomberg et al., 2012; Green et al., 2016; Blomberg et al., 2014, 2017; Coates et al., 2016; Gibson et al., 2017; Green et al., 2016), the causal pathways may be complex and involve other organisms such as parasites (Cattadori et al., 2005; Taylor et al., 2013). In fact the complexity of such pathways is one of the reasons that large-scale climate indices such as the PDO often outperform local data in predicting population dynamics and ecological process (Stenseth et al., 2002; Hallett et al., 2004). Additional studies to assess the explanatory value of the PDO index across the species range are needed (Doherty et al., 2016).

Similar Studies

In their recent paper, (Green et al., 2016, p.1) used

> ... 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.

Based on their results, they conclude that

> 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...

Although their findings apparently contradict the current study it is important to realize that they used local precipitation as opposed to a regional climate indicator. The lack of support for environmental conditions is therefore unsurprising (Stenseth et al., 2002; Hallett et al., 2004). It is also important to realize that they used their population dynamic model to analyse the impact of OAG on individual leks. As result, they provide further confirmation of the local impacts of OAG but their conclusions are not relevant at the population-level.

Conclusions

If inter-annual movement among working groups is negligible, then the results suggest that the local impacts of the increases in OAG development in Wyoming between 1985 and 2016 were largely compensated for by density-dependent processes, movement of birds and/or changes in industrial practices. This does not, however, mean that OAG development prior to 1985 had little effect nor does it mean that increasing development would be without consequence for the population. It does, however, indicate that regulations intended to benefit Sage-Grouse should not be based solely on the results of local studies.

The key finding, that regional climate, as indexed by the PDO, is an important predictor of Sage-Grouse population dynamics in Wyoming has major implications for our understanding and conservation of the species. At the very least it is expected that any long-term population declines, like those of songbirds in western North America (Ballard et al., 2003; McClure et al., 2012), will be better understood in the context of the PDO. At best, it should allow regulators to account for and predict (Stenseth et al., 2003) the effects of climatic variation on Sage-Grouse population fluctuations, and more effectively balance conservation efforts.

ACKNOWLEDGMENTS

We thank T.J. Christiansen and the State of Wyoming for providing the lek count data and R. Ranger of the American Petroleum Institute for providing partial funding. Additional funding was provided by Wildlife Science International, Poisson Consulting and Terra Cognito GIS. We also thank L. Brown and R.L. Irvine for comments and edits.

REFERENCES

Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D., and Mills Flemming, J. (2016). State-space models' dirty little secrets: even simple linear Gaussian models can have estimation problems. *Scientific Reports*, 6:26677.

Ballard, G., Geupel, G. R., Nur, N., and Gardali, T. (2003). Long-term declines and decadal patterns in population trends of songbirds in Western North America, 1979-1999. *The Condor*, 105:737–755.

Blickley, J. L., Blackwood, D., and Patricelli, G. L. (2012a). Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks: *Greater Sage-Grouse Abundance and Noise*. *Conservation Biology*, 26(3):461–471.

Blickley, J. L., Word, K. R., Krakauer, A. H., Phillips, J. L., Sells, S. N., Taff, C. C., Wingfield, J. C., and Patricelli, G. L. (2012b). Experimental Chronic Noise Is Related to Elevated Fecal Corticosteroid Metabolites in Lekking Male Greater Sage-Grouse (Centrocercus urophasianus). *PLoS ONE*, 7(11):e50462.

Blomberg, E. J., Gibson, D., Atamian, M. T., and Sedinger, J. S. (2014). Individual and environmental effects on egg allocations of female Greater Sage-Grouse. *The Auk*, 131(4):507–523.

Blomberg, E. J., Gibson, D., Atamian, M. T., and Sedinger, J. S. (2017). Variable drivers of primary versus secondary nesting; density-dependence and drought effects on greater sage-grouse. *Journal of Avian Biology*.

Blomberg, E. J., Sedinger, J. S., Atamian, M. T., and Nonne, D. V. (2012). Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. *Ecosphere*, 3(6):art55.

Blomberg, E. J., Sedinger, J. S., Nonne, D. V., and Atamian, M. T. (2013). Annual male lek attendance influences count-based population indices of greater sage-grouse: Lek Attendance of Greater Sage-Grouse. *The Journal of Wildlife Management*, 77(8):1583–1592.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., and White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3):127–135.

Bradford, M. J., Korman, J., and Higgins, P. S. (2005). Using confidence intervals to estimate the response of salmon populations (Oncorhynchus spp.) to experimental habitat alterations. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(12):2716–2726.

Braun, C. E., Oedekoven, O. O., and Cameron, L. A. (2002). Oil and Gas Development in Western North America: Effects on Sagebrush Steppe Avifauna with Particular Emphasis on Sage-grouse. In

Transactions of the 67th North American Wildlife and Natural Resources Conference, pages 337–349, Washington, D.C. Wildlife Management Institute.

Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, volume Second Edition. Springer, New York.

Cattadori, I. M., Haydon, D. T., and Hudson, P. J. (2005). Parasites and climate synchronize red grouse populations. *Nature*, 433(7027):737–741.

Coates, P. S., Ricca, M. A., Prochazka, B. G., Brooks, M. L., Doherty, K. E., Kroger, T., Blomberg, E. J., Hagen, C. A., and Casazza, M. L. (2016). Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. *Proceedings of the National Academy of Sciences*, 113(45):12745–12750.

Connelly, J. W. and Braun, C. E. (1997). Long-term changes in sage grouse Centrocercus urophasianus populations in western North America. *Wildlife Biology*, 3:229–234.

Copeland, H. E., Doherty, K. E., Naugle, D. E., Pocewicz, A., and Kiesecker, J. M. (2009). Mapping Oil and Gas Development Potential in the US Intermountain West and Estimating Impacts to Species. *PLoS ONE*, 4(10):e7400.

Copeland, H. E., Pocewicz, A., Naugle, D. E., Griffiths, T., Keinath, D., Evans, J., and Platt, J. (2013). Measuring the Effectiveness of Conservation: A Novel Framework to Quantify the Benefits of Sage-Grouse Conservation Policy and Easements in Wyoming. *PLoS ONE*, 8(6):e67261.

Davis, A. J., Hooten, M. B., Phillips, M. L., and Doherty, P. F. (2014). An integrated modeling approach to estimating Gunnison sage-grouse population dynamics: combining index and demographic data. *Ecology and Evolution*, pages n/a–n/a.

Dennis, B., Ponciano, J. M., Lele, S. R., Taper, M. L., and Staples, D. F. (2006). Estimating density dependence, process noise, and observation error. *Ecological Monographs*, 76(3):323–341.

Doherty, K. E., Evans, J. S., Coates, P. S., Juliusson, L. M., and Fedy, B. C. (2016). Importance of regional variation in conservation planning: a rangewide example of the Greater Sage-Grouse. *Ecosphere*, 7(10):e01462.

Doherty, K. E., Naugle, D. E., and Evans, J. S. (2010). A Currency for Offsetting Energy Development Impacts: Horse-Trading Sage-Grouse on the Open Market. *PLoS ONE*, 5(4):e10339.

Dzialak, M. R., Olson, C. V., Harju, S. M., Webb, S. L., Mudd, J. P., Winstead, J. B., and Hayden-Wing, L. (2011). Identifying and Prioritizing Greater Sage-Grouse Nesting and Brood-Rearing Habitat for Conservation in Human-Modified Landscapes. *PLoS ONE*, 6(10):e26273.

Fedy, B. C. and Aldridge, C. L. (2011). The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. *The Journal of Wildlife Management*, 75(5):1022–1033.

Fedy, B. C., Aldridge, C. L., Doherty, K. E., O'Donnell, M., Beck, J. L., Bedrosian, B., Holloran, M. J., Johnson, G. D., Kaczor, N. W., Kirol, C. P., Mandich, C. A., Marshall, D., McKee, G., Olson, C., Swanson, C. C., and Walker, B. L. (2012). Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. *The Journal of Wildlife Management*, 76(5):1062–1071.

Fedy, B. C. and Doherty, K. E. (2011). Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: greater sage-grouse and cottontail rabbits. *Oecologia*, 165(4):915–924.

Fedy, B. C., Kirol, C. P., Sutphin, A. L., and Maechtle, T. L. (2015). The Influence of Mitigation on Sage-Grouse Habitat Selection within an Energy Development Field. *PLOS ONE*, 10(4):e0121603.

Fodrie, F. J., Able, K. W., Galvez, F., Heck, K. L., Jensen, O. P., López-Duarte, P. C., Martin, C. W., Turner, R. E., and Whitehead, A. (2014). Integrating organismal and population responses of estuarine fishes in Macondo spill research. *BioScience*, 64(9):778–788.

Fremgen, A. L., Hansen, C. P., Rumble, M. A., Gamo, R. S., and Millspaugh, J. J. (2016). Male greater sage-grouse detectability on leks: Sightability of Male Sage-Grouse on Leks. *The Journal of Wildlife Management*, 80(2):266–274.

Fukami, T. and Wardle, D. A. (2005). Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B: Biological Sciences*, 272(1577):2105–2115.

Garton, E. O., Connelly, J. W., Horne, J. S., Hagen, C. A., Moser, A., and Schroeder, M. A. (2011). Greater Sage-Grouse Population Dynamics and Probability of Persistence. In Knick, S. T. and Connelly, J. W., editors, *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*, number no. 38 in Studies in avian biology, pages 293–374. University of California Press, Berkeley, Calif.

Garton, E. O., Wells, A. G., Baumgardt, J. A., and Connelly, J. W. (2015). Greater Sage-Grouse Population Dynamics and Probability of Persistence. Technical report, Pew Charitable Trusts.

