Recent Greater Sage Grouse (*Centrocercus urophasianus*) Population Dynamics in Wyoming Are Primarily Driven by Climate, not Oil and Gas Development

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Abstract

Effective conservation of a species requires an understanding of how human activities influence population abundance. The greater sage grouse (*Centrocercus urophasianus*) is a large tetraonid that is endemic to the sagebrush (*Artemisia* spp) habitat of western North America. A host of studies have documented the local effects of oil and gas development on greater sage grouse densities, movement, stress-levels and fitness components. However, to the best of our knowledge no one has tested whether greater sage grouse population level responses to oil and gas are consistent with the outcomes predicted by extrapolation of the results of the local studies. To test whether oil and gas results in a population-level response, hierarchical Bayesian state-space models were fitted to lek count data from Wyoming from the mid 1990s to 2012. The models indicate that climate, as indexed by the Pacific Decadal Oscillation, is the primary driver of sage grouse population dynamics across the state, explaining between 63% and 77% of the variance. Oil and gas development was not a significant driver, explaining 3% or less of the variance. Large-scale, open, collaborative, reproducible research is needed to ensure future decisions regarding oil and gas development have the intended consequences for sage grouse populations.

Introduction

Effective conservation of a species requires an understanding of how alternative human activities influence population 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, most conservation-based ecological studies attempt to infer the population-level consequences

of anthropogenic alterations from local gradients [1] in density [2], movement, habitat use, physiology, genetics, reproductive success or survival. Nonetheless, human development sometimes provides so-called "natural" experiments which can, with certain caveats, be used to test the population-level predictions of local inferences.

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 [3]. 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% [4]. In addition, mean peak counts of males on leks, which are commonly used as a population density metric [5–7], indicate long-term average declines of 33% in the remaining populations [5].

A host 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-documented phenomenon is the decline in lek counts with increasing densities of well pads [6, 8, 9]. More recently, experimental studies have suggested that noise alone can cause reduced lek attendance [10] and increased stress hormones in exposed individuals [11]. Lyon and Anderson [12] 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 [13]. 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 [14].

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 [15]. 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% [16]. 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 [6]. However, to the best of our knowledge no-one has tested whether sage grouse population level responses to OAG are consistent with the outcomes predicted by extrapolation of the results of 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 [17]. Studies on the influence of climate on the population dynamics of other tetraonid species have an illustrious past [18, 19] and climate has been used to explain regional and inter-decadal population synchrony in multiple tetraonid species with overlapping ranges [20, 21]. Consequently, the current study also considers regional

climate as a driver of sage grouse population dynamics.

Wyoming and the Pinedale Planning Area (PPA) provide "natural" experiments for testing a population-level response. Wyoming contains approximately 37% of the range-wide population of sage grouse [15, 22] and is home to substantial levels of OAG development dating to at least 1883 [23]. The PPA which is largely equivalent to the Upper Green River working group in Wyoming, was the site of several of the key local studies [12, 13]. Development of oil and gas fields in the PPA began with the first well drilled in the La Barge field in 1912. While production began there in 1924 and increased during World War II, intense development of the La Barge field took off during the 1960s, and subsequently at Jonah and Pinedale Anticline fields in the 1990s and early 2000s (S1 Video).

To test whether the local effects of OAG result in a population-level response in sage grouse, three separate analyses were performed. The first was a hierarchical analysis of the local effect of well pads, roads, and pipelines on male sage grouse lek counts in the PPA. Its primary purpose was to confirm the findings of previous studies and to provide a metric of the regional impact of OAG. The second analysis involved the fitting of a state-space model [24, 25] to test whether sage grouse population dynamics in the PPA were primarily driven by the regional OAG metric and/or climatic variation. The third, and final, analysis extended the state-space model across Wyoming to test whether the results from the PPA were corroborated.

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 all well pads were mapped statewide (Fig. 2, S1 Text). The PPA was divided into seven blocks to account for spatial autocorrelation among lek counts (Fig. 1).

