Recent local and population level responses of Greater Sage Grouse to oil and gas development in Wyoming

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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 is a large sexually dimorphic tetraonid that is endemic to the sagebrush habitat of western North America.
Methods Local and population models were used to examine whether the local effects of oil and gas result in a population-level response. The local effect of the areal disturbance within 6.44 km of individual leks was assessed using generalized linear mixed models. The population-level response was quantified using population dynamic models. An information-theoretic approach was adopted.
Results The results for both the Pinedale Planning Area and the state of Wyoming indicate that while the local areal disturbance was an important negative predictor of the lek counts between 1997 and 2012, the population dynamics over the same period were primarily driven by the climate as indexed by the Pacific Decadal Oscillation.
Conclusions If the movement of greater sage grouse between regions is low, then the results indicate that the local impacts of the increasing oil and gas development in Wyoming were largely compensated for by density-dependent processes, local movements of birds and/or changes in industrial practices. Regulators should account for, and predict, the effects of climate on sage grouse population fluctuations.

Keywords: Pacific Decadal Oscillation, Lek Counts, Population Dynamics

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 (Cooper Ornithological Society, 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.

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 indicated long-term declines in many remaining populations (WAFWA, 2015).

A multitude of studies have reported local negative effects of oil and gas (OAG) development on sage grouse densities, 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). More recently, experimental studies have suggested that noise alone can reduce lek attendance (Blickley et al., 2012b) and increase stress hormones in exposed individuals (Blickley et al., 2012a). Lyon and Anderson (2003) were among the first to provide evidence for a reduction in a fitness component. Based on the fates of radio-tracked individuals they estimated greater movement and lower nest initiation rates for females captured on leks within 3 km of a well pad or road. Radio-tracking has also been used to document lower annual survival of yearlings reared in areas where OAG infrastructure was present (Holloran et al., 2010). In addition, 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).

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. More recently 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 the actual sage grouse population-level responses are consistent with the predictions scaled-up from the local studies.

Although it has received less attention than OAG, local climate has also been shown to influence sage grouse lek counts and survival (Blomberg et al., 2012). There is a long-history of studies on the influence of climate on the population dynamics of tetraonids (Moran, 1952, 1954) and climate has been used to explain regional and inter-decadal population synchrony in multiple tetraonid species with overlapping ranges (Ranta et al., 1995; Kvasnes et al., 2010). Consequently, the current study also considers regional climate as a potential predictor of sage grouse population dynamics. Finally, although a species of concern, sage grouse in Wyoming are also a game bird and the current study therefore also considers hunting effort as a potential factor influencing population dynamics.

Wyoming 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 at least 1883 (Braun et al., 2002). Wyoming was selected for the current study for these reasons and because the lek location and lek count data are accessible to researchers. Within Wyoming, the Pinedale Planning Area (PPA), which is effectively equivalent to the Upper Green River working group, is the site of several key local historical studies (Lyon and Anderson, 2003; Holloran et al., 2010) and an area of intensive oil and gas development (S1 Video).

Local and population models were used to examine whether the local effects of OAG result in a population-level response. The local models quantified how sage grouse counts at individual lek counts are impacted by OAG development in the vicinity of each lek. The population models examined the extent to which the inter-annual survival rate is related to regional climate, hunting effort and the predicted impact of OAG from the local models. The relative importance of OAG areal disturbance, climate and hunting as explanatory variables was assessed using an information-theoretic approach (Burnham and Anderson, 2002).

METHODS

Data Collection and Preparation

Spatial Data Well location and production data were provided by the Wyoming Oil and Gas Conservation Commission (WOGCC) and rectified with field-verified data from IHS (https://www.ihs.com). All well pads, roads and pipelines associated with OAG were mapped in the PPA (Fig. 1) while just well pads were considered when calculating state wide metrics (Fig. 2, S1 Text).

Lek Counts and Working Groups The sage grouse lek count 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, and data that were collected between April

1st and May 7th as part of a survey or count were included. Lek counts for which the number of individuals of unknown sex were $\geq 5\%$ of the number of males (suggesting poor visibility) were also excluded. The State of Wyoming recognizes eight sage grouse working groups for population management and reporting purposes (Fig. 2). The working groups may only approximate population boundaries. However, the fact that hunter data is gathered by working group makes them convenient demographic units for study.

To further reduce the potential for biases, the analyses only included lek counts from 1997 onwards, as prior to this lek coverage was relatively low in most working groups (Fig. 3). To reduce the probability of stochastic events influencing the results, the entire Upper Snake River, which has just 18 known leks was also excluded from the analyses (Fig. 3). Finally, to avoid problems with model convergence, leks with no count information were excluded from the analyses.

Local Disturbance The local disturbance due to OAG development in the PPA was calculated for each calendar year in terms of the proportional areal disturbance (area of surface disturbance) due to well pads, roads, and pipelines within a 6.44 km radius (Sage-grouse National Technical Team, 2011) of each lek. State-wide the local disturbance metric was the proportional areal disturbance, within a 6.44 km radius of each lek, due to well pads only. For leks in the PPA, which were included in both analyses, the local OAG disturbance metrics were well correlated (Fig. 4). Prior to the analyses, the local OAG disturbance metrics were lead (opposite of lagged) by one year as the lek counts occur early in the calendar year. Leading the disturbance metrics is equivalent to lagging the lek counts (Walker et al., 2007; Doherty et al., 2010; Harju et al., 2010; Gregory and Beck, 2014).