Gibson, D., Blomberg, E. J., Atamian, M. T., and Sedinger, J. S. (2017). Weather, habitat composition, and female behavior interact to modify offspring survival in Greater Sage-Grouse. *Ecological Applications*, 27(1):168–181.

Gill, J. A., Norris, K., and Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, 97(2):265–268.

Green, A. W., Aldridge, C. L., and O'donnell, M. S. (2016). Investigating impacts of oil and gas development on greater sage-grouse: Oil and Gas Impacts on Sage-Grouse. *The Journal of Wildlife Management*.

Greenland, S., Senn, S. J., Rothman, K. J., Carlin, J. B., Poole, C., Goodman, S. N., and Altman, D. G. (2016). Statistical tests, P values, confidence intervals, and power: a guide to misinterpretations. *European Journal of Epidemiology*, 31(4):337–350.

Gregory, A. J. and Beck, J. L. (2014). Spatial Heterogeneity in Response of Male Greater Sage-Grouse Lek Attendance to Energy Development. *PLoS ONE*, 9(6):e97132.

Greven, S. and Kneib, T. (2010). On the behaviour of marginal and conditional AIC in linear mixed models. *Biometrika*, page asq042.

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., and Grenfell, B. T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, 430(6995):71–75.

Harju, S. M., Dzialak, M. R., Taylor, R. C., Hayden-Wing, L. D., and Winstead, J. B. (2010). Thresholds and Time Lags in Effects of Energy Development on Greater Sage-Grouse Populations. *Journal of Wildlife Management*, 74(3):437–448.

Heyerdahl, E. K., Morgan, P., and Riser, J. P. (2008). Multi-season climate synchronized historical fires in dry forests (1650–1900), northern Rockies, USA. *Ecology*, 89(3):705–716.

Hilborn, R., Bue, B. G., and Sharr, S. (1999). Estimating spawning escapements from periodic counts: a comparison of methods. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(5):888–896.

Hoenig, J. M. and Heisey, D. M. (2001). The Abuse of Power: The Pervasive Fallacy of Power Calculations for Data Analysis. *The American Statistician*, 55(1):19–24.

Holloran, M. J. (2005). Greater sage-grouse (Centrocercus urophasianus) population response to natural gas field development in western Wyoming.

Holloran, M. J., Kaiser, R. C., and Hubert, W. A. (2010). Yearling Greater Sage-Grouse Response to Energy Development in Wyoming. *Journal of Wildlife Management*, 74(1):65–72.

Johnson, D. and Rowland, M. (2007). The utility of lek counts for monitoring greater sage-grouse. In Reese, K. and Bowyer, R., editors, *Monitoring populations of sage-grouse*, pages 15–23. University of Idaho, Moscow, Idaho.

Kirol, C. P., Beck, J. L., Huzurbazar, S. V., Holloran, M. J., and Miller, S. N. (2015a). Identifying Greater Sage-Grouse source and sink habitats for conservation planning in an energy development landscape. *Ecological Applications*, 25(4):968–990.

Kirol, C. P., Sutphin, A. L., Bond, L., Fuller, M. R., and Maechtle, T. L. (2015b). Mitigation effectiveness for improving nesting success of greater sage-grouse influenced by energy development. *Wildlife Biology*, 21(2):98–109.

Kitchen, S. G. (2015). Climate and human influences on historical fire regimes (AD 1400–1900) in the eastern Great Basin (USA). *The Holocene*, page 0959683615609751.

Knape, J. (2008). Estimability of density dependence in models of time series data. *Ecology*, 89(11):2994–3000.

Knape, J. and de Valpine, P. (2012). Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance?: Density dependence in the GPDD. *Ecology Letters*, 15(1):17–23.

Knick, S. T. and Connelly, J. W., editors (2011). *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Number no. 38 in Studies in avian biology. University of California Press, Berkeley, Calif.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. (2016). **TMB** : Automatic

Differentiation and Laplace Approximation. *Journal of Statistical Software*, 70(5).

Kvasnes, M. A. J., Storaas, T., Pedersen, H. C., Bjørk, S., and Nilsen, E. B. (2010). Spatial dynamics of Norwegian tetraonid populations. *Ecological Research*, 25(2):367–374.

LaMontagne, J. M., Irvine, R. L., and Crone, E. E. (2002). Spatial patterns of population regulation in sage grouse (Centrocercus spp.) population viability analysis. *Journal of Animal Ecology*, 71(4):672–682.

Lindström, J., Ranta, E., Lindén, H., Lindstrom, J., and Linden, H. (1996). Large-Scale Synchrony in the Dynamics of Capercaillie, Black Grouse and Hazel Grouse Populations in Finland. *Oikos*, 76(2):221.

Ludwig, G. X., Alatalo, R. V., Helle, P., Linden, H., Lindstrom, J., and Siitari, H. (2006). Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proceedings of the Royal Society B: Biological Sciences*, 273(1597):2009–2016.