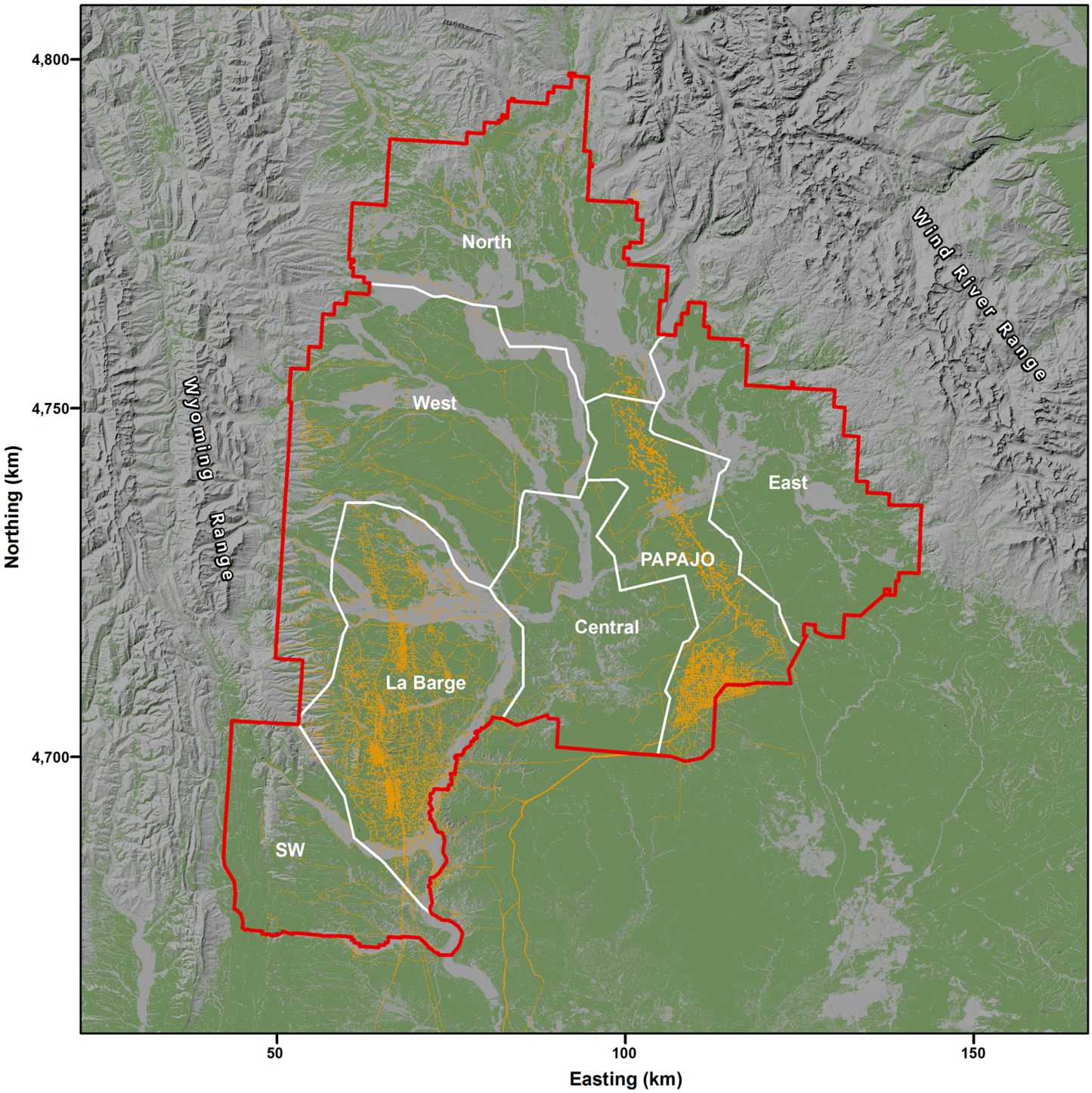

Figure 1: Map of the Pinedale Planning Area. The Pinedale Planning Area is indicated by the red polygon and the seven blocks by the white polygons. Sagebrush is in green and the oil and gas development in 2012 in orange. Lek locations are not shown. The projection is EPSG:26913.

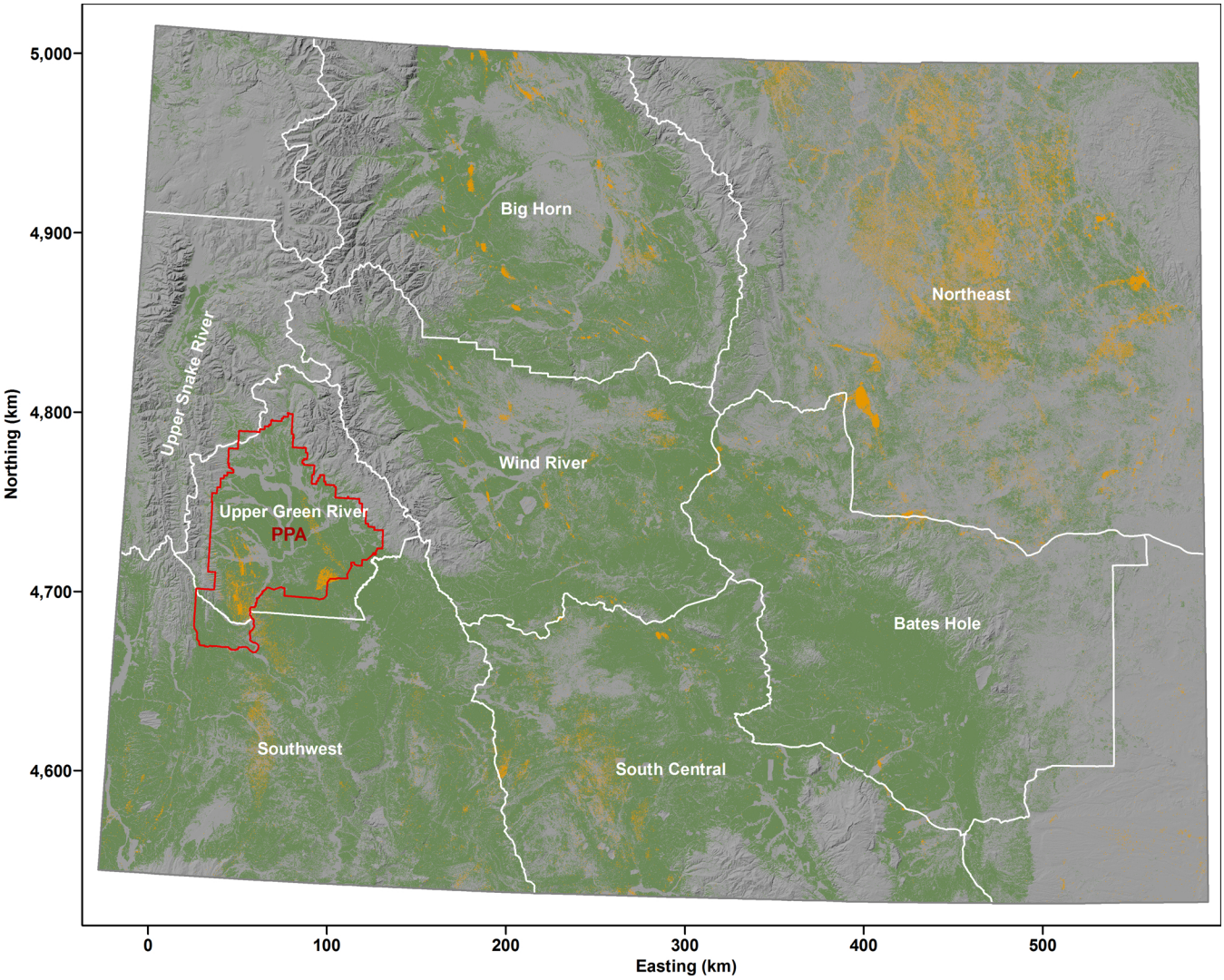

Figure 2: Map of Wyoming. The working groups are indicated by the white polygons (and the Pinedale Planning Area by the red polygon). Sagebrush is in green and the oil and gas development in 2012 in orange. Lek locations are not shown. The projection is EPSG:26913.