Sage Grouse Density We used a local lek count model both to estimate the effect of local OAG areal disturbance (within a 6.44 km radius) on individual lek counts and to estimate the average expected lek count in the PPA and individual working groups by year. The average expected lek count, which we refer to for the gth working group in the yth year as $M_{g,y}$, is a measure of the population-density (mean number of males per lek). In order to examine whether the population-level responses to OAG were consistent with the local predictions, we also used the local lek count model to estimate what the annual population density would have been with no local OAG impacts ($\hat{M}_{g,y}$). The local lek count model's estimates of the annual density, with and without OAG, were then used to calculate the expected proportional population-level difference in the annual density due to local OAG impacts ($\Theta_{g,y}$), i.e.

$$\Theta_{g,y} = \frac{M_{g,y} - \hat{M}_{g,y}}{\hat{M}_{g,y}}. \tag{1}$$

Hunting For the population models, the hunting metric was the number of hunter days per lek (Fig. 5). In the case of the PPA population models, the number of hunter days was for the Upper Green River working group (which is effectively equivalent to the PPA). Hunting effort was used instead of hunting harvest because the population dynamic models estimated the effect of hunting on the inter-annual survival rate (harvest is a function of both the survival rate and the abundance). Hunting effort was scaled by the number of leks to account for the variation in the size of the working groups.

Climate Large-scale climate indices often outperform local, temperature and precipitation 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, is potentially the most important climatic process influencing the sagebrush biome (Neilson et al., 2005). Consequently, the mean annual PDO index (Trenberth and Hurrell, 1994; Mantua et al., 1997) was chosen as the climatic metric (Fig. 6). 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). In Wyoming, a positive PDO correlates with cooler, wetter weather, while a negative phase tends to produce warmer, drier conditions (McCabe et al., 2004).

Statistical Analysis

Local Models The relationship between the local (within 6.44 km) areal disturbance and individual lek counts was estimated using a generalized linear mixed model (Bolker et al., 2009). As preliminary analysis indicated that the lek counts were overdispersed, the generalized linear mixed model (GLMM) utilized a gamma-Poisson distribution (Ntzoufras, 2009) of the form

$$\log(\lambda_{l,y}) = \text{Poisson}(\lambda_{l,y} \cdot \gamma_{i,l,y}) \tag{2}$$

$$\log(\gamma_{i,l,y}) = \text{Gamma}(\sigma_\gamma^{-2}, \sigma_\gamma^{-2}) \tag{3}$$

where the gamma distribution is parameterised in terms of its shape and rate.

The linear predictor for the PPA local lek count model was

$$\log(\lambda_{l,y}) = \beta_0 + \beta_\theta \cdot \theta_{l,y} + \alpha_{1\,y} + \alpha_{2\,l} + \alpha_{3\,l,y} \tag{4}$$

where $\lambda_{l,y}$ is the expected count at the lth lek in the yth year, β_0 is the intercept and β_θ is the relationship between the OAG disturbance ($\theta_{l,y}$) at the lth lek in the yth year and $\log(\lambda_{l,y})$. The remaining parameters, which were all assumed to be normally distributed, are the random effects of the yth year, the lth lek, and the lth lek in the yth year on the intercept.

In the case of the Wyoming local lek count model, counts at the same lek in the same year were averaged by taking the rounded mean prior to analysis to reduce the computational load. Consequently, the gamma-Poisson distribution included the lek within year variation which meant $\alpha_{3\,l,y}$ was dropped. In addition, the Wyoming lek count model included the random effects of the wth working group ($\alpha_{4\,w}$) and the wth working group within the yth year ($\alpha_{5\,w,y}$).

Population Models The PPA population model was a three-stage male-based dynamic model (Gurney and Nisbet, 1998). The distribution for the population density (mean number of males per lek) was a log-normal, i.e.,

$$\log(M_y) \sim \text{Normal}(\log(\mu_y), \sigma_M). \tag{5}$$

The expected males per lek (μ_y) was defined to be half the number of predicted adults per lek ($\mathscr{A}_y$) where adults were individuals of age two or older (Johnson and Rowland, 2007). The number of chicks per lek in the yth year ($\mathscr{C}_y$) was related to the number of adults per lek in the same year by the density-independent relationship

$$\mathscr{C}_y = \mathscr{A}_y \cdot \psi \tag{6}$$

with the number of yearlings per lek updated by

$$\mathscr{Y}_{y+1} = \mathscr{C}_y \cdot \phi_y \tag{7}$$

and the number of adults per lek by

$$\mathscr{A}_{y+1} = (\mathscr{Y}_y + \mathscr{A}_y) \cdot \phi_y. \tag{8}$$

Based on the 50:50 sex ratio (Atamian and Sedinger, 2010), a clutch size of four to eight eggs (Taylor et al., 2012; Blomberg et al., 2014), two clutches per season (Taylor et al., 2012) and a hatchling survival of 50% (Lyon and Anderson, 2003), ψ was fixed at three.

The survival from the yth year to the next was given by

$$\log\left(\frac{\phi_y}{1-\phi_y}\right) = \beta_0 + \beta_\Theta \cdot \Theta_y + \beta_\Omega \cdot \Omega_y + \beta_H \cdot H_y \tag{9}$$

where Θ_y is the OAG disturbance in the yth year, Ω_y is the PDO index and H_y is the number of hunter days per lek.

The population model for Wyoming was identical to the PPA population model, generalised to the working groups, i.e.

$$\log\left(\frac{\phi_{g,y}}{1-\phi_{g,y}}\right) = \beta_y + \beta_\Theta \cdot \Theta_{g,y} + \beta_\Omega \cdot \Omega_y + \beta_H \cdot H_{g,y} \tag{10}$$

Model Fitting and Adequacy The models were fit using Maximum Likelihood (Millar, 2011). Model adequacy was assessed by plotting and analysis of the standardized residuals and random effects (Zuur et al., 2010) from the full model (Burnham and Anderson, 2002). In particular, the spatial dependence in the random lek effects in the local models was assessed using correlograms while the temporal dependence in the residuals from the population models was assessed using autoregressive time series models.