Lyon, A. G. and Anderson, S. H. (2003). Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin*, 31(2):486–491.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C. (1997). A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. *Bulletin of the American Meteorological Society*, 78(6):1069–1079.

McCabe, G. J., Palecki, M. A., and Betancourt, J. L. (2004). Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences*, 101(12):4136–4141.

McClure, C. J. W., Rolek, B. W., McDonald, K., and Hill, G. E. (2012). Climate change and the decline of a once common bird: Climate Change and Blackbird Decline. *Ecology and Evolution*, 2(2):370–378.

Millar, R. B. (2011). *Maximum likelihood estimation and inference: with examples in R, SAS, and ADMB*. Statistics in practice. Wiley, Chichester, West Sussex. OCLC: ocn690090037.

Monroe, A. P., Edmunds, D. R., and Aldridge, C. L. (2016). Effects of lek count protocols on greater sage-grouse population trend estimates: Lek Count Timing and Trend Estimates. *The Journal of Wildlife Management*, 80(4):667–678.

Moran, P. A. P. (1952). The Statistical Analysis of Game-Bird Records. *The Journal of Animal Ecology*, 21(1):154.

Moran, P. A. P. (1954). The Statistical Analysis of Game-Bird Records. II. *The Journal of Animal Ecology*, 23(1):35.

Neilson, R., Lenihan, J., Bachelet, D., and Drapek, R. (2005). Climate change implications for sagebrush ecosystems. In *Transactions of the 70th North American Wildlife and Natural Resources Conference*, pages 145–149.

Ntzoufras, I. (2009). *Bayesian Modeling Using WinBUGS*. John Wiley & Sons Inc., Hoboken, New Jersey.

R Core Team (2017). R: A Language and Environment for Statistical Computing.

Ranta, E., Lindstrom, J., and Linden, H. (1995). Synchrony in Tetraonid Population Dynamics. *The Journal of Animal Ecology*, 64(6):767.

Ross, B. E., Haukos, D., Hagen, C., and Pitman, J. (2016). The relative contribution of climate to changes in lesser prairie-chicken abundance. *Ecosphere*, 7(6):e01323.

Row, J. R., Oyler-McCance, S. J., and Fedy, B. C. (2016). Differential influences of local subpopulations on regional diversity and differentiation for greater sage-grouse (*Centrocercus urophasianus*). *Molecular Ecology*, 25(18):4424–4437.

Schoennagel, T., Veblen, T. T., Kulakowski, D., and Holz, A. (2007). Multidecadal climate variability and climate interactions affect subalpine fire occurrence, western Colorado (USA). *Ecology*, 88(11):2891–2902.

Schroeder, M. A., Aldridge, C. L., Apa, A. D., Bohne, J. R., Braun, C. E., Bunnell, S. D., Connelly, J. W., Deibert, P. A., Gardner, S. C., Hilliard, M. A., and others (2004). Distribution of sage-grouse in North America. *The Condor*, 106(2):363–376.

Sedinger, J. S., White, G. C., Espinosa, S., Partee, E. T., and Braun, C. E. (2010). Assessing Compensatory Versus Additive Harvest Mortality: An Example Using Greater Sage-Grouse. *Journal of Wildlife Management*, 74(2):326–332.

Selås, V., Sonerud, G. A., Framstad, E., Kålås, J. A., Kobro, S., Pedersen, H. B., Spidsø, T. K., and Wiig, O. (2011). Climate change in Norway: warm summers limit grouse reproduction. *Population Ecology*, 53(2):361–371.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., and Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, 297(5585):1292–1296.

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N. G., and Adlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Nino Southern Oscillation and beyond. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1529):2087–2096.

Taylor, R. L., Tack, J. D., Naugle, D. E., and Mills, L. S. (2013). Combined Effects of Energy Development and Disease on Greater Sage-Grouse. *PLoS ONE*, 8(8):e71256.

Trenberth, K. E. and Hurrell, J. W. (1994). Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics*, 9(6):303–319.

Vaida, F. and Blanchard, S. (2005). Conditional Akaike information for mixed-effects models. *Biometrika*, 92(2):351–370.

Viterbi, R., Imperio, S., Alpe, D., Bosser-peverelli, V., and Provenzale, A. (2015). Climatic control and population dynamics of black grouse (*Tetrao tetrix*) in the Western Italian Alps: Population Dynamics of Alpine Black Grouse. *The Journal of Wildlife Management*, 79(1):156–166.

Walker, B. L., Naugle, D. E., and Doherty, K. E. (2007). Greater Sage-Grouse Population Response to Energy Development and Habitat Loss. *Journal of Wildlife Management*, 71(8):2644–2654.

Walsh, D. P., White, G. C., Remington, T. E., and Bowden, D. C. (2004). Evaluation of the lek-count index for greater sage-grouse. *Wildlife Society Bulletin*, 32(1):56–68.

