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 Spatial scale is important when studying ecological processes. The Greater sage-grouse (*Centrocercus urophasianus*) is a large sexually dimorphic tetraonid that is endemic to the sagebrush biome 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 the areal disturbance due to well pads as well as climatic variation on individual lek counts and Greater sage-grouse populations (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 using Frequentist and Bayesian methods. An information-theoretic approach was used to identify the most importance spatial scale and time lags. The relative importance of oil and gas and climate at the local and population-level scales was assessed using information-theoretic (Akaike's weights) and estimation (effect size) statistics.
Results At the local scale, oil and gas was an important negative predictor of the lek count. At the population scale, there was no evidence for an effect of oil and gas although the possibility of a strong negative effect consistent with summation of the local effect impacts could not be excluded. Regional climatic variation, as indexed by the Pacific Decadal Oscillation, was a important positive predictor of density changes at both the local and population-level.
Conclusions Additional studies to reduce the uncertainty in the range of possible effects of oil and gas at the population scale are required. Wildfile agencies need to account for the effects of regional climatic variation when managing sage-grouse populations.

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

INTRODUCTION

> If we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale. Because we are clever at devising explanations of what we see, we may think we understand the system when we have not even observed it correctly.
>
> Wiens (1989)

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, practical and statistical 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, local gradients may not accurately predict the population-level response (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.) biome of western North America (Knick and Connelly, 2011). Each spring, adult males aggregate in open areas called leks where they display for females. Fertilized females then nest on the ground among the sagebrush (Holloran and Anderson, 2005). 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. Mean peak counts of males on leks are commonly used as an abundance metric (Connelly and Braun, 1997; Doherty et al., 2010; Fedy and Aldridge, 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). 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) have been detected using radio-tracking. 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).

However, to date no-one has examined whether sage-grouse population-level responses are consistent with the local studies. Although Green et al. (2016) claim that they model sage-grouse populations, they use their population dynamic models to analyse the effects of OAG on changes in abundance at individual leks. Even authors such as Walker et al. (2007) and Gamo and Beck (2017) who analyse aggregations of leks, group their leks by level of OAG development as opposed to population boundaries. Depending on the scales over which density-dependence and movement occur, such sub-population-level analyses can lead to over or under-estimation of the actual population-level impacts.

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 includes 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), has experienced substantial levels of OAG development dating to the late 1800s (Braun et al., 2002) and because the lek location and count data were 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 only 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 multiple counts exist for 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) 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, June 7, 2017 and August 1, 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 proportional areal disturbance due to well pads within a specific distance of the leks. The areal disturbance was calculated at lek distances of 0.8, 1.6, 3.2 and 6.4 km with the areal disturbance of each well pad considered to have a radius of 60 m (Green et al., 2016). The annual areal disturbances for individual leks with lek counts 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 areal disturbance due to OAG and the PDO index as fixed effects and year and lek as random effects. The areal disturbance and PDO index were standardised (centered and divided by the standard deviation) to facilitate comparison. As preliminary analysis indicated that the lek counts were overdispersed, the GLMMs utilized a negative binomial distribution.

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

$$M_{i,y} \sim \text{NegBin}(\mu_{i,y}, \phi) \tag{1}$$

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

$$\alpha_{Li} \sim \text{Normal}(0, \sigma_L) \tag{3}$$

$$\alpha_{Y\,y} \sim \text{Normal}(0, \sigma_Y) \tag{4}$$

where $M_{i,y}$ is the rounded mean count of males for the ith lek in the yth year, β_A and β_P are the fixed effects of the standardised areal disturbance due to well pads ($\text{AREA}_{i,y}$) and PDO index (PDO_y) on the expected count ($\mu_{i,y}$), σ_L and σ_Y are the standard deviations (SDs) of the random effects of lek and year. In our parameterization of the negative binomial the parameter ϕ controls the overdispersion scaled by the square of μ, i.e.,

$$SD[M] = \sqrt{\mu + \phi \cdot \mu^2} \tag{5}$$

Key model parameters are also described in Table 1.

To identify the most important spatial scale (distance from each lek when calculating the areal disturbance) and temporal lags, a total of 64 models were fitted to the lek count data representing all combinations of the four lek distances (0.8, 1.6, 3.2 and 6.4 km) and independent lags of one to four years in the areal disturbance (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 64 models (Burnham and Anderson, 2002).

Once the model with the most important spatial scale and temporal lags was identified, the relative importance of β_A 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) and by calculating their effect sizes with 95% confidence/credible limits (CLs Bradford et al., 2005; Claridge-Chang and Assam, 2016). The effect sizes, which represent the expected percent change in the lek count with an increase in the predictor of one SD, were calculated for the final full model and by averaging across all four models (Burnham and Anderson, 2002; Turek, 2015).

Population Models The calculated 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 areal disturbance and 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 performed well in explaining rates of change for sage-grouse in general and for Wyoming sage-grouse in particular (Garton et al., 2011).

The population model is described by the following equations

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

$$\log(\mu_{g,y}) = \beta_0 + (\beta_D + 1 + \alpha_{Gg}) \cdot \log(\mu_{g,y-1}) + \beta_A \cdot \text{AREA}_{g,y} + \beta_P \cdot \text{PDO}_y + \alpha_{Y_y} + \alpha_{\eta_{g,y}} \tag{7}$$

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

$$\alpha_{Gg} \sim \text{Normal}(0, \sigma_G) \tag{9}$$

$$\alpha_{Y_y} \sim \text{Normal}(0, \sigma_Y) \tag{10}$$

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

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

$$\log(N_\infty) = \frac{-(\beta_0 + \beta_A \cdot \text{AREA}_{g,y} + \beta_P \cdot \text{PDO}_y)}{\beta_D + \alpha_{Gg}}. \tag{12}$$

The primary question this study attempts to answer is whether the sage-grouse population-level responses to oil and gas are consistent with the local studies. Consequently, the average areal disturbance in each working group was calculated at the spatial scale that was most important in the local analyses. However, as the timing of effects could differ between the local count models and the population dynamic models, the Akaike's weight for each lag of one to four years in the areal disturbance and one to four years in the PDO index was calculated across the 16 models representing all lag combinations. Once the full model with the most important temporal lags had been identified, the relative importance of β_A and β_P was once again quantified from their effect sizes with 95% CLs and their Akaike's weights across the full model and the three reduced variants.

Predicted Population Impacts

To examine whether the population-level responses are consistent with the lek-level results, the expected effect of OAG on the long-term mean densities in each working group was calculated for the local and population models. In the case of the local model, the predicted population impacts represent the percent difference in the sum of the expected counts for the observed levels of OAG versus no OAGacross all leks in the working group after accounting for annual and climatic effects. In the case of the population model, the predicted population impacts represent the percent difference in the expected carrying capacity with the observed levels of OAG versus no OAGaccounting for annual and climatic effects. Finally, to test whether the results are consistent, the odds ratio that the predicted Wyoming-wide impact from the population model is less than the summation of the Wyoming-wide local impacts was calculated for the most recent year.

Statistical Methods

For reasons of computational efficiency, the intial 64 local and 16 population-level models were fit using the frequentist method of Maximum Likelihood (ML, Millar, 2011). The Akaike's weights were calculated from the marginal Akaike's Information Criterion values corrected for small sample size (mAICc, 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 final full ML model (Burnham and Anderson, 2002) with the most important spatial scale and lags. As both the local and population models used log-link functions, the effect sizes (percent change in the response for an increase in one SD) were calculated from $\exp(\beta) - 1$ where β is the fixed effect of interest or its upper or lower CL. The ML effect sizes were calculated from the full model and averaged across the full model and three reduced variants (Lukacs et al., 2010).

To allow the predicted population impacts to be estimated with CLs, the final full models were also fitted using Bayesian methods (Gelman et al., 2014). The prior for all paramaters was an uninformative (Gelman et al., 2014) normal distribution with a mean of 0 and a SD of 5. A total of 2,000 MCMC samples were drawn from the second halves of four chains. Convergence was confirmed by ensuring that Rhat was less than 1.05 (Gelman et al., 2014) for all the estimated parameters.

Software

The data preparation, analysis and plotting were performed using R version 3.4.2 (R Core Team, 2017) and the R packages TMB (Kristensen et al., 2016) and rstan (Stan Development Team, 2016). The clean and tidy analysis data and R scripts are archived at https://doi.org/10.5281/zenodo.837866. The raw sage-grouse data, which provide the lek locational information, are available from the Wyoming Department of Fish and Game. The raw data are not required to replicate the analyses.

RESULTS

Local Models

The Akaike weights for the spatial scales indicate that 3.2 km is unanimously supported (w_i = 1.00) as the most important lek distance for predicting individual lek counts from the areal disturbance due to well pads (Table S1). The Akaike weights for the lags in the areal disturbance also provided unanimous support for a single candidate with the lag of one year receiving a weight of 1.00 (Table S2). The situation with the PDO index lags was less clear-cut (Table 2), although a lag of two years received the majority of the support (w_i = 0.73). Consequently, the local model with a lek distance of 3.2 km and lags of one and two years years in the areal disturbance due to well pads and the PDO index, respectively, was selected as

the final model. The standardized residuals, with the exception of a small number of high outliers, were approximately normally distributed and displayed homogeneity of variance. Most leks had an expected count of male sage-grouse in the absence of OAG of approximately 10 birds (Fig. S1).

The Akaike weights for β_A ($w_i = 1$) and β_P ($w_i = 0.98$) across the final full model and the three reduced models indicate that both are very strongly supported as predictors of individual lek counts. The effect size estimates (Fig. 5) indicate that β_A and β_P have large negative (Fig. 6) and positive (Fig. 7) impacts of similar magnitudes on the lek counts and that the estimates are insensitive to the statistical framework (ML of Bayesian) or model-averaging (Tables S3-S5). Despite the inclusion of the PDO index as an important predictor there was still substantial remaining annual variation in the lek counts (Fig. S2) which was modelled by the random effect of year.