Model Comparison Alternative models were compared using Akaike's Information Criterion (Burnham and Anderson, 2002) and, in the case of the population models, the proportion of the variance explained (R^2) by each model. R^2 was not calculated for the lek count models because they included multiple nested random effects. Akaike's Information Criterion (AIC) was calculated using the marginal AIC corrected for small sample size (Burnham and Anderson, 2002; Vaida and Blanchard, 2005; Greven and Kneib, 2010). The AIC differences (Δ_i) and Akaike's weights (w_i) were also calculated for each set of models (Burnham and Anderson, 2002).

Variable Importance The relative importance of the explanatory variables β_θ, β_Θ, β_Ω and β_H (Table 1) was assessed by 1) standardizing the variables to allow direct comparison of the coefficients within and between models (Schielzeth, 2010); 2) summing the Akaike's weight (w_i) of all models with the explanatory variable (Burnham and Anderson, 2002); 3) estimating the effect size with 95% confidence intervals (Bradford et al., 2005); 4) and, in the case of the population models, comparing the proportion of the variance explained by each of the models with and without the variable. The variables were standardised by subtracting the mean and dividing by the standard deviation. The total Akaike weight (w_i) for a variable is the probability that the actual Kullback-Leibler best model includes the variable, conditional on one of the models being the Kullback-Leibler best model (Burnham and Anderson, 2002). The parameter estimates, effect sizes and approximate lower and upper 95% confidence intervals (CIs) were averaged across all models weighted by the w_is (Burnham and Anderson, 2002).

Software The data manipulation, analyses and plotting were performed using R version 3.4.0 (R Core Team, 2015) and the R packages TMB (Kristensen et al., 2016) and sgpd2 (S2 Text).

RESULTS

PPA Local Models

The local areal disturbance due to well pads, roads and pipelines was an important negative predictor of the lek counts in the PPA (Fig. 7). In particular, a percent areal disturbance of 5% was associated with a decline of approximately 50%, while a 10% disturbance was associated with a decline of roughly 80% (Fig. 7). There was no support for the base model (Table 2) which meant that β_θ had an Akaike's weight of 1.00 (Table 3).

If the lek count model results are extrapolated across the PPA, then the best supported model predicts that the population of sage grouse in the PPA was approximately 30% lower in 1997 and over 45% lower in 2012 than it would have been with no OAG disturbance (Fig. 8). There was no evidence for any spatial correlation in the size of the leks. The standardised residuals, which were approximately normally distributed, displayed homogeneity of variance.

Wyoming Local Models

There was also strong support for the importance of the areal disturbance due to well pads as a predictor of lek counts across Wyoming. A percent areal disturbance of 2.5% was associated with a decline of approximately 50%, while a 5% disturbance was associated with a decline or roughly 75% (Fig. 9). Once again there was no support for the base model (Table 4) and w_i was 1.00 for β_Θ (Table 5).

The best supported local model predicted that the population-response to local OAG development varied between working groups with Bates Hole, Southwest and Wind River experiencing little disturbance and the Northeast and Upper Green River being increasingly impacted through time (Fig. 10). There was no evidence for any substantive spatial correlation in the size of the leks. The standardized residuals, with the possible exception of a negligible number of high outliers, were well-behaved.

PPA Population Models

The best-supported population dynamic model for the Pinedale Planning Area explained 77% of the variance in the population density (Table 6; Fig. 11). All the models with support included the PDO as a predictor (Table 6) which meant β_Ω had a w_i of 1.00 (Table 7). In contrast, there was little support ($w_i \leq 0.25$) for oil and gas (β_Θ) or hunting (β_H) as predictors of the inter-annual survival rate between 1997 and 2012. In fact, at best, model's without β_Ω explained just 23% of the variance (Table 6).

The estimated model averaged effect sizes indicate that an increase in the PDO of one standard deviation (from the mean of -0.2 to 0.6) was predictive of an increase in the survival (Fig. 12) of 13.8 to 25.4% (Fig. 13). In contrast, the estimated effect sizes ruled out any negative effects of an increase of one standard deviation in OAG (38 to 43%) or hunting (10 to 14.4 hunter days per lek) on the inter-annual survival rate greater than -0.3%.

There was no evidence for any temporal correlation in the standardized residuals which were approximately normally distributed with homogeneity of variance.

Wyoming Populations Model

Once again the results for Wyoming were consistent with those for the Pinedale Planning Area. The best-supported population dynamic model explained 81% of the variance in the population density (Table 8; Fig. 14), β_Ω had a w_i of 1.00 (Table 9) and there was little support ($w_i \leq 0.20$) for β_Θ or β_H. The model averaged effect sizes (not shown) ruled out any negative effects of OAG or hunting greater than -0.7% and the lower and upper bounds for the PDO were 18.1% and 24.6%.

The only temporal correlation was for the Upper Green River working group. The residuals were once again reasonably consistent with the assumptions of the model.

DISCUSSION

The results for both the Pinedale Planning Area and the state of Wyoming suggest that while the local areal disturbance was an important negative predictor of the count at individual leks between 1997 and 2012, it had little to no effect on the population abundance.

Potential Explanations There are three potential explanations for the apparent discrepancy 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-level analyses lack statistical power and the third, and ecologically most interesting explanation, is that the populations were able to compensate for the local impacts. Distinguishing between these alternatives is critical for understanding the effects of human activities on a species of concern.