FIGURES

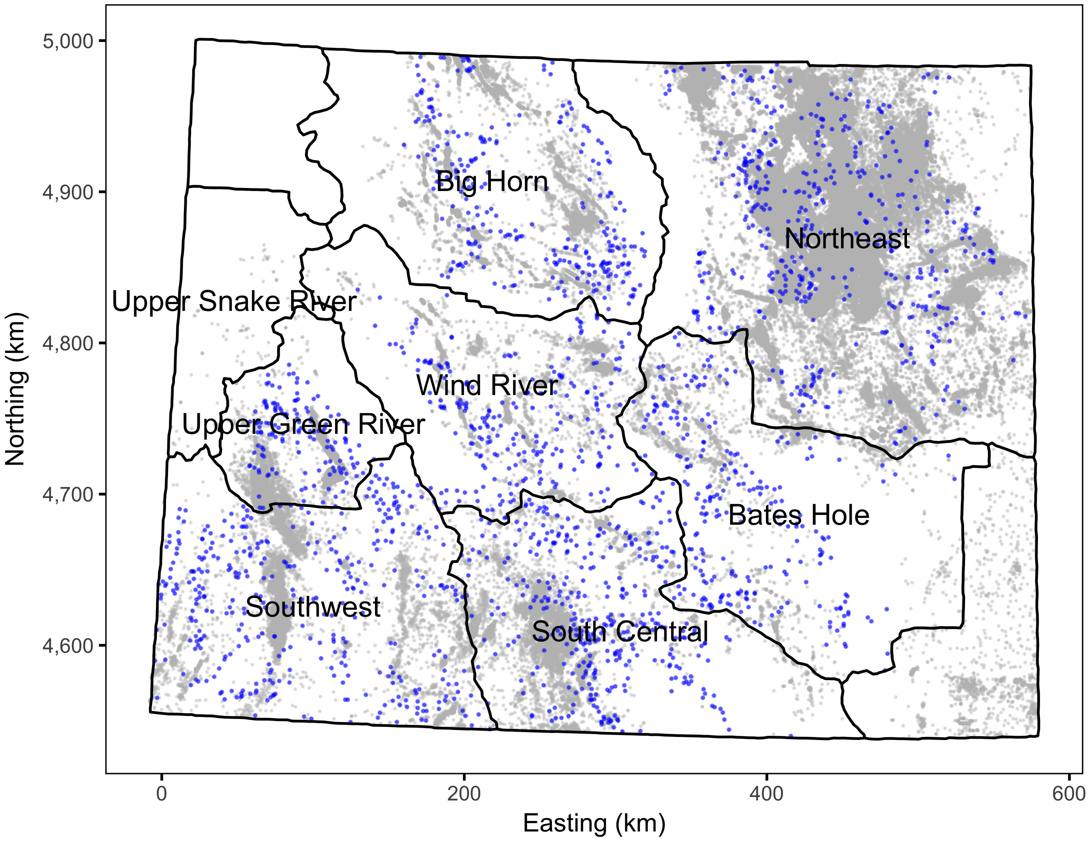

Figure 1. Map of Wyoming and its working groups. Leks are indicated by blue points and wells pads by grey points. Only leks and wells pads that are included in the analyses are shown. The leks and well pads are not to scale. The projection is EPSG:26913.

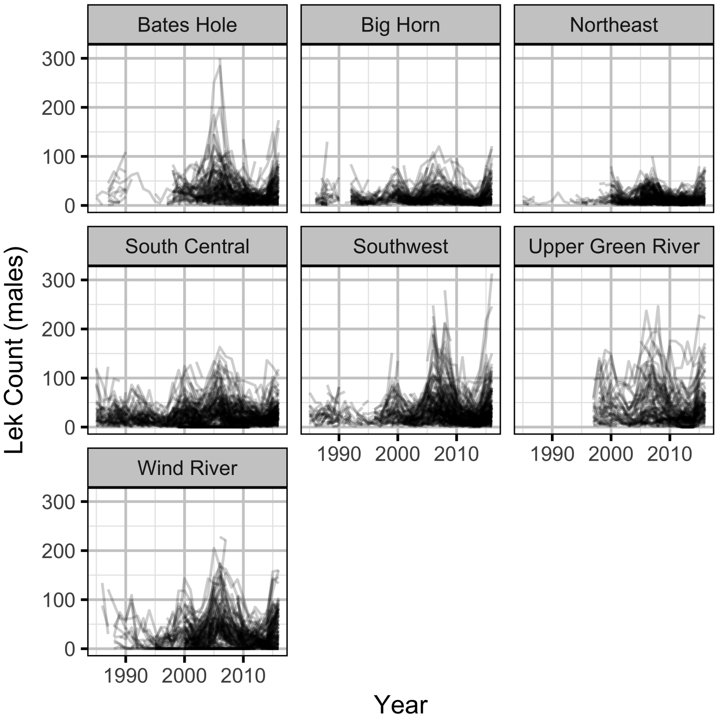

Figure 2. Mean counts of male Sage-Grouse at individual leks by year and working group.