Lek Counts The sage grouse lek count data were provided by the State of Wyoming. To ensure the analyses were based on the most reliable data, only checked ground counts that were collected between April 1st and May 7th as part of a survey or count were included in the analysis. For the same reason, counts for which the number of individuals of unknown sex were $\geq 5\%$ of the number of males, were also excluded.

PPA Lek Counts Reliable counts were available in at least one year for 136 of the 152 documented leks from the PPA (Fig. 3). The local disturbance due to OAG development was calculated for each calendar year in terms of the proportional areal disturbance due to well pads, roads, and pipelines within a 6.44 km radius [26] of each lek (Fig. 3).

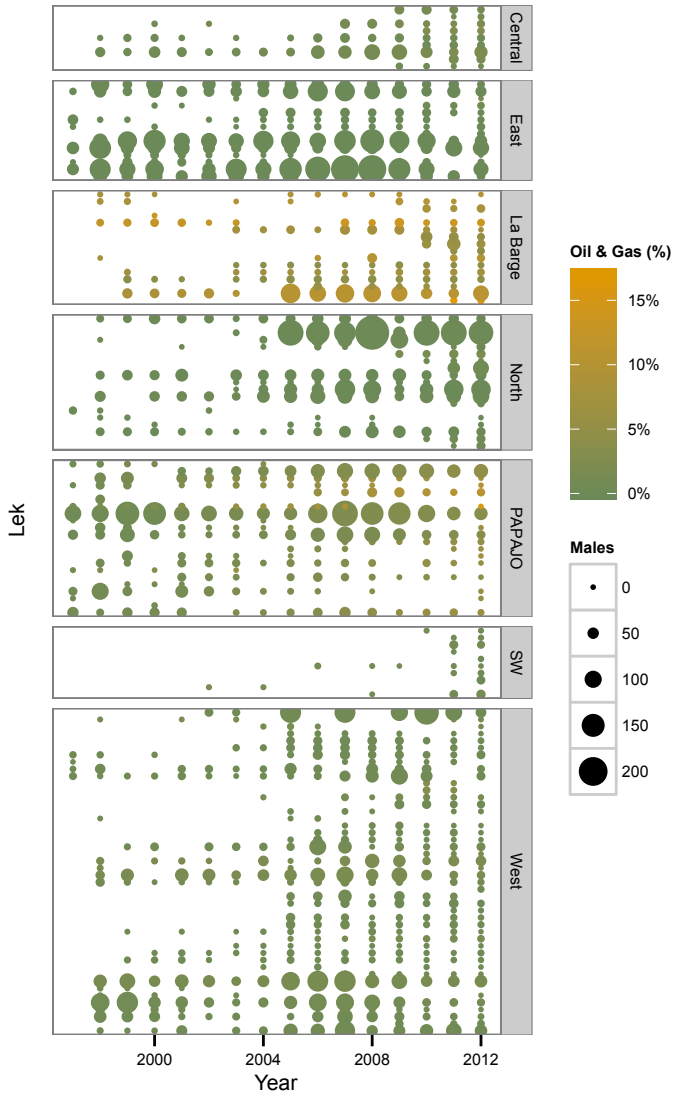

Figure 3: Mean lek counts of male sage grouse by lek, block, year and oil and gas disturbance for the Pinedale Planning Area. The number of males is indicated by the radius of the points, and the percentage areal oil and gas disturbance within 6.44 km is indicated by the color. Only leks with at least one reliable count are shown.

PPA Population The population density in the PPA was assumed to be the mean lek count predicted by the PPA lek count model. The disturbance due to OAG development was the unlagged percent population-level impact as predicted by the lek count model (which can be thought of as the mean areal disturbance within 6.44 km of each lek weighted by its size and the relationship between areal disturbance and lek attendance).

Wyoming Populations For the purpose of estimating the dynamics of sage grouse populations across Wyoming, working groups were considered to be separate populations. The population density in each working group was assumed to be the estimated mean average number of males per lek, where lek counts were excluded based on the same criteria as for the PPA. Population density estimates were only considered to be reliable if ten or more leks were

counted in a given year.

The regional disturbance due to OAG development in each working group was calculated for each calendar year in terms of the proportional areal disturbance due to well pads within a 6.44 km buffer of all known leks. The habitat quality of each working group was the proportion of the buffer that was sagebrush where well pads were replaced with the pre-settlement sagebrush layer (S1 Text).

The State of Wyoming also provided annual data on hunter days and the numbers of chick wings in hunter-harvested wing counts [27] by working group. Preliminary analyses indicated that hunter days per unit area of sage grouse habitat was not a significant predictor of survival and that inclusion of the chick proportions did not improve the model's explanatory power.

Climatic Data Following preliminary analyses in which regional temperature and precipitation time series were considered, the mean annual Pacific Decadal Oscillation (PDO) index [28] was chosen as the metric of regional climatic variation (Fig. 4). The PDO index is derived from the large-scale spatial pattern of sea surface temperature in the North Pacific Ocean. When the PDO index is in the warm (positive) phase, the eastern portion of the North Pacific Ocean is warmer than the west-central portion, while the opposite is the case for the cool (negative) phase.

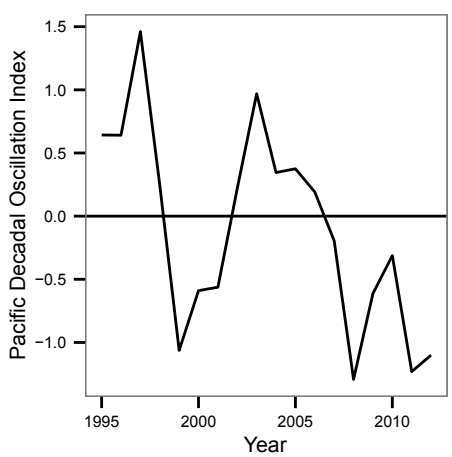

Figure 4: Pacific Decadal Oscillation Index by year. Positive values indicate a warm phase and negative values a cool phase.