Overestimation of Local Impacts Due to the fact that multiple studies (Walker et al., 2007; Doherty et al., 2010; Harju et al., 2010), including the current one, all detected a strong negative effects of OAG on local lek counts, there is little doubt that OAG development has a substantial impact on local lek counts. Therefore, the apparent discrepancy between the local impacts and the absence of an biologically important population-level response requires an alternative explanation.

Statistical Power The second explanation for the mismatch between the local impact of OAG and the apparent absence of a population-level response is that the population-level analyses lack statistical power. Although some authors perform additional 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 indicate that, if all the model assumptions hold (Greenland et al., 2016), then the analyses have sufficient power to rule out a population-level effect of any biologically meaningful size.

This key finding leaves us with two possibilites. The first, which we discuss below, is that the population models' assumptions are fundamentally violated rendering the results unreliable. The second possibility, which we discuss in the next section, is that the sage grouse populations were able to compensate for the local impacts.

The population models, which included three life-stages (chick, yearling and adult) and density independent recruitment (LaMontagne et al., 2002), are based on sage grouse life history (Atamian and Sedinger, 2010; Taylor et al., 2012; Blomberg et al., 2014; Taylor et al., 2012). For tractability, the models make various simplifying assumptions such as a 1:1 sex ratio (while the sex ratio at hatch is 1:1, by the fall it appears to be 1.5:1 (Guttery et al., 2013b)), 100% lek attendance by male adults and 100% observer efficiency, no lek attendance by male yearlings (Walsh et al., 2004; Johnson and Rowland, 2007), and identical fall to fall survival for chicks, yearlings and adults.

However, despite the simplifying assumptions, the residuals seem to contain little to no remaining signal and the best supported models explain the majority of the variance in the data. Furthermore the results are consistent with other studies that indicate climate is the primary driver of many tetraonid populations and that sage grouse are resiliant to moderate harvest (Sedinger et al., 2010). We are therefore reasonably confident that the model results are reliable with one caveat.

The population models assume that there is negligible movement of individuals among the working groups. 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). Movement among working groups is a potential issue because the resultant source-sink dynamics (Kirol et al., 2015a) may diminish the estimated population-level effects of OAG.

Ecological Compensation The third explanation for the mismatch between the local impacts of OAG and the absence of a population-level response is that the sage grouse populations compensated for local losses. Studies examining density dependence in sage grouse have concluded that sage grouse in Colorado and Nevada 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 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 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 compensation was partly due to more ecological practices.

Similar Studies Several studies have documented an effect of precipitation on sage grouse survival (Blomberg et al., 2013; Guttery et al., 2013a). However, to the best of our knowledge, prior to the release of our initial preprint in 2015, only one paper had estimated the relative importance of the effect of precipitation on sage grouse abundance. Based on male counts at 13 leks spanning 7 years, Blomberg et al. (2012) concluded that precipitation explained 75% of the variance in the annual counts. The current study estimated the equivalent value to be 77% for the PDO index in the PPA.

A more recent result was reported by Green et al. (2016) who use

> ... 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

Given the similarity with the current study, the contradictory findings on the impact of OAG on sage grouse populations warrants further comment. In particular it is important to realize that Green et al. (2016) apply their population dynamic model to individual leks. As result, they provide further confirmation of the local impacts of OAG on lek counts but their conclusions are not relevant at the population-level.

Conclusions If inter-annual movement between working groups is negligible, then the results indicate that the local impacts of the increases in OAG development in Wyoming between 1997 and 2012 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 1997 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, was the primary predictor of recent 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 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 climate on sage grouse population fluctuations, and more effectively balance conservation efforts.