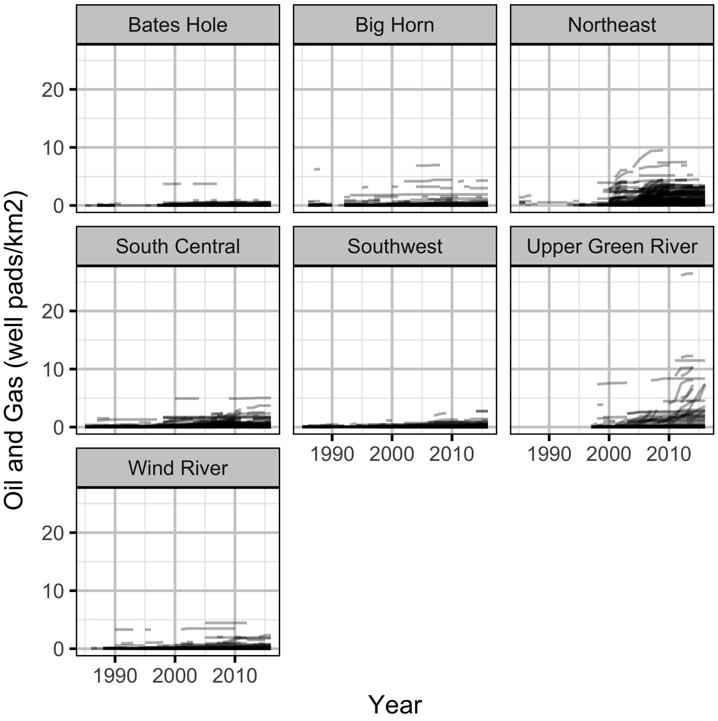

Figure 3. Well pad densities within 3.2 km of individual leks with one or more counts by year and working group.

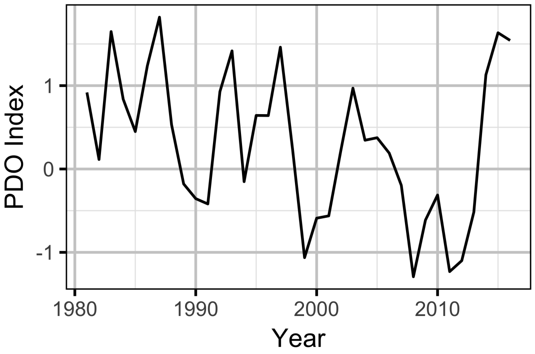

Figure 4. Pacific Decadal Oscillation index by year. Positive values indicate a warm phase and negative values a cool phase.

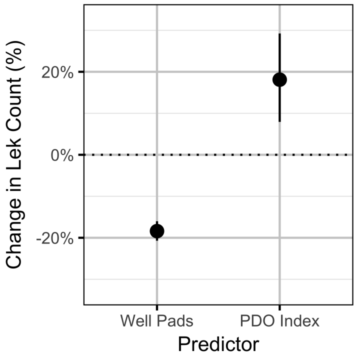

Figure 5. Model averaged estimates (with 95% CIs) of the effect of an increase in one standard deviation in well pad density within 3.2 km (0.89 well pads/km^2) and the Pacific Decadal Oscillation index (0.82) on the expected count of male Sage-Grouse at an individual lek.

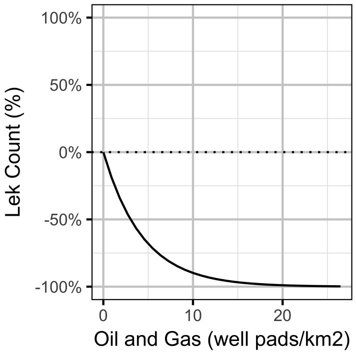

Figure 6. Model averaged estimate of the effect of well pad density within 3.2 km on the expected count of male Sage-Grouse at an individual lek.

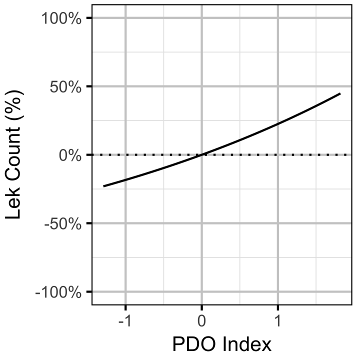

Figure 7. Model averaged estimate of the effect of the Pacific Decadal Oscillation on the expected count of male Sage-Grouse at an individual lek.