Population Models

Based on the results of the local models, the level OAG development in each working group was calculated in terms of the average areal disturbance due to well pads within 3.2 km of each lek (Fig. 8). The Akaike weights for the lag in the areal disturbance (Table 3) were largely indifferent (w_i between 0.23 and 0.27) although a lag of one year had the most support while the Akaike weights for the PDO index (Table 4) clearly supported a lag of one year ($w_i = 0.83$). Due in part to the presence of process error, the model predictions provided a tight fit to the annual mean lek counts which exhibit large cyclical fluctuations (Fig. 9). The residuals were approximately normally distributed with homogeneity of variance. The carrying capacities in the absence of OAG varied between 10 birds per lek in the Northeast to 30 birds per lek in the Upper Green River (Fig. S3).

The Akaike weights for β_A and β_P (Table 1) across the final full model and the three reduced models indicate that while the PDO index is well supported ($w_i = 0.28$) as a predictor of population changes, there is little support ($w_i = 0.92$) for the areal disturbance.

The effect size estimates (Fig. 10), which are sensitive to the statistical framework and model-averaging (Tables S6-S8), indicate that while β_P has a large positive influence the effect of β_A on the subsequent year's density is relatively small. However, despite a relatively small influence on the subsequent year's density, β_A may have quite a large effect on the long-term carrying capacity (Fig. 11). The effect of β_P on the carrying capacity (Fig. S4) is comparable to its effect on the counts at individual leks (Fig. 7). Once again, the random effect of year accounted for substantial unexplained annual variation (Fig. S5). The effect of density on the subsequent year's density, i.e., density-dependence, is relatively minor - in a typical working group a reduction in the density to 10 males (half the carry capacity) results in an average of just 12.5 males the following year (Fig. S6).

Predicted Population Impacts

The predicted population impacts from the Bayesian full models indicate that although β_A has a relatively minor influence on the change in the population density, the possibility of a large negative effect of OAG on the carrying capacity that is consistent with summation of the local lek-level impact cannot be excluded (Fig. 12). However, the odds ratios that the 2016 state-wide predicted population impact was less than the summation of the local impacts is 5.1:1.

DISCUSSION

Oil and Gas

The results confirm the importance of OAG as a predictor of male attendance at individual leks in Wyoming over the past 32 years. The population-level results are less clear-cut. In particular, the low Akaike's weights indicate a lack of support for a population-level impact of OAG. However, although relatively unlikely, the possibility of a large negative population-level effect that is consistent with sum of the local impacts cannot be excluded.

There are four reasons why local impacts may not result in a population-level response (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; the third is that predictions of the population models are unreliable; and the fourth, and perhaps ecologically most interesting, is that the populations are able to compensate. 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 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 population-level models lack the power to exclude impacts that are consistent with summation of the local lek-level reductions.

Model Reliability The third possible explanation is that the estimates from the GSSPMs are unreliable. 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 CLs indicate that the observational and process errors are a similar magnitude and that both are relatively well defined. Another 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). 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 geographic scale of working groups is less than 1.1% per year (Row et al., 2016).

Ecological Compensation The fourth explanation for a mismatch between the local impacts of OAG and a 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, previous studies have demonstrated that sage-grouse can compensate for hunting (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 compensation was partly due to more ecological practices.

Climatic Variation

The current study indicates that the PDO index is an 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).

Conclusions

Ours is not the first study to extrapolate local impacts to population declines. 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% while 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. 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.

Ours is however the first to examine whether the actual population response is consistent with extrapolation of the local impacts. Although we find no evidence for a population-level response the possibility of a large negative impact that is consistent with the local impacts cannot be excluded. In order to guide future management decisions, additional studies are urgently required to determine the extent to which the absence of a detectable population-level response is due to ecological compensation vesus a lack of statistical power. To enable this, sage-grouse lek count data should be made available to researchers by all states and provinces.

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.

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FIGURES

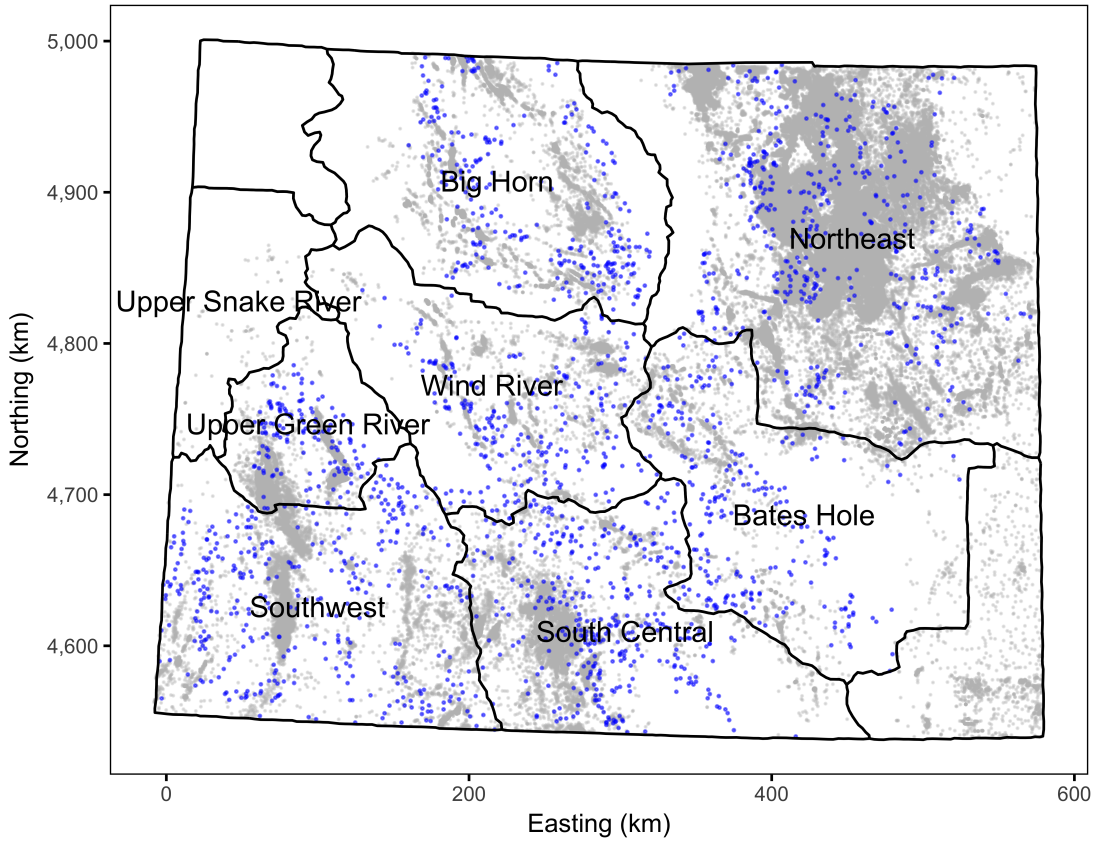


Figure 1. Map of Wyoming and its working groups. Leks are indicated by blue points and well pads by grey points. Only leks and wells pads that are included in the analyses are shown. The leks and well pads are not to scale. The projection is EPSG:26913.

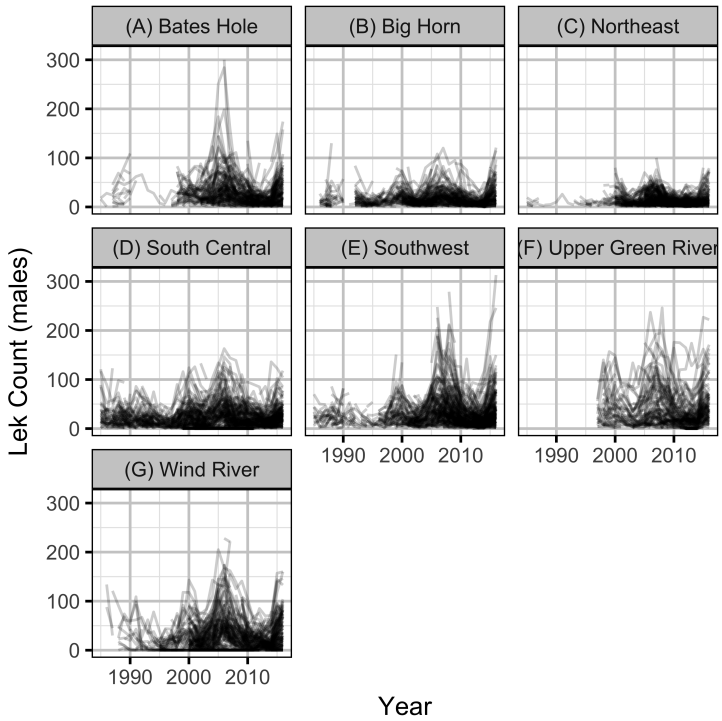


Figure 2. Mean counts of male sage-grouse at individual leks by year and working group.