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FIGURES

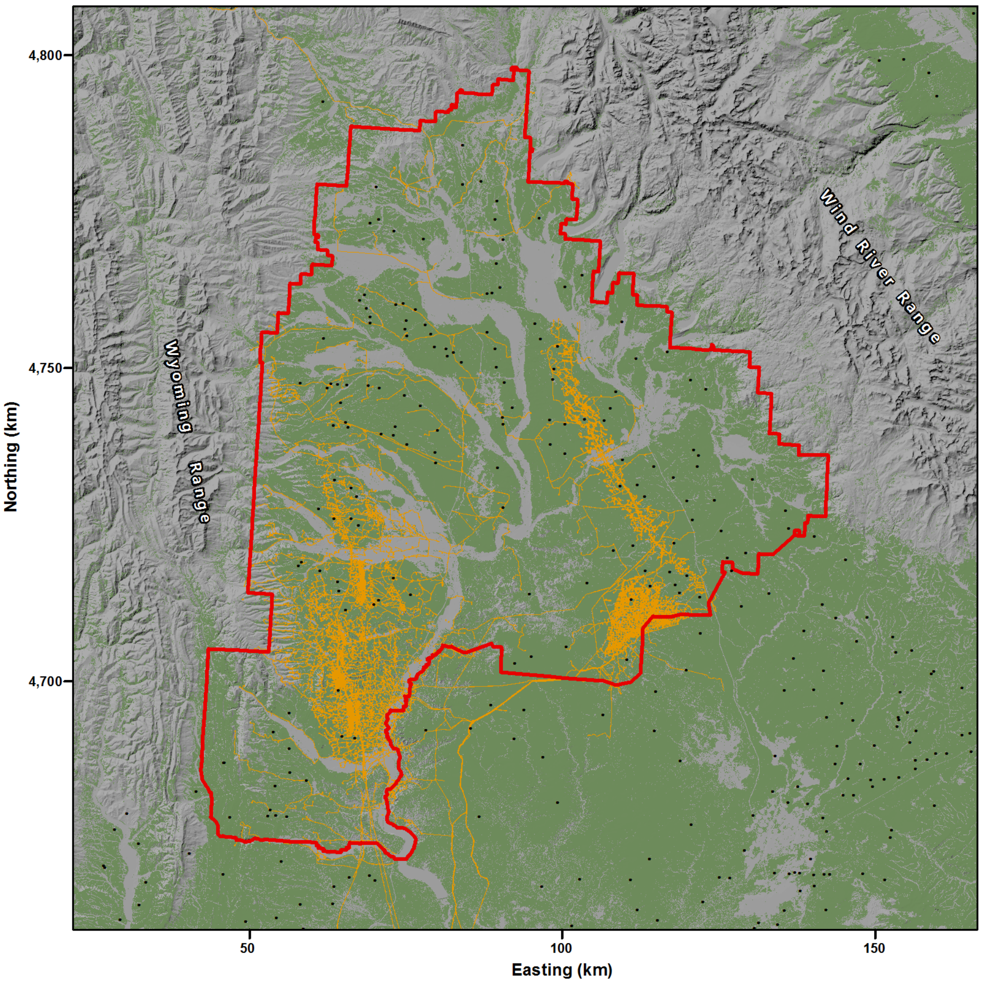

Figure 1. Map of the Pinedale Planning Area. The Pinedale Planning Area is indicated by the red polygon. Sagebrush is in green, the oil and gas development in 2012 is in orange and leks are indicated by black dots. The projection is EPSG:26913.

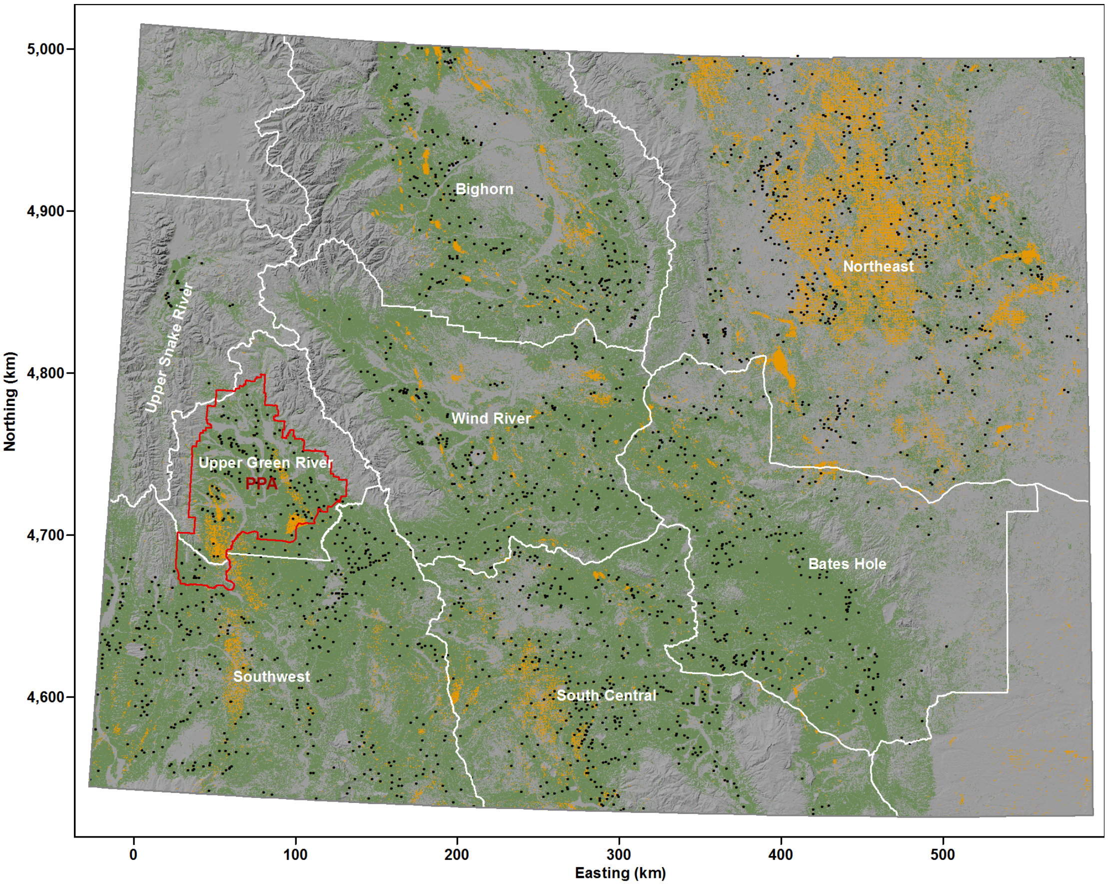

Figure 2. Map of Wyoming. The working groups are indicated by the white polygons (and the Pinedale Planning Area by the red polygon). Sagebrush is in green, the oil and gas development in 2012 is in orange and leks are indicated by black dots. The projection is EPSG:26913.