Statistical Analysis

Model Definitions The effect on individual lek counts of the local (within 6.44 km) areal disturbance due to well pads, roads, and pipelines was estimated using a generalized linear mixed model [29]. As preliminary analysis indicated that the lek counts were overdispersed, the model used a gamma-Poisson distribution [30] of the form

$$C_{i,l,b,y} \sim \text{Poisson}(\lambda_{l,b,y} * \gamma_{i,l,b,y}) \tag{1}$$

$$\gamma_{i,l,b,y} \sim \text{gamma}(\sigma_\gamma^{-2}, \sigma_\gamma^{-2}) \tag{2}$$

where $C_{i,l,b,y}$ is the ith count for the lth lek from the bth block in the yth year and σ_γ is the standard deviation of the corresponding overdispersion terms. The linear predictor (with the canonical log link function) was

$$\log(\lambda_{l,b,y}) = \beta_{\lambda 0_y} + \beta_{\lambda\Theta} * \Theta_y + \beta_{\lambda 1_l} + \beta_{\lambda 2_{l,y}} + \beta_{\lambda 3_{b,y}} \tag{3}$$

where $\beta_{\lambda 0_y}$ is the intercept for each year and $\beta_{\lambda\Theta}$ is the effect of the OAG disturbance (Θ_y) on the expected lek count. The remaining parameters are the random categorical effects of the lth lek, the lth lek in the yth year, and the bth block in the yth year. The standard deviations of the random effects, which were all bias-corrected (log-)normal distributions, i.e., with an expectation of $-\sigma^2/2$ [25], were $\sigma_{\lambda 1}$ to $\sigma_{\lambda 3}$, respectively. The lek counts were lagged by one year [6, 8, 9, 31].

The PPA population dynamic model was a three-stage male-based state-space model [24, 25, 32] in which the observational distribution for the mean number of males per lek in the yth year (M_y) was a bias-corrected log-normal [25]

$$M_y \sim \text{lognormal}(\log(\mu_y) - \sigma_M^2/2, \sigma_M^2). \tag{4}$$

The expected males per lek (μ_y) was in turn defined to be half the number of predicted adults per lek ($\mathcal{A}_y$) where adults were individuals of age two or older [33]. The number of chicks per lek in the yth year ($\mathcal{C}_y$) was related to the number of adults per lek in the same year by the density-independent relationship

$$\mathcal{C}_y = \mathcal{A}_y * \psi \tag{5}$$

with the number of yearlings per lek updated by

$$\mathcal{Y}_{y+1} = \mathcal{C}_y * \phi_y \tag{6}$$

and the number of adults per lek by

$$\mathcal{A}_{y+1} = (\mathcal{Y}_y + \mathcal{A}_y) * \phi_y. \tag{7}$$

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

$$\log\left(\frac{\phi_y}{1-\phi_y}\right) = \beta_{\phi 0} + \beta_{\phi\Theta} * \Theta_y + \beta_{\phi\Omega} * \Omega_y \tag{8}$$

where Θ_y is the OAG disturbance in the yth year and Ω_y is the PDO index.

The population dynamics model for Wyoming was identical to the PPA population model, generalised to the

working groups with one exception. The inter-annual survival was

$$\log\left(\frac{\phi_{g,y}}{1-\phi_{g,y}}\right) = \beta_{\phi 0} + \beta_{\phi\Theta} * \Theta_{g,y} + \beta_{\phi\Omega} * \Omega_y + \beta_{\phi\Upsilon} * \Upsilon_g \tag{9}$$

where Υ_g is the habitat quality at the gth working group.

Parameter Estimation The parameters were estimated using Bayesian methods [24, 29]. With the exception of the number of chicks per adult (ψ), vague (low information) prior distributions were used [24]. The vagueness of the priors was confirmed by ensuring they did not constrain the posterior distributions [24]. Based on a 50:50 sex ratio [34], a clutch size of four to eight eggs [35, 36], two clutches per season [35], and a hatchling survival of 50 % [12], the prior distribution for ψ was a uniform$(2, 4)$ for both population models.

The posterior distributions of the parameters were estimated using a Monte Carlo Markov Chain (MCMC) algorithm. To guard against non-convergence of the MCMC process, five chains were run, starting at randomly selected initial values. Each chain was run for a minimum of 100,000 iterations with the first half of the chain discarded for burn-in followed by further thinning to leave at least 2,000 samples from each chain. Convergence was confirmed by by ensuring the Brooks-Gelman-Rubin convergence diagnostic $\hat{R} \leq 1.05$ for each of the parameters in the model [24, 37].

The posterior distributions are summarized in terms of a point *estimate* (mean), *lower* and *upper* 95% credible limits (2.5 and 97.5% quantiles [38]), the standard deviation (*SD*), percent relative *error* (half the 95% credible interval [CRI] as a percent of the point estimate) and statistical *significance* (Bayesian equivalent of a two-sided p-value [24, 39, 40]).

Model Evaluation Model selection was achieved by dropping fixed variables with two-sided p-values ≥ 0.05 [24, 39, 40]. Model adequacy was confirmed by examination of plots of standardised residuals or plots of predictions with observed values. Model fit was quantified in terms of the coefficient of determination (R^2). The contribution of particular predictor variables to the model fit was determined by refitting the model with the variable set to zero in the input data.

The results are displayed graphically by plotting the modeled relationship between a particular variable and the response with the remaining variables held constant. The areal disturbance and PDO index are held constant at 0% and the habitat quality at 75%. Random variables are held constant at their typical values (expected arithmetic means of the underlying hyper-distributions [24]). Where informative, the influence of particular variables is plotted in terms of the effect size (i.e., percent change in the response variable) with 95% CRIs [41].

Replicability The analyses were performed using R version 3.2.2 [42], JAGS 3.4.0 [43] and the sglekwy and sgpd R packages (S1 Software).