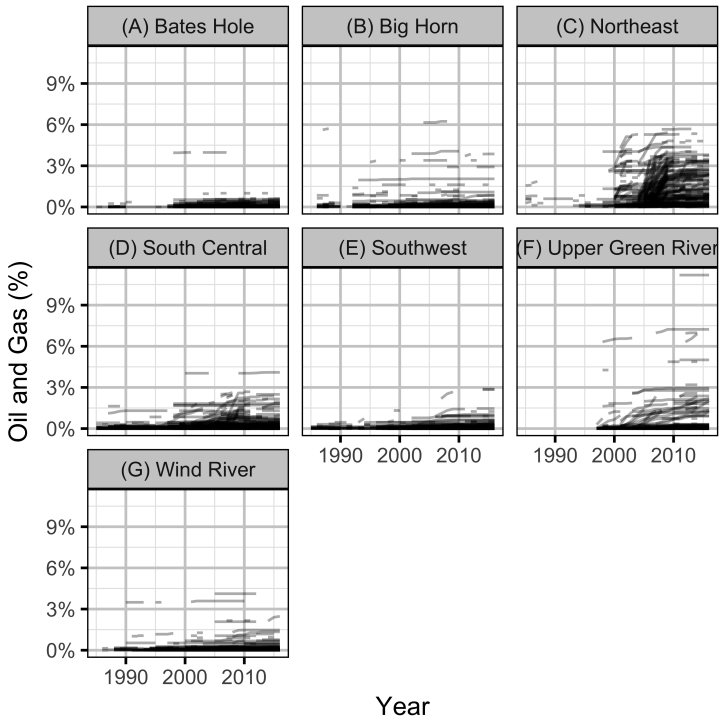


Figure 3. Percent areal disturbance due to well pads within 3.2 km of individual leks with one or more counts by year and working group.

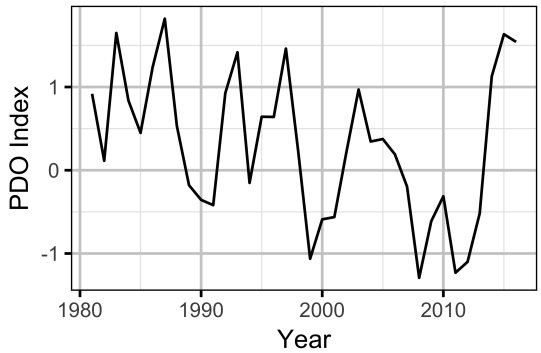


Figure 4. Pacific Decadal Oscillation index by year. Positive values indicate a warm phase and negative values a cool phase.

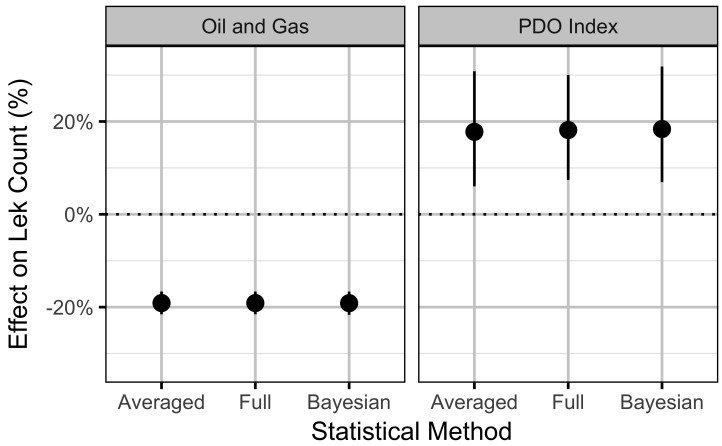


Figure 5. Estimates (with 95% CIs) of the effect of an increase in one SD (0.8 %) in the areal disturbance due to well pads within 3.2 km and the Pacific Decadal Oscillation index (0.82). The effect is on the expected count of male sage-grouse at an individual lek.

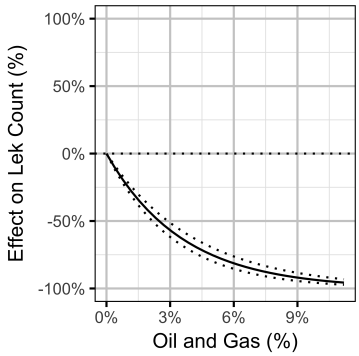


Figure 6. Bayesian estimates (with 95% CIs) of the effect of the percent areal disturbance due to oil and gas well pads on the expected count of male sage-grouse at a typical lek.

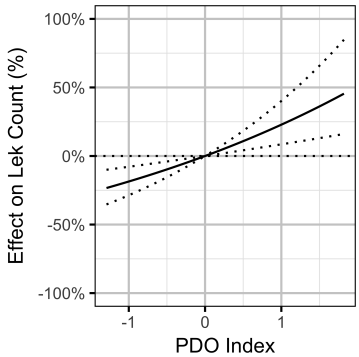


Figure 7. Bayesian estimates (with 95% CIs) of the effect of the Pacific Decadal Oscillation index on the expected count of male sage-grouse at a typical lek.

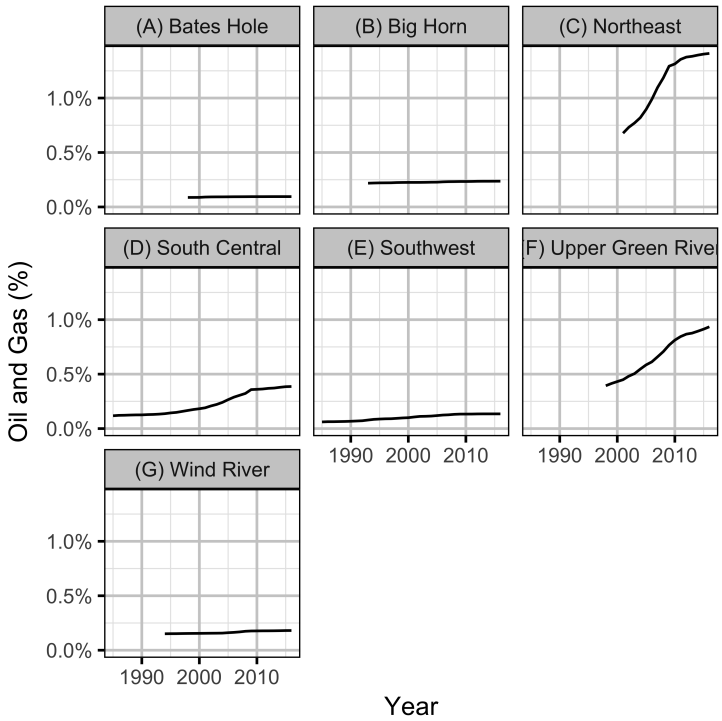


Figure 8. Mean areal disturbances due to well pads within 3.2 km of all leks by year and working group.

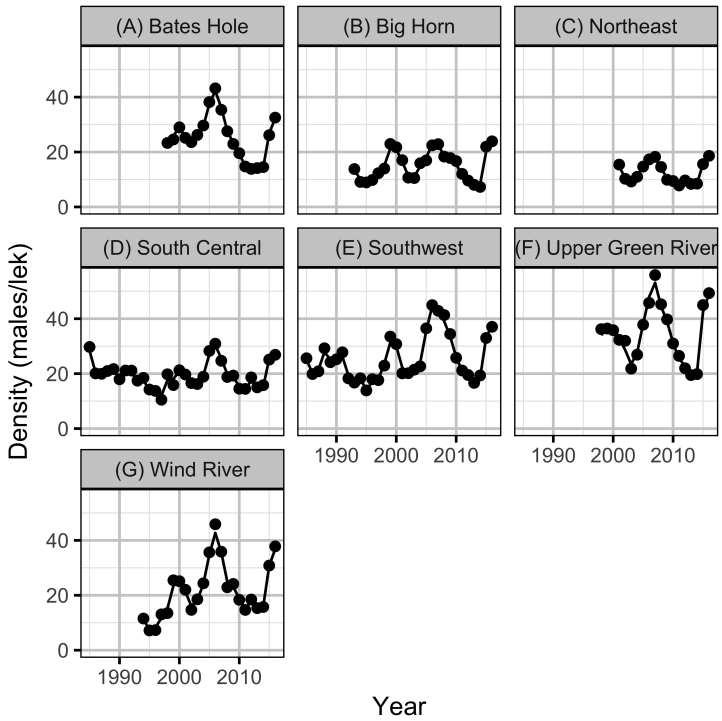


Figure 9. Mean lek counts by year and working group. The solid line is the Maximum Likelihood estimate of the population density based on the final full model.

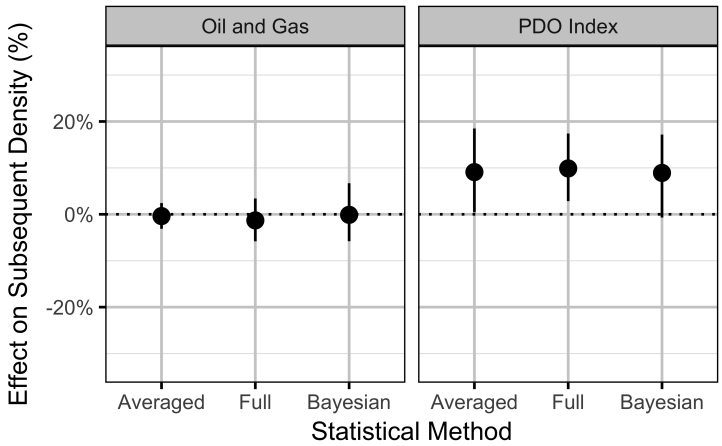


Figure 10. Estimates (with 95% CIs) of the effect of an increase in one SD (0.34%) in the areal disturbance due to well pads within 3.2 km of all leks and the Pacific Decadal Oscillation index (0.87). The effect is on the expected subsequent population density.

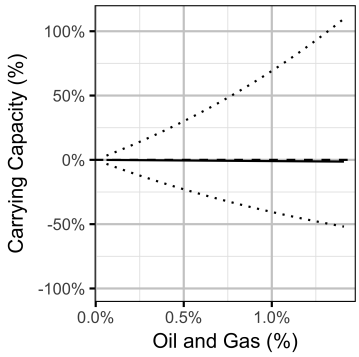


Figure 11. Bayesian estimates (with 95% CIs) of the effect of the percent areal disturbance due to oil and gas well pads on the expected carrying capacity at a typical working group.