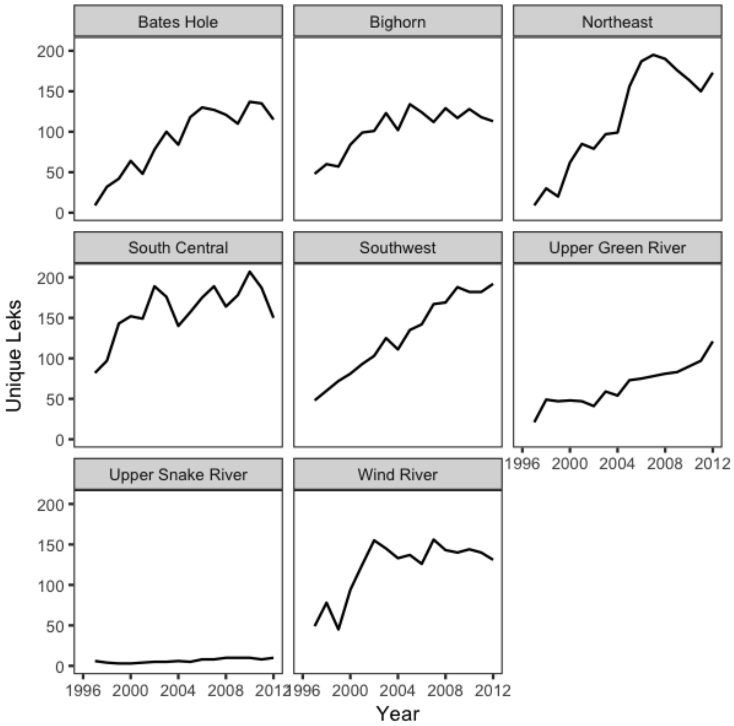

Figure 3. The number of unique leks with a reliable male count by year and working group.

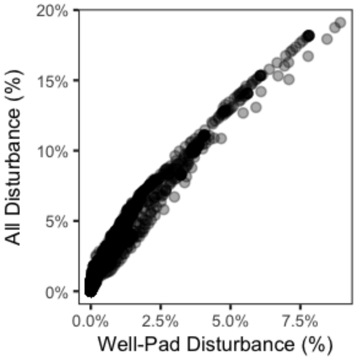

Figure 4. The proportional areal disturbance within 6.44 km due to well pads, roads and pipelines by the proportional areal disturbance within 6.44 km due to well pads only for leks in the PPA.

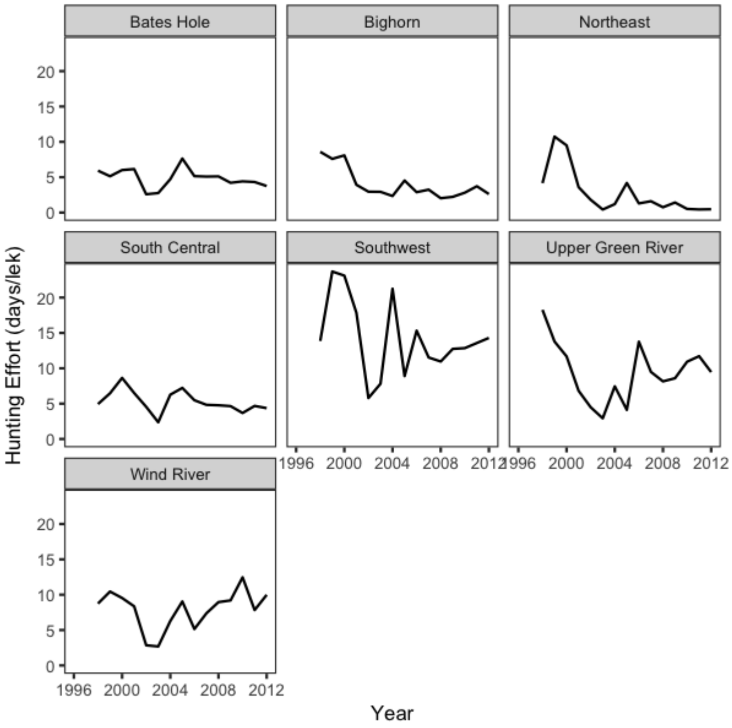

Figure 5. Hunting effort as hunter days per lek by working group and year.

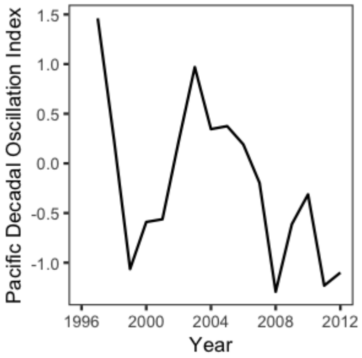

Figure 6. Pacific Decadal Oscillation Index by year. Positive values indicate a warm phase and negative values a cool phase.

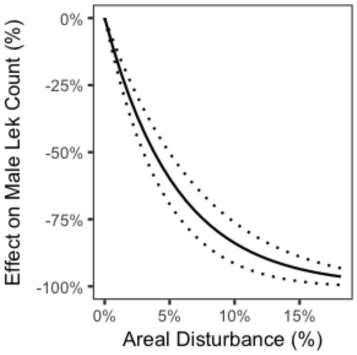

Figure 7. Estimated relationship between the count of male sage grouse at a typical lek in a typical year in the Pinedale Planning Area and the areal disturbance. The areal disturbance is the proportional areal disturbance due well pads, roads and pipelines within 6.44 km. The solid line indicates the point estimates and the dotted lines the 95% CIs.

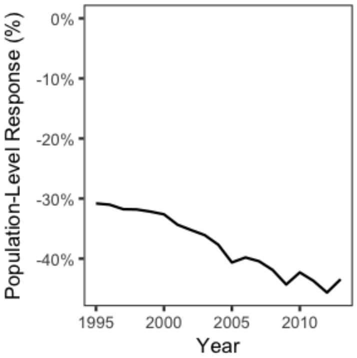

Figure 8. Predicted population-level response of sage grouse in the Pinedale Planning Area to well pads, roads and pipelines within 6.44 km of the leks by year.