Results

PPA Lek Counts

The parameter estimates table for the PPA lek count model (Table 1) indicates that, consistent with previous studies [6,8,9], the effect of the local OAG areal disturbance on the lek count ($\beta_{\lambda\Theta}$) was negative and highly significant. Table 1 also indicates that the among lek variation ($\sigma_{\lambda 1}$) was greater than the among lek within year variation ($\sigma_{\lambda 2}$) which was in turn greater than the among block within year variation ($\sigma_{\lambda 3}$). In addition, the point estimate for the gamma distributed overdispersion term (σ_{γ}) indicates that the residual variance about the expected count (λ) was approximately $\lambda + (\lambda * 0.5)^2$.

Table 1: **Key fixed parameter estimates for the Pinedale Planning Area lek count model.** $\beta_{\lambda\Theta}$ is the effect of OAG disturbance, σ_{γ} is the SD of the overdispersion, $\sigma_{\lambda 1}$ is the SD of the effect of lek, $\sigma_{\lambda 2}$ is the SD of the effect of lek within year and $\sigma_{\lambda 3}$ is the SD of the effect of block. The columns are the *parameter* name, the point *estimate*, the *lower* and *upper* 95% credible intervals, the standard deviation (*SD*), the percent relative *error*, and the statistical *significance*.

Parameter	Estimate	Lower	Upper	SD	Error	Significance
$\beta_{\lambda\Theta}$	-0.3990	-0.5301	-0.2701	0.0662	33	0.000
σ_{γ}	0.5018	0.4803	0.5238	0.0112	4	0.000
$\sigma_{\lambda 1}$	0.9923	0.8612	1.1435	0.0721	14	0.000
$\sigma_{\lambda 2}$	0.4365	0.3933	0.4788	0.0221	10	0.000
$\sigma_{\lambda 3}$	0.1749	0.1105	0.2463	0.0345	39	0.000

When plotted in terms of the effect on the expected count, the results indicate that a percent areal disturbance within 6.44 km of a lek of 5% was associated with a 50% decline, while a 10% disturbance was associated with a 75% decline, and a 15% disturbance with a 90% decline (Fig. 5). If the lek count model results are extrapolated across the PPA then the model predicts that the population of sage grouse in the PPA was 22% lower in 1997 and 33% lower in 2012 than it would have been with no areal disturbance from OAG (Fig. 6).

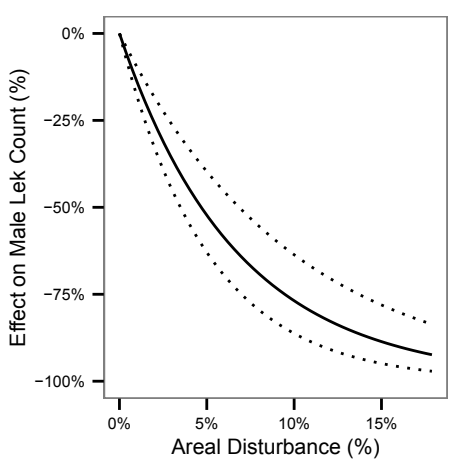

Figure 5: Estimated change in the count of male sage grouse at a typical lek in the Pinedale Planning Area by areal disturbance. The areal disturbance is the proportional areal disturbance due to OAG development within 6.44 km. The solid line indicates the point estimate and the dotted lines the 95% CRIs.

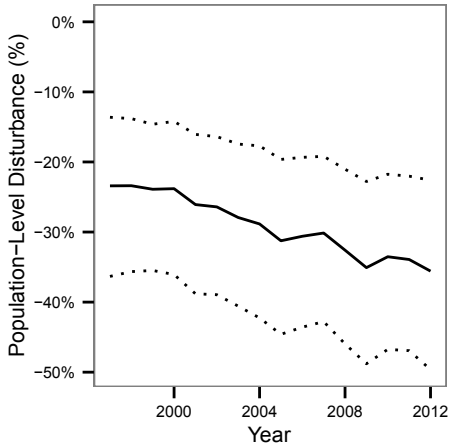

Figure 6: Estimated population-level impact to sage grouse in the Pinedale Planning Area due to oil and gas by year. The solid line indicates the point estimate and the dotted lines 95% CRIs.

The lek count model estimated that the mean number of males per lek, which provides a metric of population density, peaked in 1999 and 2007 (Fig. 7). For comparison, the lek count model predictions are plotted with the mean average counts.

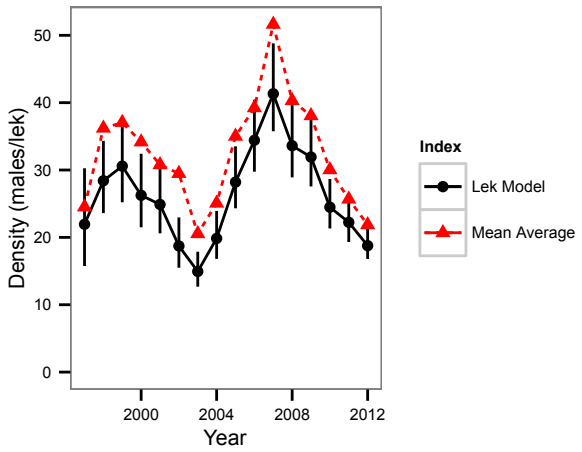

Figure 7: Density of male sage grouse in the Pinedale Planning Area by year. The lek model values are the expected male count at a typical lek as estimated by the lek count model with 95% CRIs. The mean average values are the calculated mean average male lek counts.

PPA Population

The parameter estimates table for the PPA population state-space model (Table 2) indicates that the regional OAG disturbance ($\beta_{\phi\Theta}$) was not a significant ($p > 0.05$) predictor of the population-level inter-annual survival (ϕ). In contrast, the PDO index ($\beta_{\phi\Omega}$) was a highly significant positive predictor (Fig. 8).