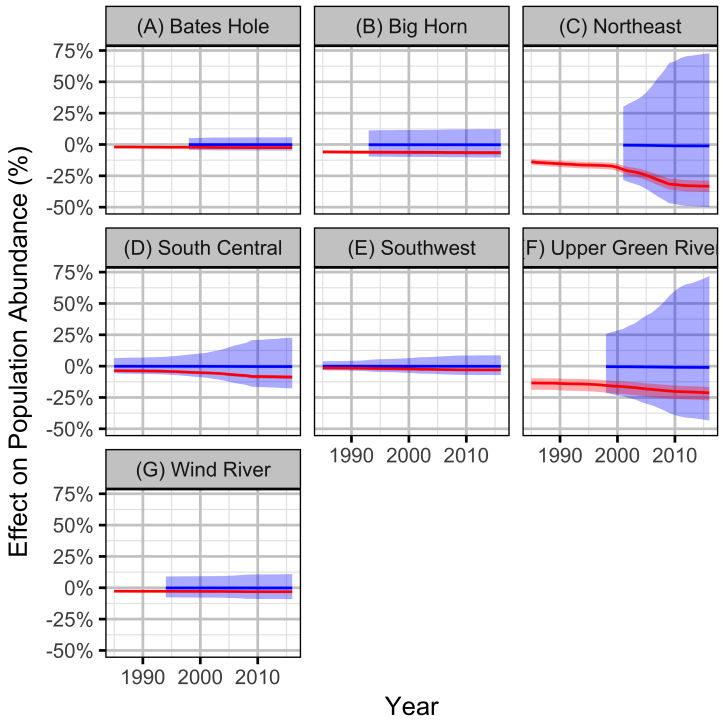


Figure 12. Bayesian estimates (with 95% CIs) of the effect of the observed levels of oil and gas on the population abundance of sage-grouse based on the local (red) and population (blue) models.

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_A	The effect of the standardised areal disturbance due to well pads on β_0.
ϕ	The overdispersion term.
σ_ε	The SD of the observer error.
σ_η	The SD of the process error.
σ_G	The SD of the random effect of working group on β_0.
σ_I	The SD of the random effect of working group on β_I.
σ_L	The SD of the random effect of lek on β_0.
σ_Y	The SD of the random effect of year on β_0.

Table 1. Descriptions of key model parameters.

PDO Lag (yr)	Models	Proportion	w_i
2	16	0.25	0.73
3	16	0.25	0.17
4	16	0.25	0.05
1	16	0.25	0.04

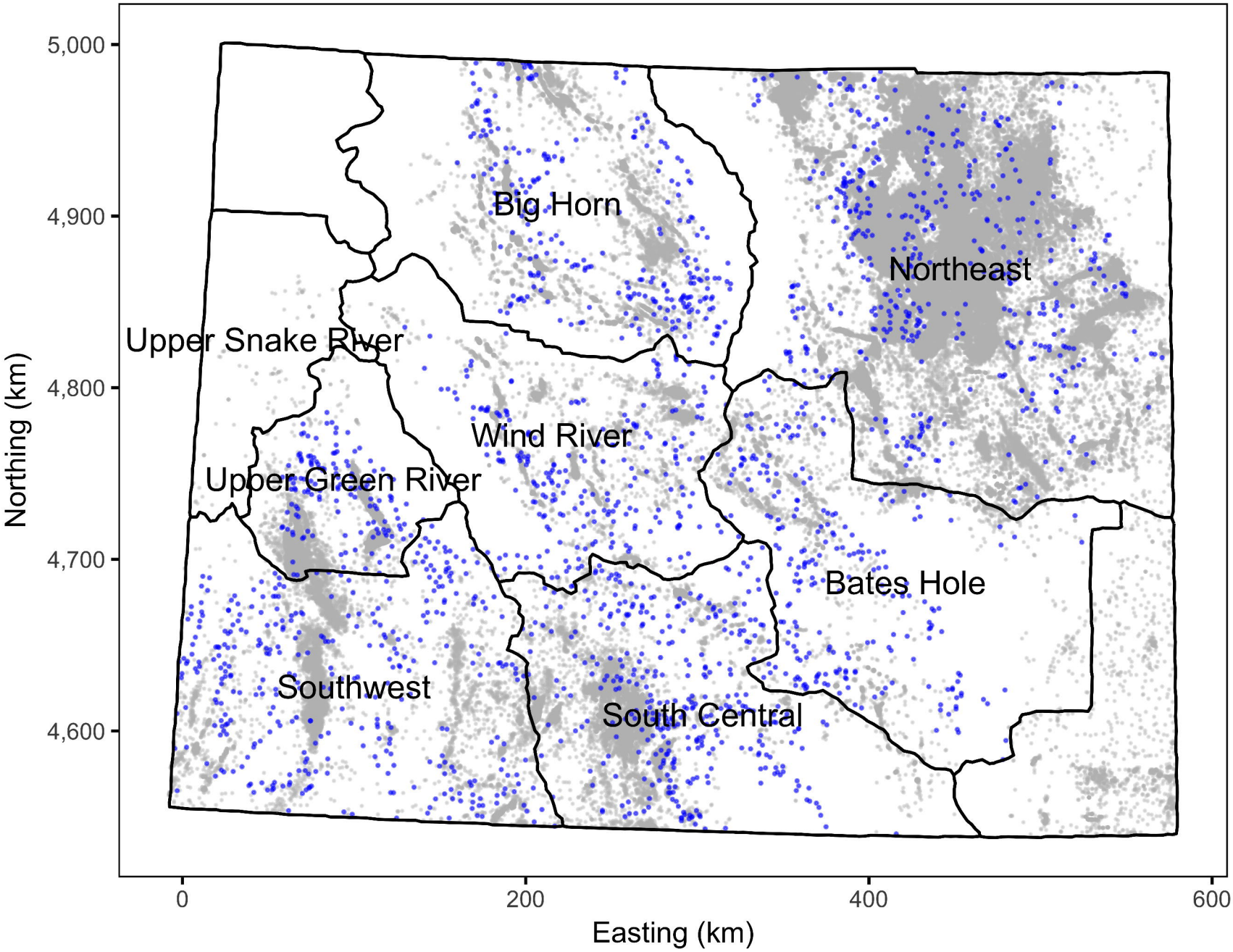
Table 2. The relative importance (w_i) of the lag in the Pacific Decadal Oscillation index density as a predictor of the count of males sage-grouse at individual leks across all models with a lek distance of 0.8, 1.6, 3.2, 6.4 and 12.8 km and the areal disturbance due to well pads independently lagged one to four years.

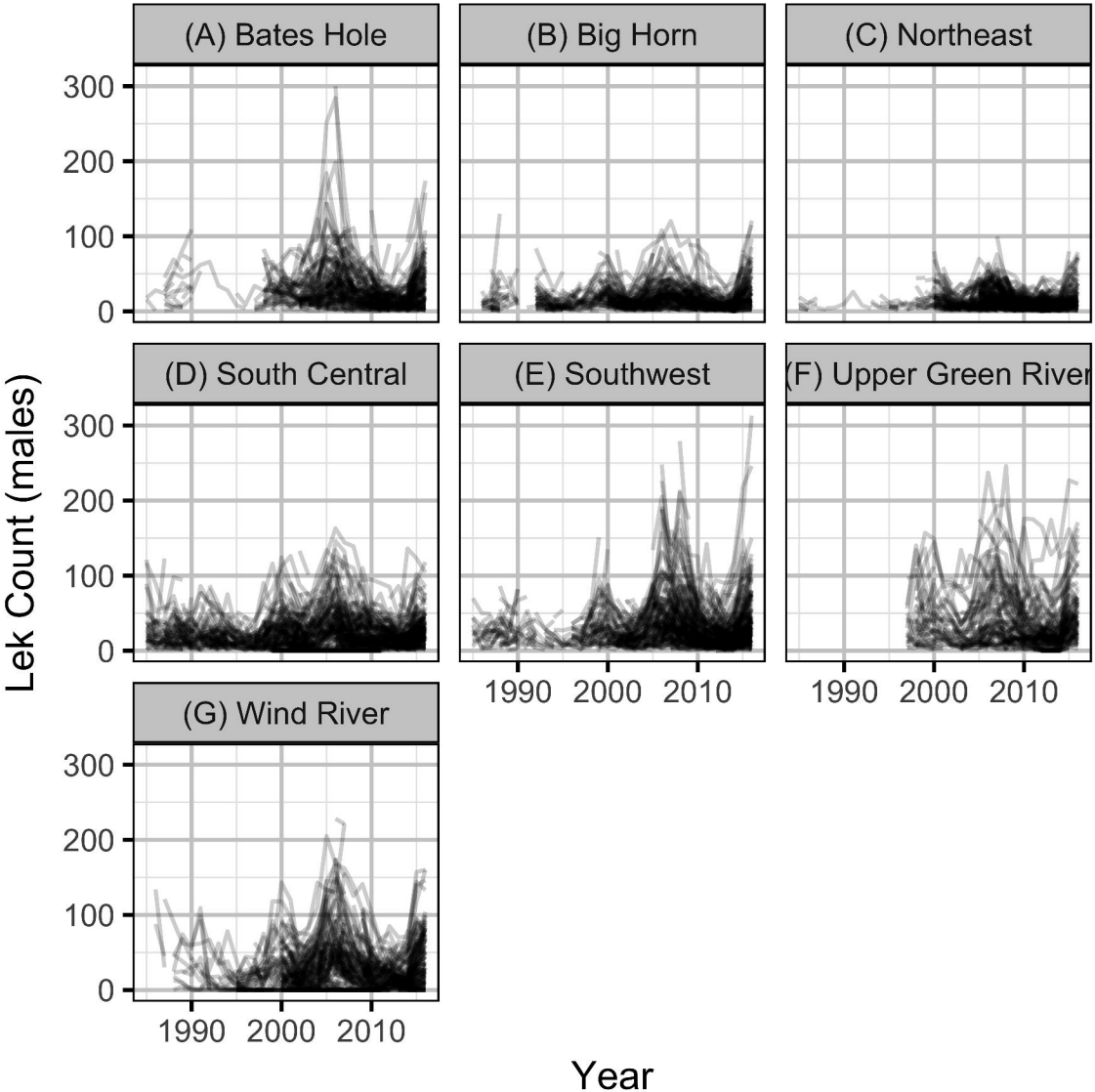
Area Lag (yr)	Models	Proportion	w_i
1	4	0.25	0.27
2	4	0.25	0.26
3	4	0.25	0.24
4	4	0.25	0.23