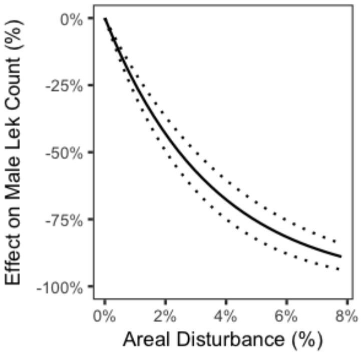

Figure 9. Estimated relationship between the count of male sage grouse at a typical Wyoming lek in a typical year and the areal disturbance. The areal disturbance is the proportional areal disturbance due to well pads within 6.44 km. The solid line indicates the point estimates and the dotted lines the 95% CIs.

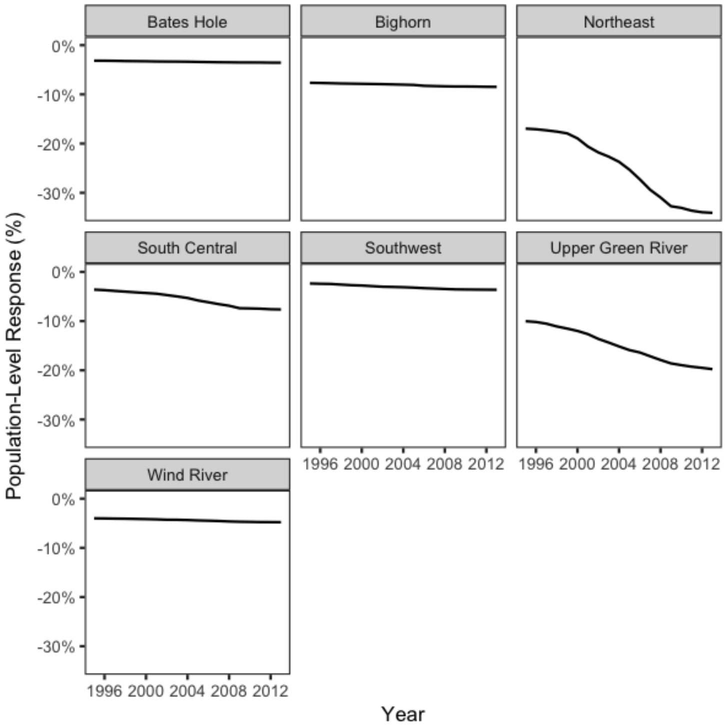

Figure 10. Predicted population-level response of sage grouse in Wyoming to well pads within 6.44 km of the leks by working group and year.

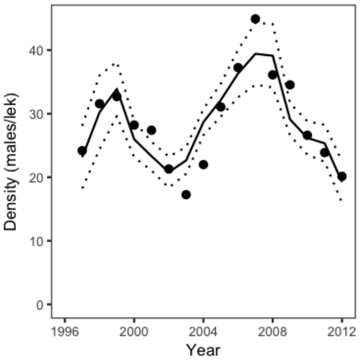

Figure 11. Estimated density of sage grouse in the Pinedale Planning Area by year. The points are the densities from the Pinedale Planning Area lek count model. The solid line is the fit from the Pinedale Planning Area population model.

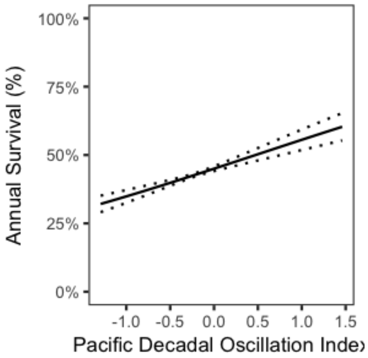

Figure 12. Estimated relationship between annual survival and the Pacific Decadal Oscillation Index for sage grouse in the Pinedale Planning Area. The solid line indicates the point estimates and the dotted lines the 95% CIs.

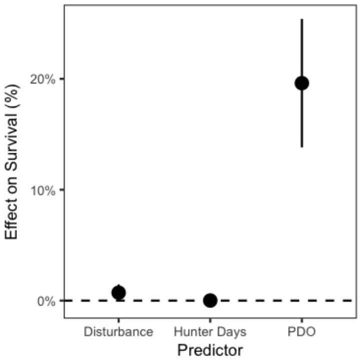

Figure 13. Estimated effect of disturbance, hunting effort and the Pacific Decadal Oscillation Index on annual survival in the Pinedale Planning Area. The points indicate the model averaged estimates of the change in survival for an increase in each variable of one standard deviation. The lines the 95% CIs.

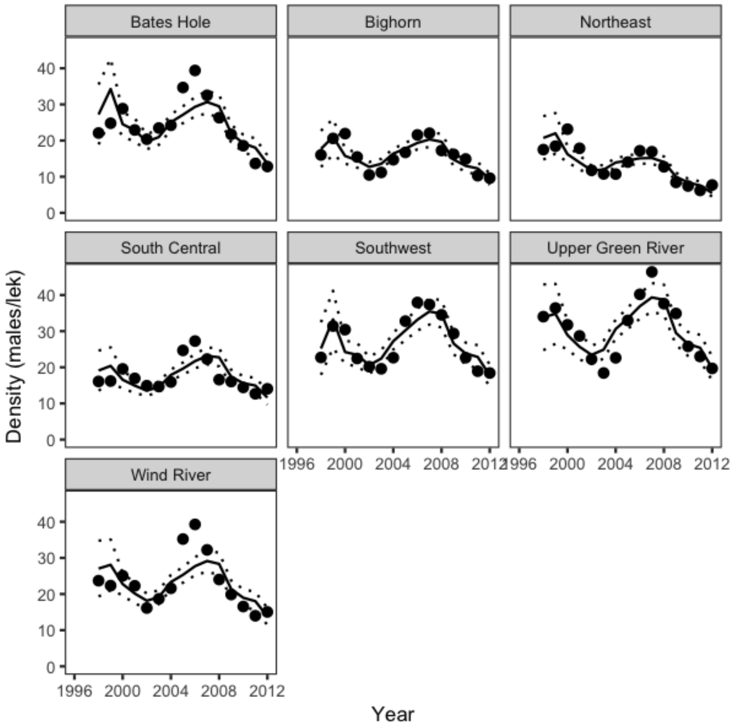

Figure 14. Estimated density of male sage grouse in Wyoming by working group and year. The points are the densities from the Wyoming lek count model. The solid line is the fit from the Pinedale Planning Area population model.

