Hierarchical Bayesian Analyses of Greater Sage Grouse Population Dynamics in the Pinedale Planning Area and Wyoming Working Groups: 1997-2012.

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Introduction

Statistical analyses were conducted, using hierarchical Bayesian models, to test hypotheses as a follow up to the report, *Spatial and Temporal Analysis of Oil and Gas Development, Mitigation, and Sage Grouse Lek Attendance in the Pinedale Planning Area, Wyoming: 1990-2012* (Ramey and Ivey 2014). The objectives of this study were to:

1) Test the significance and effect size of surface disturbance from oil and gas development (hereafter, areal disturbance) on male sage grouse lek counts.

2) Test the alternative hypotheses that oil and gas areal disturbance and/or regional climate variation (Pacific Decadal Oscillation), are the primary drivers of sage grouse population trends in the Pinedale Planning Area.

3) Test alternative hypotheses that oil and gas areal disturbance, large-scale climate phenomena (the Pacific Decadal Oscillation), hunting harvest, and/or habitat quality are the primary drivers of sage grouse population trends in sage grouse working groups across the State of Wyoming.

The analyses in this report initially focused on Pinedale Planning Area (Objectives 1 and 2), and then expanded across other regions of Wyoming (Objective 3) in order to provide a further test of earlier results (Ramey and Ivey 2014). To ensure the highest quality lek count data and the inclusion of wing composition data from hunting harvests, analyses in this study were limited to the period of 1997 to 2012.

The primary question that this study attempts to answer is: What effect has oil and gas development had on the abundance of Wyoming's sage grouse populations?

Results and Significance

The lek count data are the same as used in Ramey and Ivey (2014), except that mean number of males observed at leks was used in analyses rather than peak male attendance (Figure 1).

1) Key findings of the Pinedale lek count analysis (which assumes no movement of male sage grouse among leks) are as follows:

1.1) A 5% areal disturbance within 6.44km (4 miles) of leks was associated with ~50% decline in the male lek count at those leks. A 10% disturbance was associated with ~75% decline, and a 15% disturbance with ~90% decline (Figure 2).

Significance: This result is consistent with previously reported observations of decreased lek attendance locally in areas of intensive development, including the graphical results reported by Ramey and Ivey (2014).

1.2) If we extend these model results across the Pinedale population, the model predicts that the Pinedale population would have been ~12% lower in 1997 and ~22% lower in 2012 than would be expected with no areal disturbance from oil and gas. Again, assuming that there is no movement of male sage grouse among leks.

Significance: This analysis underscores the problem of extending the results of lek counts in locally disturbed areas to trends across whole population. The lek count model predicted that the Pinedale population was 12 and 22% lower as a result of areal disturbances in 1997 and 2012 than would have been expected if there was no areal disturbance (and assuming no movement of male sage grouse among leks). However, this predicted population decrease, due to proportion surface area disturbance within 6.44 km of each lek, by year, is the result of two commonly used but unrealistic assumptions. First, that males do not move among leks, and second, that localized negative effects of surface disturbance on lek attendance in the affected area automatically extends across the population as a whole, even if the majority of the population resides in undisturbed or minimally disturbed habitat. As with Pinedale (results presented below) predictions of population declines based on these assumptions have failed to come true.

1.3) The model predictions are close to the mean average lek counts (Figures 3 and 4).

Significance: The mean of peak lek counts, which are traditionally used to compile and analyze lek count data, are biased. This bias is due to a statistical artifact of an inappropriate calculation. During the lekking season, lek counts rise and then fall as birds congregate at leks before dispersing again. There are two appropriate ways to account for this phenomenon when estimating abundance. The first is to explicitly model the change in lek counts through time, while the second is to exclude early and late season counts so there is little variation due to date within the data. We chose the second option. Unfortunately many biologists attempt to deal with

the seasonal variation in lek attendance by taking the peak (maximum value) of all the counts at a given lek in a particular year. This method is not statistically valid because such a calculation fails to take into account the fact that there is variation in the lek counts due to factors other than date.