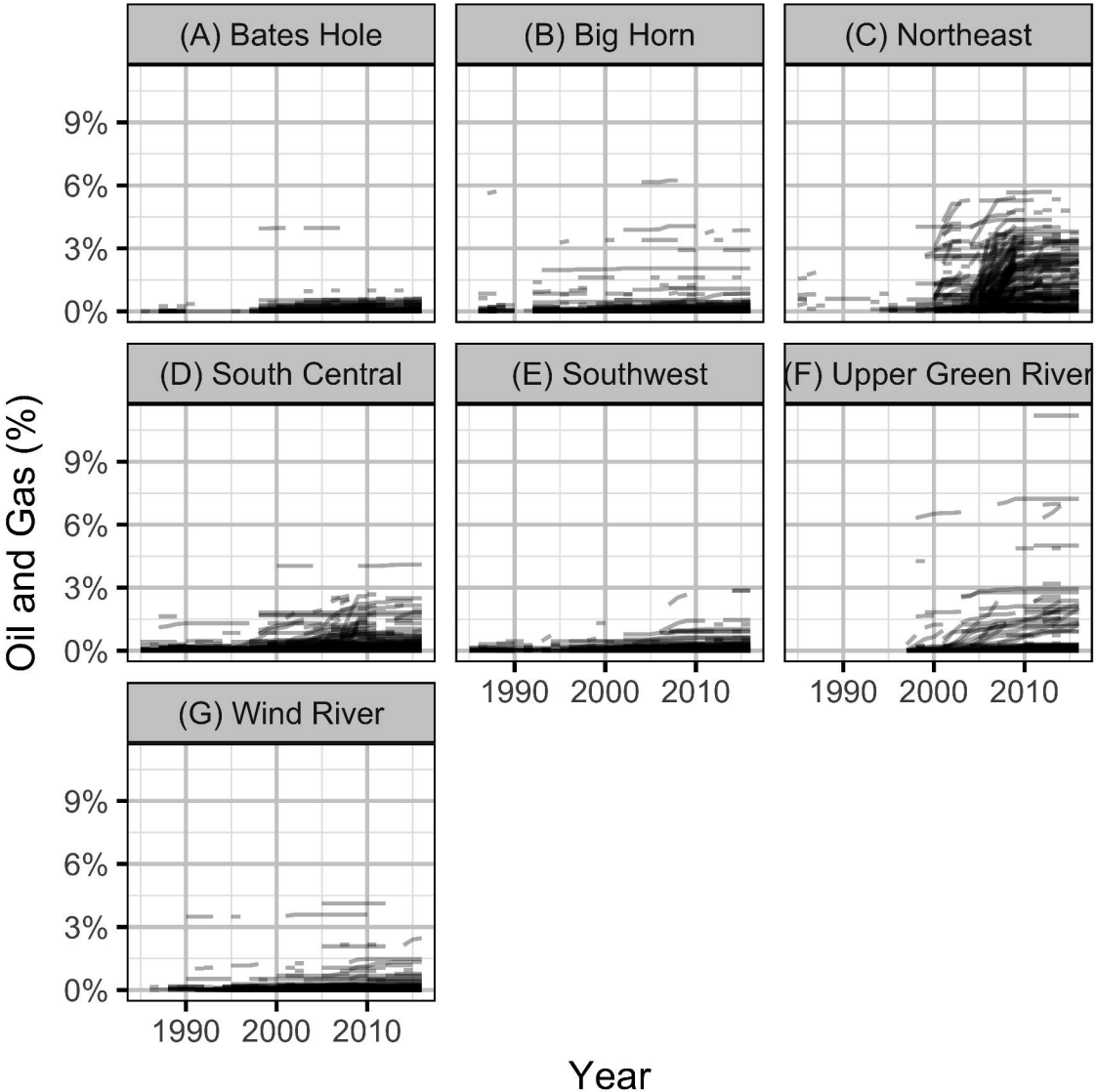
Table 3. The relative importance (w_i) of the lag in the areal disturbance due to well pads as a predictor of the change in the population density across all models with a lek distance of 3.2 km and the Pacific Decadal Oscillation index independently lagged one to four years.

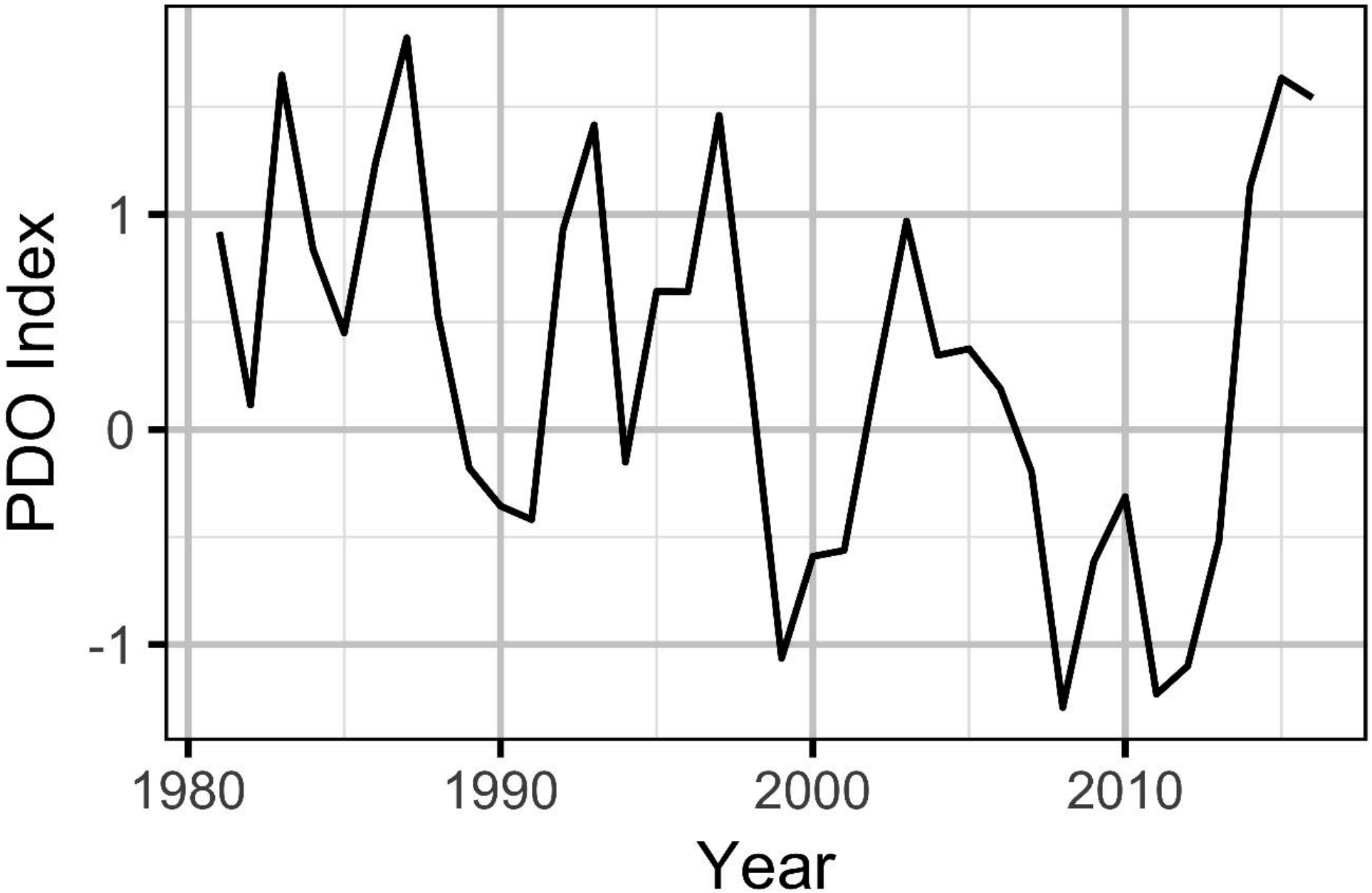
PDO Lag (yr)	Models	Proportion	w_i
1	4	0.25	0.83
2	4	0.25	0.11
4	4	0.25	0.03
3	4	0.25	0.03