Table 2: **Key fixed parameter estimates for the Pinedale Planning Area population model.** $\beta_{\phi 0}$ is the intercept for the annual survival, $\beta_{\phi\Theta}$ is the effect of OAG on the annual survival, $\beta_{\phi\Omega}$ is the effect of the PDO on the annual survival, ψ is the number of chicks per adult and σ_M is the residual variation in the population density metric. The columns are the *parameter* name, the point *estimate*, the *lower* and *upper* 95% credible intervals, the standard deviation (*SD*), the percent relative *error*, and the statistical *significance*.

Parameter	Estimate	Lower	Upper	SD	Error	Significance
$\beta_{\phi 0}$	-0.5223	-1.0127	-0.0233	0.2473	95	0.039
$\beta_{\phi\Theta}$	1.217	-0.323	2.921	0.800	130	0.112
$\beta_{\phi\Omega}$	0.4766	0.2908	0.6686	0.0948	40	0.000
ψ	2.979	2.046	3.943	0.574	32	0.000
σ_M	0.1661	0.1084	0.2660	0.0408	47	0.000

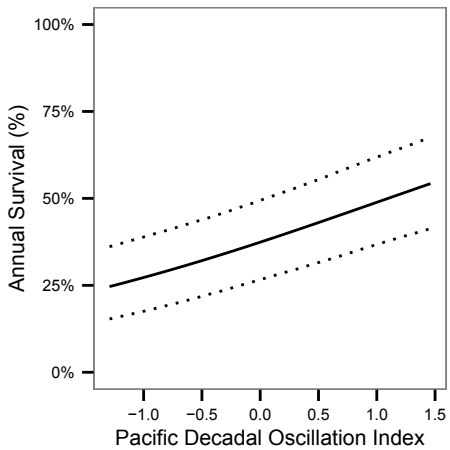

Figure 8: Estimated relationship between annual survival and the Pacific Decadal Oscillation Index for sage grouse in the Pinedale Planning Area. The solid line is the relationship as estimated by the Pinedale single population model and the dotted lines are 95% CRIs.

The PPA population model explained 80% of the variance in the sage grouse density metric (Table 3, Fig. 9). When the regional OAG metric was eliminated, the model still explained 77% of the variance in population density. In contrast, when the PDO index was eliminated, the model explained 1% of the variance (Table 3). The null model without OAG and the PDO index had a negative R^2 value because it was a worse fit than a straight line.

Table 3: **Proportion of the variance in the density of sage grouse explained by variables in the Pinedale Planning Area population model.** OAG is the areal disturbance due to oil and gas and PDO is the Pacific Decadal Oscillation Index. *Model* indicates the included variables and R^2 the proportion of the variance explained. The null model excludes both variables.

Model	R^2
OAG + PDO	80
PDO	77
OAG	1
Null	-1

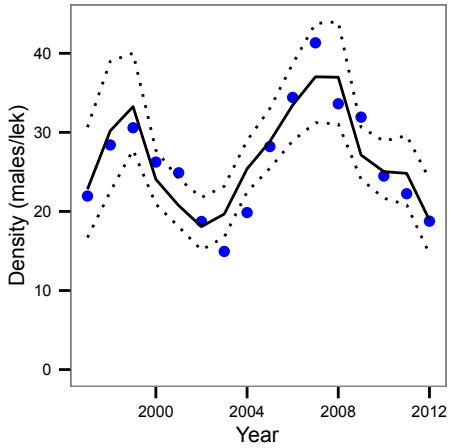

Figure 9: Density of sage grouse in the Pinedale Planning Area by year. The points are the densities from the lek count model. The solid line is the density as estimated by the single population model with 95% CRIs as dotted lines.

Wyoming Populations

The state-wide metric of OAG disturbance indicates that habitat losses due to well pads are greatest in the Upper Green River, which roughly corresponds to the PPA, and the Northeast (Fig. 10).

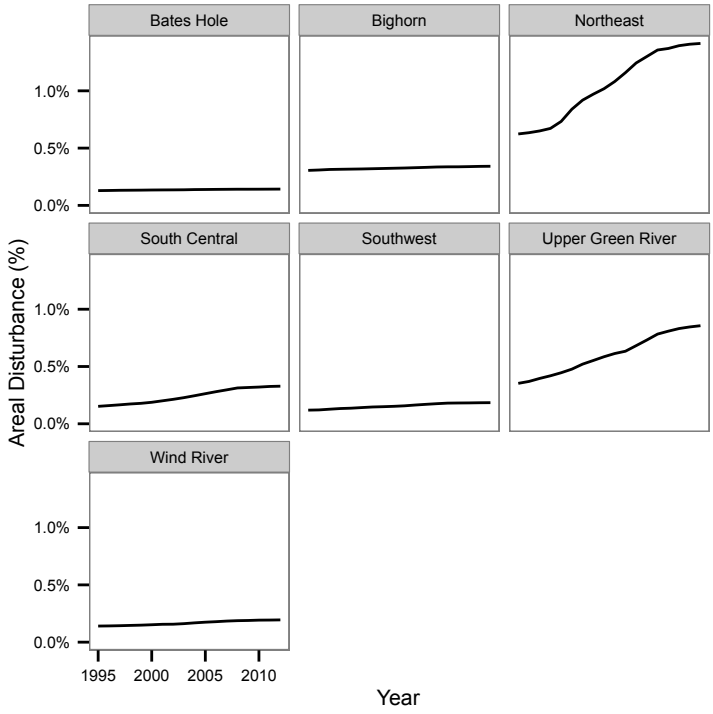

Figure 10: Areal disturbance due to oil and gas development by working group and year. The areal disturbance is the proportional areal disturbance to sage grouse habitat by well pads.

The Wyoming populations model produced very similar results to the PPA population model (Table 4). OAG

disturbance (in this case proportional areal disturbance to sage grouse habitat) was not a significant predictor of survival ($\beta_{\phi\Theta}$) while the PDO index was once again a highly significant positive predictor ($\beta_{\phi\Omega}$; Fig. 11). The habitat qualtiy was also a significant positive predictor of survival ($\beta_{\phi\Upsilon}$).