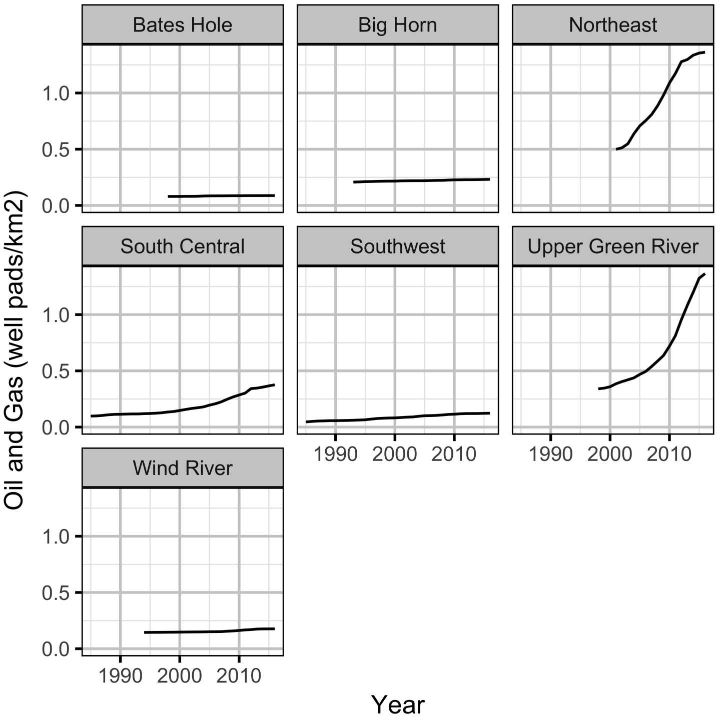

Figure 8. Mean well pad densities within 3.2 km of all leks by year and working group.

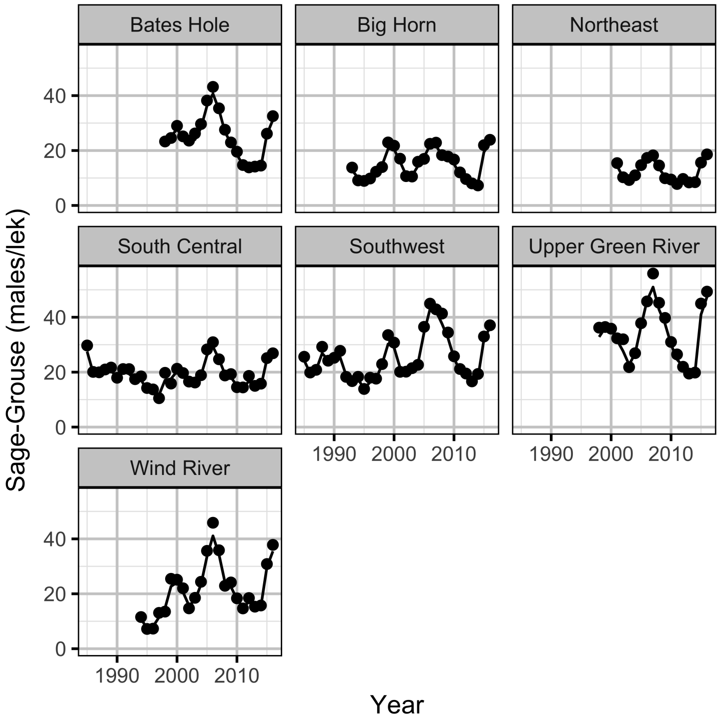

Figure 9. Mean lek counts by year and working group. The solid line is the model averaged estimate of the population density.

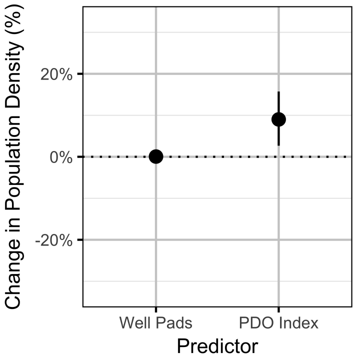

Figure 10. Model averaged estimates (with 95% CIs) of the effect of an increase in one standard deviation in the mean well pad density (0.32 well pads/km^2) within 3.2 km of all leks and the Pacific Decadal Oscillation index (0.82) on the expected population density.

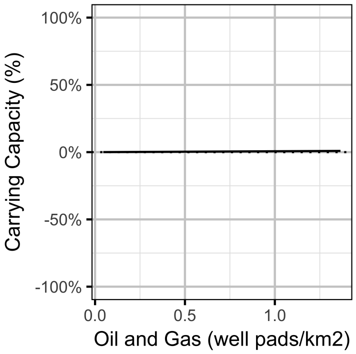

Figure 11. Model averaged estimate of the effect of the mean well pad density within 3.2 km of all leks on the expected carrying capacity at a typical working group in a typical year.

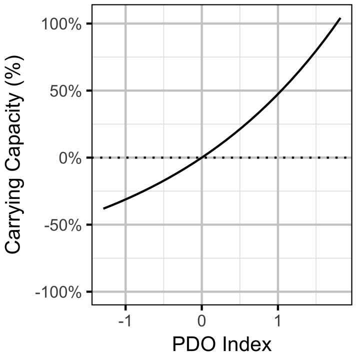

Figure 12. Model averaged estimate of the effect of the Pacific Decadal Oscillation index on the expected carrying capacity at a typical working group with no oil and gas development.