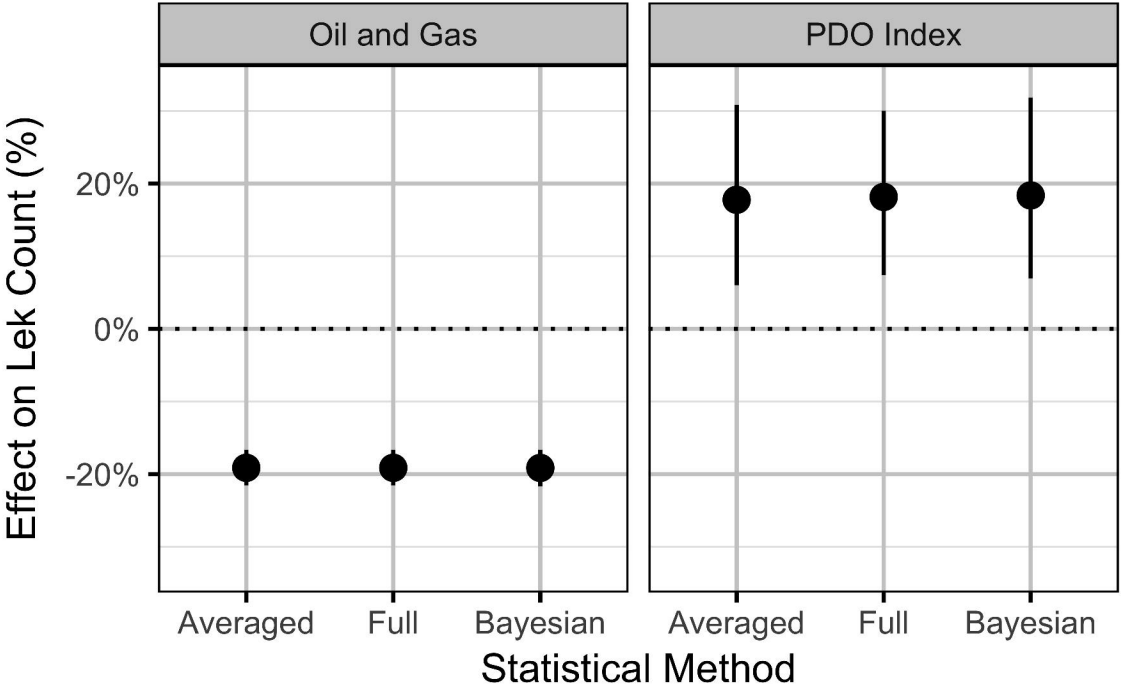
Table 4. The relative importance (w_i) of the lag in the Pacific Decadal Oscillation index as a predictor of the change in the population density across all models with a lek distance of 3.2 km and the areal disturbance due to well pads lagged one to four years.

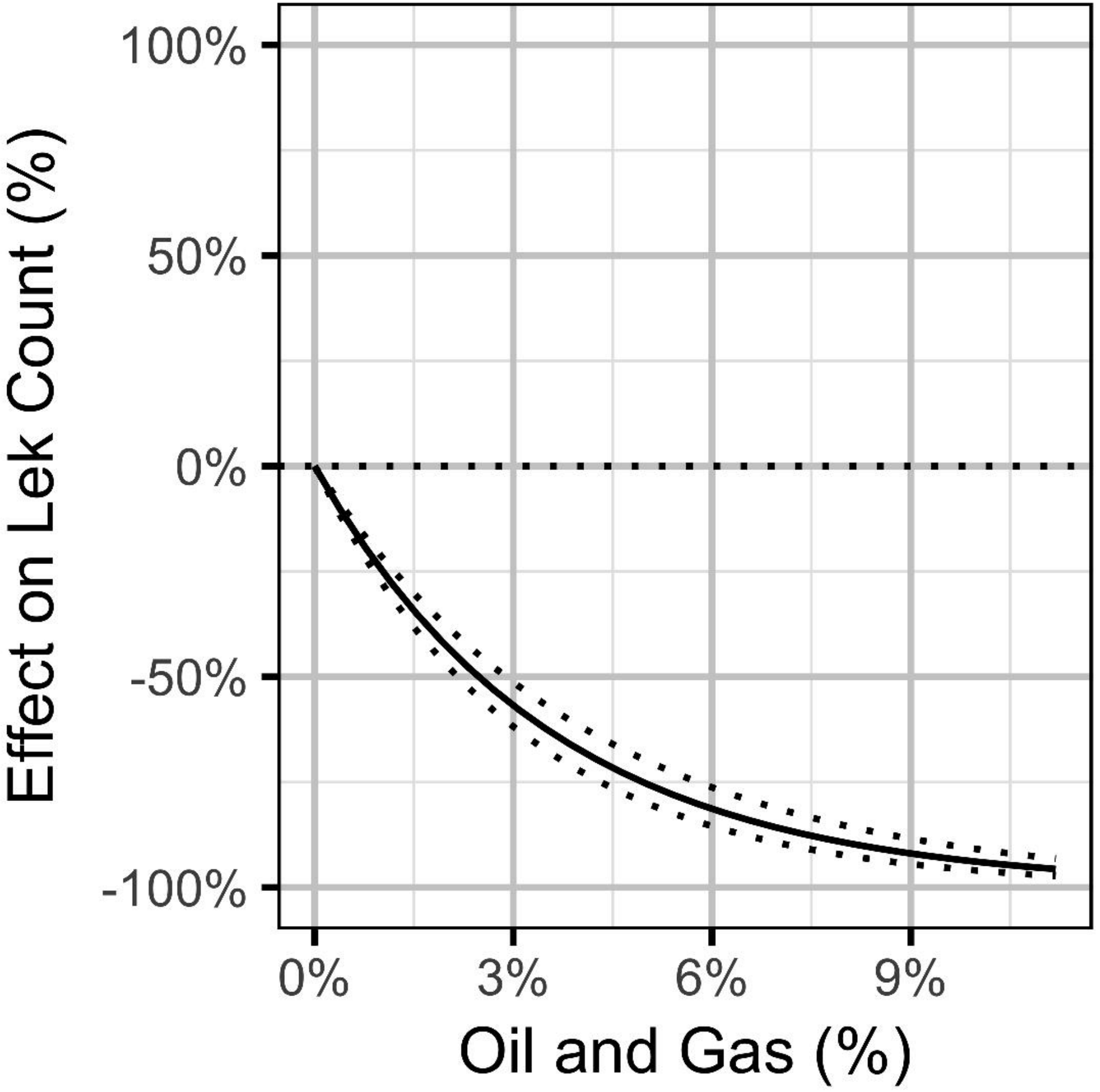

Big Horn
Northeast
Upper Snake River
Wind River
Upper Green River
Bates Hole
Southwest
South Central
5,000
4,900
4,800
4,700
4,600
Northing (km)
0
200
400
600
Easting (km)

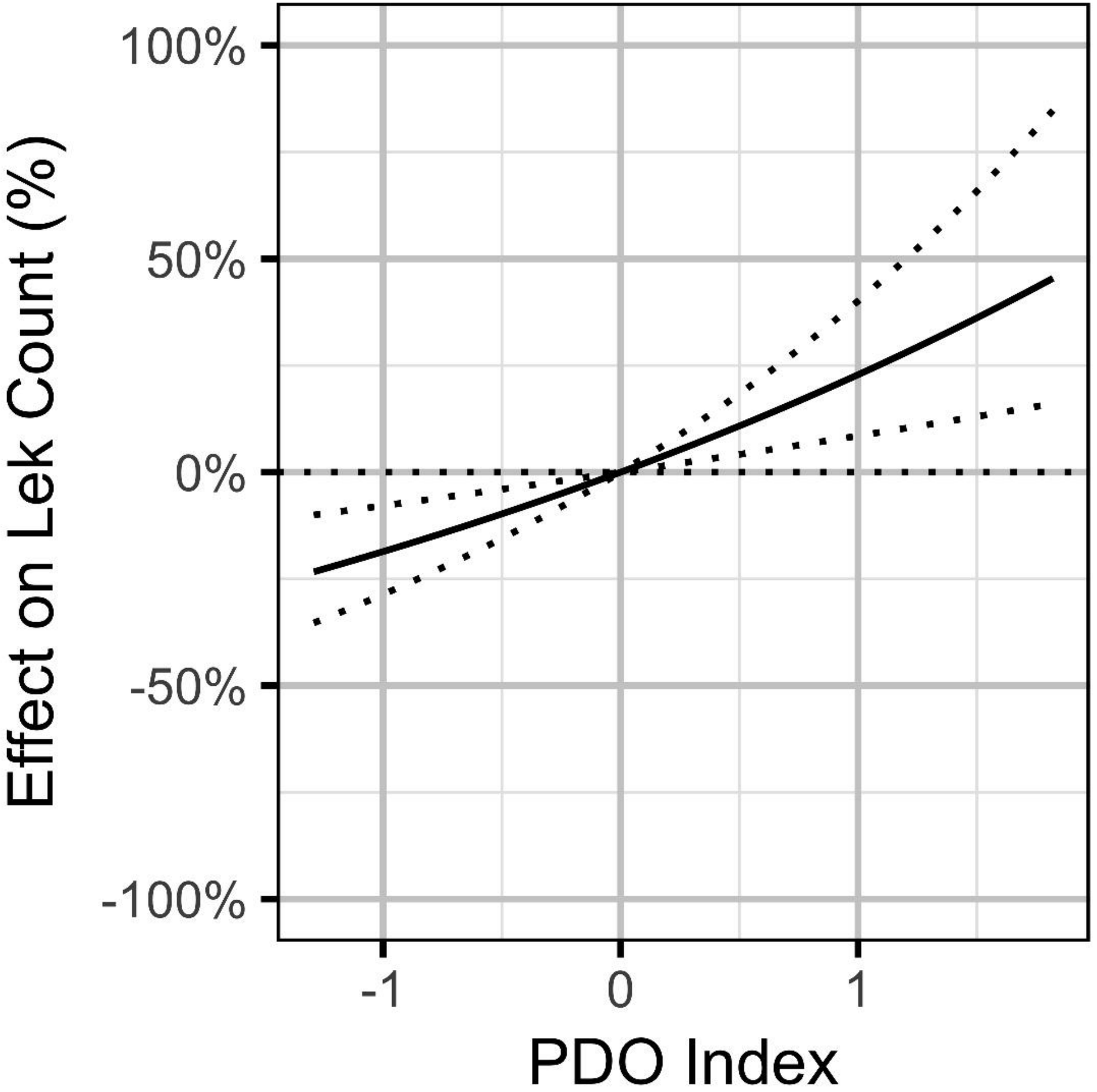

(A) Bates Hole
(B) Big Horn
(C) Northeast
(D) South Central
(E) Southwest
(F) Upper Green River
(G) Wind River
Lek Count (males)
0
100
200
300
1990
2000
2010
Year