Table 4: **Key fixed parameter estimates for the Wyoming populations model.** $\beta_{\phi 0}$ is the intercept for the annual survival, $\beta_{\phi\Upsilon}$ is the effect of habitat quality on the annual survival, $\beta_{\phi\Theta}$ is the effect of OAG on the annual survival, $\beta_{\phi\Omega}$ is the effect of the PDO on the annual survival, ψ is the number of chicks per adult and σ_M is the residual variation in the population density metric. The columns are the *parameter* name, the point *estimate*, the *lower* and *upper* 95% credible intervals, the standard deviation (*SD*), the percent relative *error*, and the statistical *significance*.

Parameter	Estimate	Lower	Upper	SD	Error	Significance
$\beta_{\phi 0}$	-0.2603	-0.3942	0.0154	0.1128	79	0.068
$\beta_{\phi\Theta}$	-0.5227	-4.0698	3.0592	1.8117	680	0.772
$\beta_{\phi\Omega}$	0.4050	0.3295	0.4893	0.0405	20	0.000
$\beta_{\phi\Upsilon}$	0.01838	0.00162	0.03556	0.00871	92	0.031
ψ	3.313	2.162	3.976	0.516	27	0.000
σ_M	0.2241	0.1952	0.2580	0.0161	14	0.000

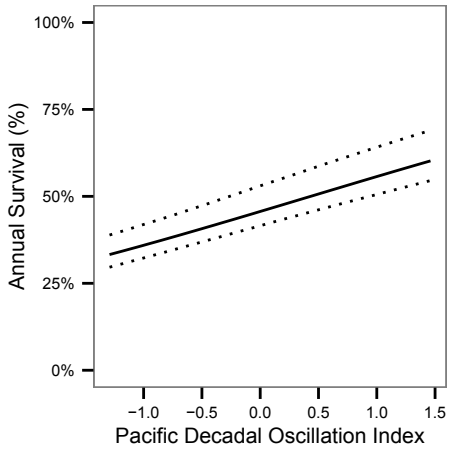

Figure 11: Estimated relationship between annual survival and the Pacific Decadal Oscillation Index for sage grouse in Wyoming. The solid line is the relationship as estimated by the multiple populations model and the dotted lines are 95% CRIs.

The Wyoming populations model also explained most of the variation in the population densities (Fig. 12). The coefficient of determination values indicate that the full model again explained 80% or more of the variance in the population density and elimination of OAG had no effect on the predictive capacity of the model (Table 5). The null model explained 48% of the variance because habitat quality is a significant predictor and each population is initiated with its own chick, yearling and adult densities. The PDO Index explained 63% of the variance not accounted for by the null model, i.e., $(81 - 48)/(100 - 48)$.

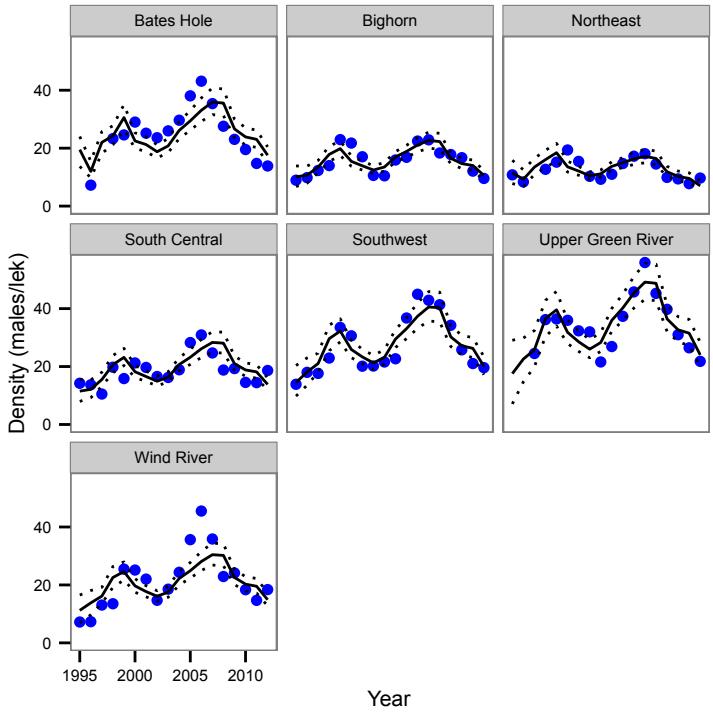

Figure 12: Density of male sage grouse by working group and year. The points are the calculated mean average lek density. The solid line is the density as estimated by the multiple populations model with 95% CRIs as dotted lines.

Table 5: **Proportion of the variance explained by variables in the Wyoming populations model.** OAG is the areal disturbance due to oil and gas and PDO is the Pacific Decadal Oscillation Index. *Model* indicates the included variables and R^2 the proportion of the variance explained. The null model excludes both variables.

Model	R^2
OAG + PDO	81
PDO	81
OAG	48
Null	48

Discussion

The Absence of a Population-Level Response

The current study replicates previous findings that lek attendance is reduced by proximity to, and density of, OAG disturbance [6, 8, 9]. When the results are extrapolated across the PPA population, they predicted that in 1997 the population density would have been 22% lower than without OAG, and that over the next decade and a half it would have declined by a further 11%. The prediction of a decline, however, is inconsistent with the population data and models and underscores the problem with extrapolating lek attendance trends in locally disturbed areas to predict trends across whole populations.

Across Wyoming, the proportional areal disturbance to sage grouse habitat due to well pads varies across an order of magnitude from 0.1% in Bates Hole to over 1.2% in the Northeast. Given the large variation in the areal disturbance due to OAG among and within working groups, it is not unreasonable to expect that the state-space models would detect an effect on the dynamics of the sage grouse populations. However, in contrast to expectations [6, 15, 16], OAG development was not a significant predictor of population dynamics and explained just 3% and 0% of the variance in the population density for the PPA population and Wyoming populations, respectively. There are at least four possible explanations for this absence of a population-level response: 1) the population models are structurally inadequate, 2) the lek counts are unreliable, 3) the OAG metrics are inaccurate, 4) the populations are not discrete, and 5) the results of the local studies are not reliable predictors of the population response. Each of these explanations is discussed in turn below.