To better understand the problem, consider a six-sided unweighted die. It should be clear to the reader that the expected mean throw of such a die is 3.5. Now imagine the die was thrown five times and the mean value calculated, and this process repeated thousands of times, and the mean of the means from each set of five throws calculated. The expected value would still be 3.5. In contrast, if the mean was calculated using only the peak value from each set of five throws, the value would be 5.4, which is upwardly biased by over 30%.

Our analyses indicate that the lek count data exhibit extra-Poisson variation which we model using a gamma-Poisson distribution. Given the gamma-Poisson variation, if the expected value was 10 males then the expected mean of the mean counts would also be 10 while the expected mean of the peak counts would be biased upwards by 32% for two counts per lek and biased upwards by 52% for three counts per lek. Clearly if the number of counts per lek was not constant over time, such an artifact could lead to a substantial trend bias.

In addition to the gamma-Poisson variation in the counts at a lek in a particular year, there is also variation among leks with some leks having consistently higher counts than others. It is also important to take this lek variation into account because failure to do so will lead to temporal biases in the population estimates if leks are not sampled at random through time.

A third type of variation is that among leks within years. While a model that ignores lek within-year variation would not exhibit temporal biases in population estimates, it would underestimate the uncertainty in the predicted abundances.

2. Key findings of the Pinedale population dynamics analysis (which assumes no density-dependence) are as follows:

2.1) Annual survival (of chicks, yearlings and adults) is strongly driven by the Pacific Decadal Oscillation (PDO), which explained 78% of the variation in the Pinedale Planning Area population abundance as estimated from lek attendance (Tables 1 and 3b; Figures 5 - 9).

Significance: The PDO is the primary predictor of population fluctuations and trends in the Pinedale population from 1997 to 2012. The Pacific Decadal Oscillation (PDO) is a climate index derived from the large-scale spatial pattern of sea surface temperature in the North Pacific Ocean. When the PDO is in the “warm (+)” phase, the eastern portion of the North Pacific Ocean is warmer than the west-central portion, and the opposite is the case for the “cool (-)” phase. Shifts in the PDO

between a warm and cool phase strongly affect patterns of temperature, and precipitation in western North America. A warm phase of the PDO can be expected to result in cooler, wetter winters in Wyoming. Such favorable climatic conditions for sage grouse can be expected to result in larger cohorts, with individuals in better body condition, which may survive and reproduce at a higher rate, thus contributing to an overall population increase.

Our results are consistent with those of previous research that periodic sage grouse population fluctuations are driven by variation in abiotic factors, including regional precipitation and temperature (Fedy and Doherty 2010; Blomberg 2012; Guttery et al. 2013; WG&F 2006-2012). Although documentation exists that the PDO has affected populations of other terrestrial species in western North America (i.e. Ballard et al. 2003; Morrison and Hik 2007; McClure et al. 2012), our study is the first reported use of it as a predictive variable in modeling sage grouse population trends.

While the exact mechanism(s) of the PDO operating on sage grouse populations in Wyoming has not been fully elucidated (and is outside the scope of this paper), we note that large-scale climate indices such as the PDO and El Niño/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 ecological processes. Such predictions include plant phenology, demographic rates, and population dynamics of affected species (Stenseth et al. 2002 and 2003; Hallett et al. 2004).

2.2) There is no evidence of a long-term change in the population when PDO influence on survival is accounted for.

Significance: Although areal disturbance was shown to have an effect at a local level on lek attendance, it did not have a significant effect on inter-annual survival as estimated by the population dynamics model. Furthermore, inclusion of areal disturbance explained just 2% additional variation in all lek attendance beyond that explained by the PDO alone (Table 1). Therefore, we reject the hypotheses that areal disturbance has negatively affected the Pinedale population or that it has been the primary driver of population trends.