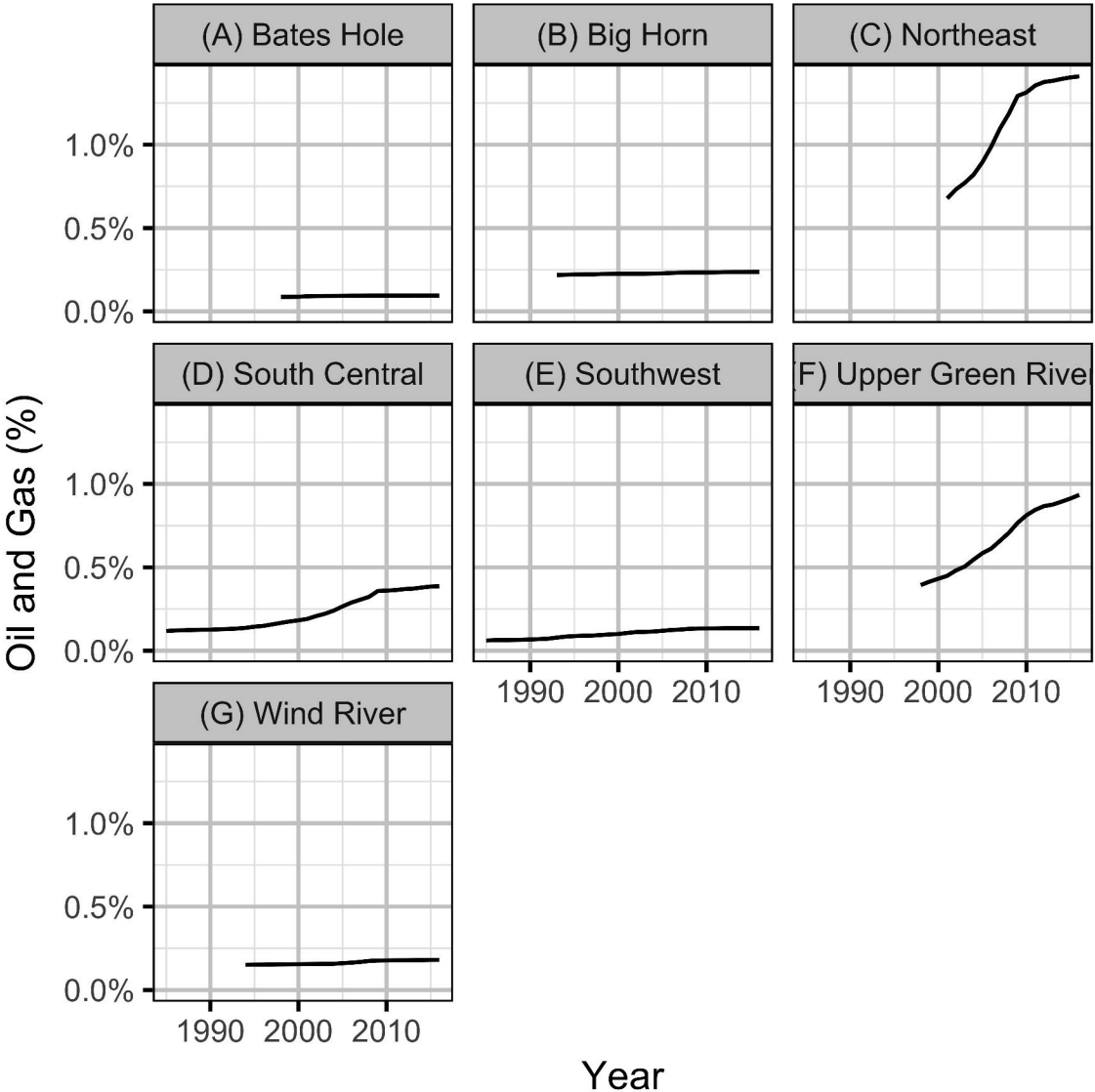

(A) Bates Hole
(B) Big Horn
(C) Northeast
(D) South Central
(E) Southwest
(F) Upper Green River
(G) Wind River
9%
6%
3%
0%
1990
2000
2010
Oil and Gas (%)
Year

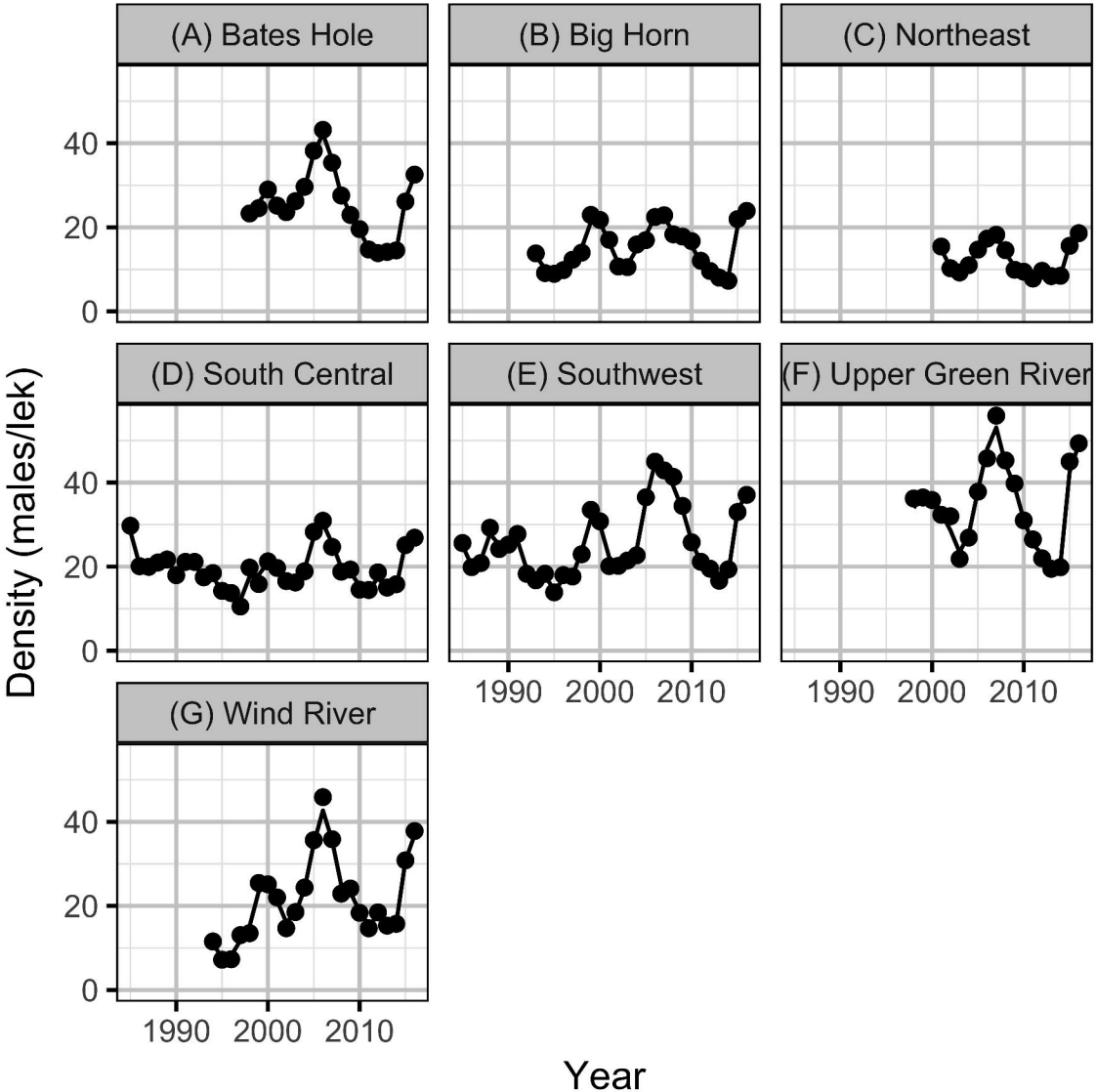

PDO Index
1
0
-1
1980
1990
2000
2010
Year

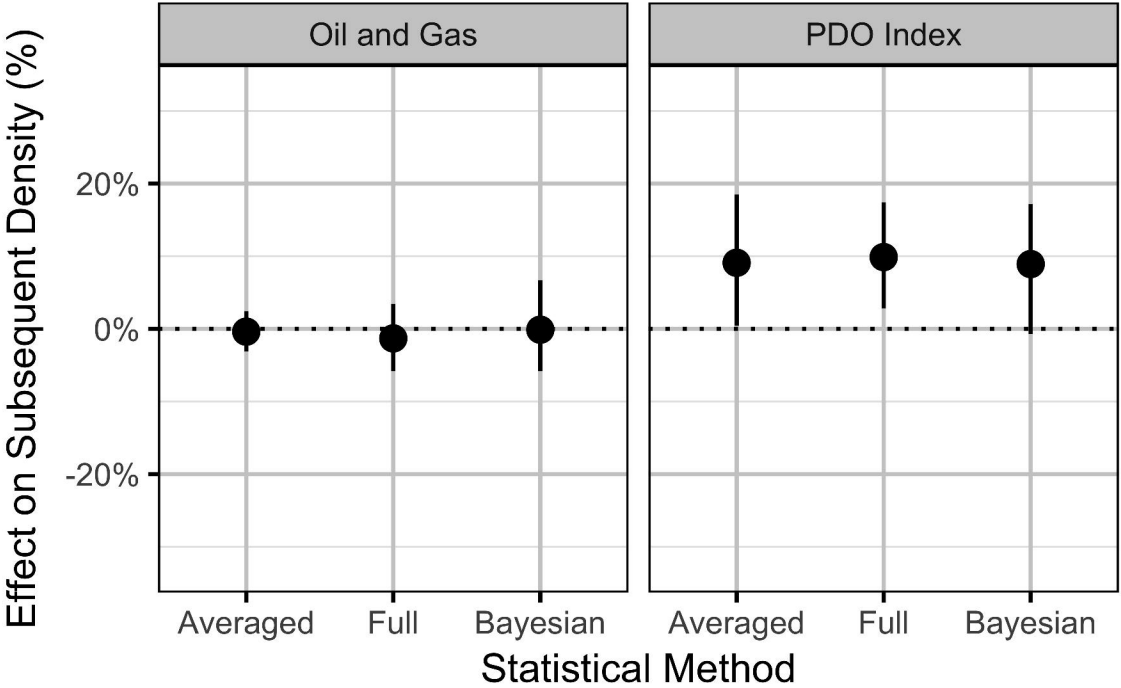

Oil and Gas
PDO Index
Effect on Lek Count (%)
20%
0%
-20%
Averaged
Full
Bayesian
Averaged
Full
Bayesian
Statistical Method