The population models appear to be sufficiently structurally adequate to be "useful" [44]. The models, which included three life-stages (chick, yearling and adult) and density dependent recruitment [45], are based on sage grouse life history [34, 35, 35, 36]. Due to limited data, 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 [46]), 100% lek attendance by male adults, no lek attendance by male yearlings [33, 47], and identical fall to fall survival for chicks, yearlings and adults. However, despite the simplifying assumptions the models identified climate as the major driver and explained 80% or more of the variance in the population density metrics. Consequently it in reasonable to conclude that the population models are structurally adequate.

The second possible explanation is that the lek count data are unreliable. Despite concerns [33, 47] lek counts are the primary metric of sage grouse population density in most studies [5–7, 45]. To minimize the potential for biases the analysis was restricted to the most reliable lek counts. The resultant population density metrics appear to contain useful information because they exhibit patterns of temporal and spatial synchrony consistent with climate [18–21]. It is also important to note that if lek counts are not reliable indices of population density then most studies of sage grouse status are invalidated.

The third possible explanation for the insignificance of OAG as a predictor of sage grouse population dynamics is that the areal disturbance metrics do not capture the actual impacts [31]. The uncertainty arises because of the existence of multiple causal pathways by which OAG development can potentially reduce reproduction or survival [48]. For example noise [10] and predation are two mechanisms by which OAG development can reduce abundance that are not necessarily directly associated with areal disturbance. In fact, since 1996, OAG companies have increasingly adopted various mitigation and conservation measures (S2 Text). It is therefore possible that an effect was not detected because mitigation and conservation substantially reduced the population-level impact from OAG over the course of the study.

A fourth possible explanation is that the large-scale movement of birds among the working groups (and the PPA) swamped any regional differences in reproduction or survival. In a recent study, Fedy et al. (2012) concluded that sage

grouse in Wyoming make substantial movements between critical life stages [22]. It is therefore likely that movement may have reduced some regional differences. However, Fedy et al. (2012) also found that some individuals remained year-round in the same vicinity and the current populations model was nonetheless able to detect inter-regional survival differences related to habitat quality. If movement is acting to compensate for inter-regional differences, then the spatial and temporal scales at which OAG impacts are assessed must be rethought.

The final explanation is that extrapolation of the results of the local studies do not provide useful predictors of the population-level response. In particular, small-scale movement in the form of avoidance [2] or attraction [49] may have acted to complicate the relationship between lek abundance, individual fitness, and the consequences for the population.

If it is accepted that the current population dynamics model are sufficiently structurally adequate to be useful, then whichever of the four remaining explanations is chosen has major implications for our current understanding of the impact of OAG development on sage grouse populations. Either most studies of sage grouse status are questionable, or mitigation and conservation have substantially reduced the impact of OAG, or the scales at which OAG impacts are assessed are too small, or the results of the local studies are not reliable when scaled up. In reality, the actual question is, to what extent have each of these possible explanations contributed to the lack of a population-level response.

Regional Climate as the Primary Driver

The finding that regional climate, as captured by the PDO index, has been the primary driver of sage grouse population dynamics in Wyoming over the past 18 years also has major implications for our understanding. Although several studies have documented an effect of precipitation on sage grouse survival [50, 51], to the best of our knowledge only one previous study has estimated the magnitude of the effect of regional climate on sage grouse numbers [17]. Based on male counts at 13 leks spanning 7 years, Blomberg et al. (2012) concluded that precipitation was correlated with 75% of the variance in the annual counts [17]. Our results are consistent with other studies that have reported that large-scale climate indices such as the PDO and El Nino/Southern Oscillation (ENSO) regularly outperform crude summaries of local climatic conditions (i.e. monthly data on temperature and precipitation gathered from local weather stations) in predicting population dynamics and ecological processes [52, 53].

A key question to emerge from the current study is to what extent have long-term fluctuations in other areas [5] been driven by changes in the PDO? At the very least it is expected that some long-term declines, like those of songbirds in western North America [54, 55], will be better understood in the context of the PDO. Finally we note that identification of the PDO as the primary driver opens the possibility for more accurate predictions of future sage grouse numbers [56]. At the very least, the finding that climate is the primary driver explains the synchrony between Wyoming cottontail rabbits (*Sylvilagus* spp) and sage grouse that intrigued Fedy et al. [57]. At best, it will allow decision makers and regulators to more effectively balance conservation efforts, energy development and other forms

of human activity on the landscape.

Future Research

Large-scale, open, collaborative, reproducible research is needed [58] to ensure future decisions regarding OAG development have the intended consequences for sage grouse populations. In particular, it is critical that other authors attempt to replicate the results of the current study both in Wyoming and across the species range. To facilitate the process we have produced software packages that include the data and scripts to replicate the current analyses (S1 Software). However, a species wide assessment of sage grouse population dynamics also requires government biologists from other states to open the lek count data, which was collected using public funds, to all individuals.

Supporting Information

S1 Software

R Packages. Instructions on how to install the sglekwy (`http://dx.doi.org/10.5281/zenodo.31476`) and sgpd (`http://dx.doi.org/10.5281/zenodo.31625`) R packages. The packages, which were developed for the current paper, allow the results to be easily replicated and the models fitted to other datasets. (MD)

S1 Text

Spatial Data. Description of how the spatial data (`http://dx.doi.org/10.5281/zenodo.31526`) were collected and prepared using GIS analysis. (DOCX)

S2 Text

Mitigation of Oil and Gas Impacts. Overview of the recent improvements in OAG technologies that have likely reduced the impact to sage grouse populations. (DOCX)

S1 Video

Oil and Gas Development in the Pinedale Planning Area. Animation of the development of OAG in the PPA from 1912 to 2012. (MP4)

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Author Contributions

Conceived the study: RRR ASI. Collected the data: ASI RRR. Analyzed the data: JLT ASI RR. Wrote the paper: JLT RRR.

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