TABLES

Parameter	Description
θ	The local disturbance due to oil and gas.
Θ	The standardised population-level disturbance due to oil and gas.
Ω	The standardised Pacific Decadal Oscillation Index.
H	The standardised number of hunter days per lek.
$\log(\lambda)$	The expected log lek count.
β_θ	The relationship between θ and $\log(\lambda)$.
$\log(\phi/(1-\phi))$	The expected logistic inter-annual survival rate.
β_Θ	The relationship between Θ and $\log(\phi/(1-\phi))$.
β_Ω	The relationship between Ω and $\log(\phi/(1-\phi))$.
β_H	The relationship between H and $\log(\phi/(1-\phi))$.

Table 1. Descriptions of key model parameters.

Model	K	AIC_c	Δ_i	w_i
β_θ	6	43007.6	0.0	1.00
$\varnothing$	5	43069.3	61.7	0.00

Table 2. Pinedale Planning Area lek count model values. K is the number of fixed parameters, AIC is the Akaike's Information Criterion, Δ_i is the AIC difference and w_i is the Akaike's weight. The base model is indicated by $\varnothing$

Variable	Estimate	Lower	Upper	nmodels	w_i
β_θ	-0.49	-0.62	-0.37	2	1.00

Table 3. Pinedale Planning Area lek count parameter values. Estimate is the model-averaged estimate, Lower and Upper are the model-averaged approximate 95% lower and upper confidence limits and w_i is the Akaike's weight.

Model	K	AIC_c	Δ_i	w_i
β_θ	7	93305.2	0.0	1.00
$\varnothing$	6	93400.8	95.6	0.00

Table 4. Wyoming lek count model values. K is the number of fixed parameters, AIC is the Akaike's Information Criterion, Δ_i is the AIC difference and w_i is the Akaike's weight. The base model is indicated by $\varnothing$

Variable	Estimate	Lower	Upper	nmodels	w_i
β_θ	-0.20	-0.24	-0.16	2	1.00

Table 5. Wyoming lek count parameter values. Estimate is the model-averaged estimate, Lower and Upper are the model-averaged approximate 95% lower and upper confidence limits and w_i is the Akaike's weight.

Model	K	AIC_c	Δ_i	w_i	R^2
$\varnothing + \beta_\Omega$	5	-4.3	0.0	0.70	0.77
$\varnothing + \beta_\Theta + \beta_\Omega$	6	-2.1	2.1	0.24	0.80
$\varnothing + \beta_H + \beta_\Omega$	6	1.0	5.3	0.05	0.77
$\beta_\Theta + \beta_H + \beta_\Omega$	7	3.5	7.8	0.01	0.79
$\varnothing$	4	12.2	16.5	0.00	0.02
$\varnothing + \beta_H$	5	14.1	18.4	0.00	0.15
$\varnothing + \beta_\Theta$	5	16.3	20.6	0.00	0.05
$\varnothing + \beta_\Theta + \beta_H$	6	18.4	22.7	0.00	0.23

Table 6. Pinedale Planning Area population model values. K is the number of fixed parameters, AIC is the Akaike's Information Criterion, Δ_i is the AIC difference, w_i is the Akaike's weight and R^2 is the proportion of the variance explained by the model. The base model is indicated by $\varnothing$

Variable	Estimate	Lower	Upper	nmodels	w_i
β_Ω	0.34	0.24	0.44	8	1.00
β_Θ	0.01	-0.00	0.03	8	0.25
β_H	0.00	-0.01	0.01	8	0.06

Table 7. Pinedale Planning Area population parameter values. Estimate is the model-averaged estimate, Lower and Upper are the model-averaged approximate 95% lower and upper confidence limits and w_i is the Akaike's weight.

Model	K	AIC_c	Δ_i	w_i	R^2
$\varnothing + \beta_\Omega$	23	-27.3	0.0	0.68	0.81
$\varnothing + \beta_H + \beta_\Omega$	24	-24.4	2.9	0.16	0.81
$\varnothing + \beta_\Theta + \beta_\Omega$	24	-24.0	3.3	0.13	0.81
$\beta_\Theta + \beta_H + \beta_\Omega$	25	-21.5	5.8	0.04	0.81
$\varnothing + \beta_\Theta + \beta_H$	24	59.0	86.3	0.00	0.55
$\varnothing + \beta_H$	23	64.0	91.4	0.00	0.53
$\varnothing + \beta_\Theta$	23	64.1	91.4	0.00	0.52
$\varnothing$	22	64.4	91.7	0.00	0.51

Table 8. Wyoming population model values. K is the number of fixed parameters, AIC is the Akaike's Information Criterion, Δ_i is the AIC difference, w_i is the Akaike's weight and R^2 is the proportion of the variance explained by the model. The base model is indicated by $\varnothing$

Variable	Estimate	Lower	Upper	nmodels	w_i
β_{Ω}	0.37	0.31	0.43	8	1.00
β_H	0.00	-0.01	0.02	8	0.20
β_{Θ}	0.00	-0.01	0.02	8	0.17

Table 9. Wyoming population parameter values. Estimate is the model-averaged estimate, Lower and Upper are the model-averaged approximate 95% lower and upper confidence limits and w_i is the Akaike's weight.