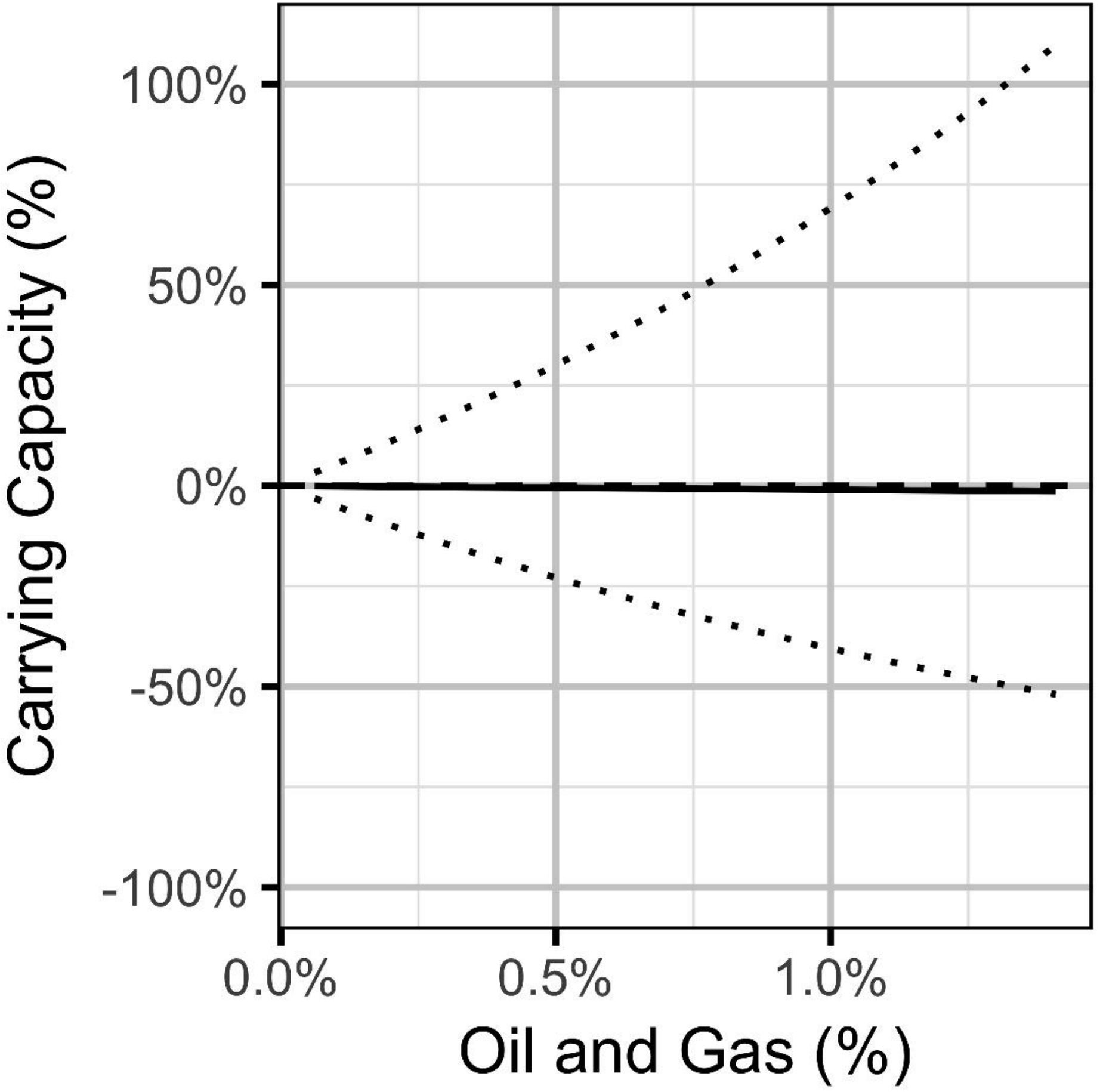

100%
50%
0%
-50%
-100%
Effect on Lek Count (%)
0%
3%
6%
9%
Oil and Gas (%)

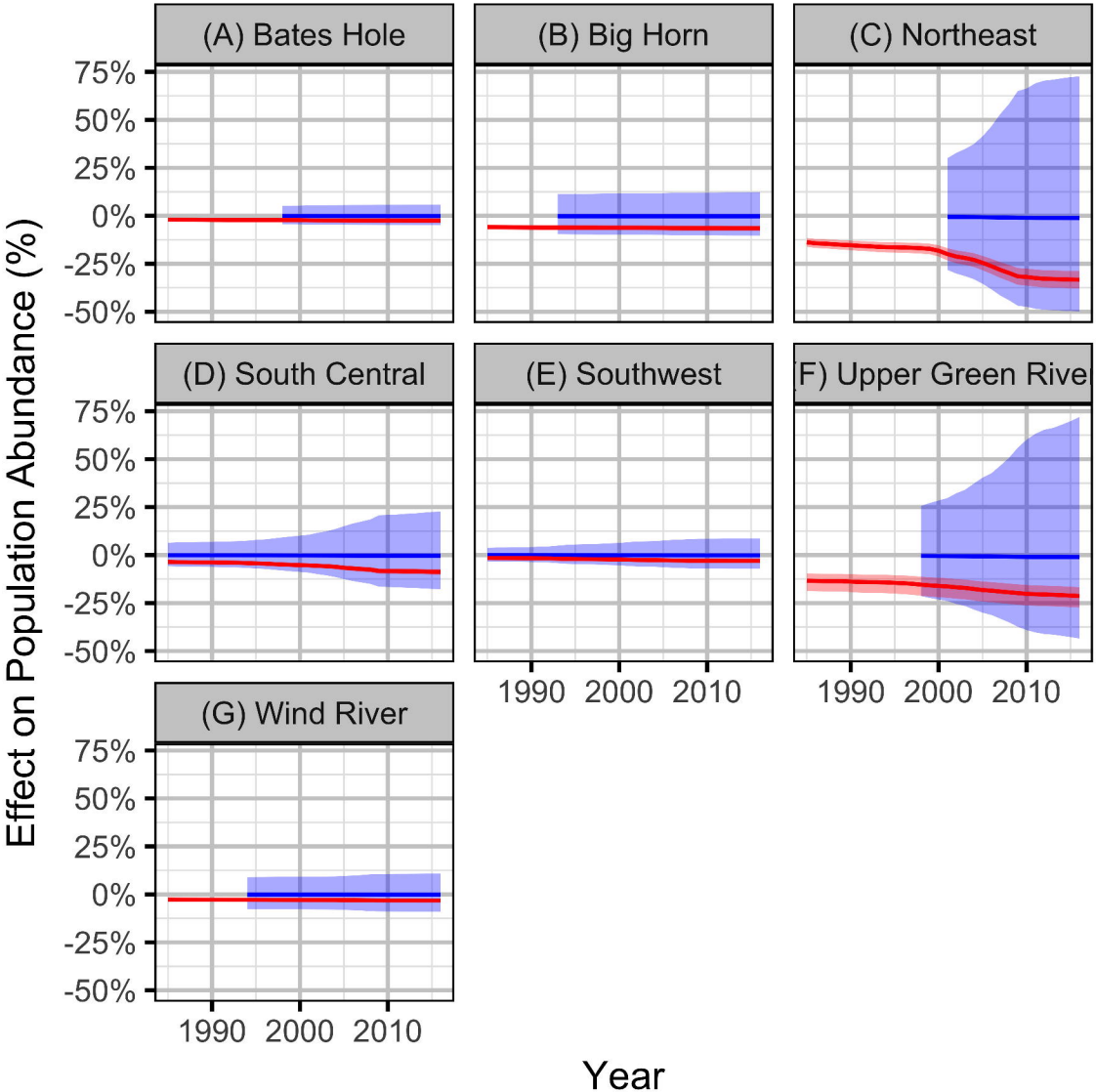

100%
50%
0%
-50%
-100%
Effect on Lek Count (%)
-1
0
1
PDO Index


(A) Bates Hole
(B) Big Horn
(C) Northeast
(D) South Central
(E) Southwest
F) Upper Green Rive
(G) Wind River
1.0%
0.5%
0.0%
1990
2000
2010
Oil and Gas (%)
Year


(A) Bates Hole
(B) Big Horn
(C) Northeast
(D) South Central
(E) Southwest
(F) Upper Green River
(G) Wind River
Density (males/lek)
0
20
40
1990
2000
2010
Year


Oil and Gas
PDO Index
Effect on Subsequent Density (%)
20%
0%
-20%
Averaged
Full
Bayesian
Averaged
Full
Bayesian
Statistical Method


100%
50%
0%
-50%
-100%
Carrying Capacity (%)
0.0%
0.5%
1.0%
Oil and Gas (%)


(A) Bates Hole
(B) Big Horn
(C) Northeast
(D) South Central
(E) Southwest
F) Upper Green Rive
(G) Wind River
75%
50%
25%
0%
-25%
-50%
1990
2000
2010
Effect on Population Abundance (%)
Year