TABLES

Parameter	Description
β_0	The intercept for the log lek count or log population density.
β_I	The intercept for the log initial population density.
β_D	The effect of population density on β_0.
β_P	The effect of the standardised Pacific Decadal Oscillation index on β_0.
β_W	The effect of the standardised well pad density on β_0.
σ_γ	The standard deviation of the overdispersion.
σ_ε	The standard deviation of the observer error.
σ_η	The standard deviation of the process error.
σ_G	The standard deviation of the random effect of working group on β_0.
σ_I	The standard deviation of the random effect of working group on β_I.
σ_L	The standard deviation of the random effect of lek on β_0.
σ_Y	The standard deviation of the random effect of year on β_0.

Table 1. Descriptions of key model parameters.

Distance (km)	Models	Proportion	w_i
3.2	16	0.20	0.95
1.6	16	0.20	0.05
0.8	16	0.20	0.00
6.4	16	0.20	0.00
12.8	16	0.20	0.00

Table 2. The relative importance (w_i) of spatial scale as a predictor of the count of males Sage-Grouse at individual leks across all models with both well pad density and the Pacific Decadal Oscillation index independently lagged one to four years.

Wells Lag (yr)	Models	Proportion	w_i
1	20	0.25	0.92
2	20	0.25	0.08
3	20	0.25	0.00
4	20	0.25	0.00

Table 3. The relative importance (w_i) of the lag in well pad density as a predictor of the count of males Sage-Grouse at individual leks across all models with a lek distance of 0.8, 1.6, 3.2, 6.4 and 12.8 km and the Pacific Decadal Oscillation index independently lagged one to four years.

PDO Lag (yr)	Models	Proportion	w_i
2	20	0.25	0.77
3	20	0.25	0.15
4	20	0.25	0.04
1	20	0.25	0.03

Table 4. The relative importance (w_i) of the lag in the Pacific Decadal Oscillation index density as a predictor of the count of males Sage-Grouse at individual leks across all models with a lek distance of 0.8, 1.6, 3.2, 6.4 and 12.8 km and the well pad density independently lagged one to four years.

Parameter	Estimate	Lower	Upper	Models	Proportion	w_i
β_0	2.479	2.370	2.587	4	1.00	1.00
β_P	0.166	0.076	0.256	4	0.50	0.99
β_W	-0.203	-0.232	-0.174	4	0.50	1.00
σ_Y	0.270	0.211	0.346	4	1.00	1.00
σ_γ	0.619	0.611	0.627	4	1.00	1.00
σ_L	0.998	0.962	1.035	4	1.00	1.00

Table 5. The model averaged parameter estimates for the lek count model with approximate lower and upper 95% CIs for a lek distance of 3.2 km, well pad density lag of one year and Pacific Decadal Oscillation index lag of two years. The Akaike's weights (w_i) are based on all four combinations of models with and without well pads (β_W) and the Pacific Decadal Oscillation index (β_P).

Wells Lag (yr)	Models	Proportion	w_i
4	4	0.25	0.25
1	4	0.25	0.25
2	4	0.25	0.25
3	4	0.25	0.25

Table 6. The relative importance (w_i) of the lag in well pad density as a predictor of the change in the population density across all models with a lek distance of 3.2 km and the Pacific Decadal Oscillation index independently lagged one to four years.

PDO Lag (yr)	Models	Proportion	w_i
1	4	0.25	0.83
2	4	0.25	0.11
4	4	0.25	0.03
3	4	0.25	0.03

Table 7. The relative importance (w_i) of the lag in the Pacific Decadal Oscillation index as a predictor of the change in the population density across all models with a lek distance of 3.2 km and the well pad density lagged one to four years.

Parameter	Estimate	Lower	Upper	Models	Proportion	w_i
β_D	-0.262	-0.437	-0.087	4	1.00	0.99
β_I	2.880	2.564	3.197	4	1.00	0.99
β_0	0.769	0.261	1.277	4	1.00	0.99
β_P	0.086	0.026	0.146	4	0.50	0.91
β_W	0.001	-0.009	0.010	4	0.50	0.24
σ_Y	0.176	0.132	0.234	4	1.00	0.99
σ_G	0.031	0.013	0.076	4	1.00	0.99
σ_I	0.317	0.139	0.721	4	1.00	0.99
σ_ε	0.085	0.054	0.136	4	1.00	0.99
σ_η	0.112	0.078	0.161	4	1.00	0.99

Table 8. The model averaged parameter estimates for the population dynamic model with approximate lower and upper 95% CIs for a lek distance of 3.2 km, well pad density lag of four years and Pacific Decadal Oscillation index lag of one year. The Akaike's weights (w_i) are based on all four combinations of models with and without well pads (β_W) and the Pacific Decadal Oscillation index (β_P).