If regional population fluctuations and their primary drivers are not taken into account, erroneous conclusions regarding population trends and their driver(s) may result. The data and analyses presented here show that the PDO, and not patterns of oil and gas development, has been the primary driver of population trends.

3. Key findings of the Wyoming population dynamics analysis (which assumes density-dependence and uses harvest composition data) are as follows:

3.1) The Wyoming working group results were similar to results obtained in the Pinedale population dynamics analysis, with the majority of variation in lek attendance accounted

for by inclusion of the PDO index in the population model while areal disturbance did not have a significant effect (Tables 2 and 3c; Figures 10 - 13).

3.2) Chick productivity is strongly driven by the PDO, and habitat quality, but not areal disturbance (Figures 14 - 16).

3.3) Annual survival (of chicks, yearlings and adults) is strongly driven by the PDO but not areal disturbance (Figures 17 and 18).

3.6) There is no evidence of long-term change in the populations as a result of oil and gas surface disturbance when PDO and habitat quality influences are accounted for (which explain 67% of the variation in abundance) (Tables 2 and 3c).

Significance: Our analysis of working groups utilized population composition data that was obtained from hunter-harvested wings compiled by the State of Wyoming. Consistent with the results from the Pinedale population dynamics analysis, the PDO was found to be the major driver of population fluctuations and trends across groups. Again, areal disturbance effects explained just 2% more variation than that explained by PDO alone and were not statistically significant (Table 2). Therefore, we reject the hypothesis that areal disturbance has negatively affected lek attendance at a population level across the working groups included in this analysis.

Hunting harvest was found to not have a significant effect in our population dynamics analysis.

Conclusions

In conclusion, within the Pinedale Planning Area and across working groups in Wyoming, climate was found to be the primary driver of population trends in greater sage grouse. Oil and gas surface disturbance, while having a local negative effect on male lek attendance, was not a significant factor at the population level, as has been conjectured by numerous authors.

Until this study, the focus on human impacts to greater sage grouse has been primarily based on comparisons of lek counts in disturbed vs. undisturbed areas, or tracking the fate of selected leks in disturbed and undisturbed areas, without taking into account the bigger picture of trends in lek distribution and attendance across the population. As we have pointed out previously, one of the most difficult misconceptions to overcome in the study of sage grouse is the belief that sage grouse are tied to specific leks, and therefore, a change in attendance at an individual lek indicates a loss or gain of individuals to the population as a whole.

The results of the Pinedale Planning Area and Wyoming population dynamics analyses were consistent with the graphical results from the previous study by Ramey and Ivey (2014), thus providing confidence in the earlier conclusions.

This study uncovered bias in how lek counts are currently utilized (i.e. taking a mean of peak male lek attendance), and we have proposed alternative approaches.

The PDO (and the ENSO) are well-documented drivers of other animal populations in North America. This study was the first to formally incorporate the PDO phenomenon into a model of greater sage grouse population dynamics. The fact that the PDO, incorporated into the population model, accounted for 78% of population variation in Pinedale (and 67% in Wyoming working groups), should call into question many of the conjectures regarding purported anthropogenic drivers of population trends and threats to this species. If natural climatic drivers of population abundance are not taken into account, then erroneous conclusions will be arrived at. This comes at great expense to conservation efforts, the public, and mitigating bona-fide threats to this and other species.

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Methods

Data Preparation

The lek count, harvest, environmental and oil and gas developmental data were developed as described in Ramey and Ivey (2014). The data were cleansed, tidied and manipulated prior to analysis using R version 3.1.2 (Team, R Core 2013).

During the lek count data preparation it was assumed that:

- Only checked ground counts and surveys conducted between April 1st and May 7th where the number of individuals of unknown sex was not recorded or less than 5% of the number of males were reliable (unreliable counts were excluded from the analysis).

During the Pinedale population dynamics data preparation it was assumed that:

- The population abundance in each year was the males per lek predicted by the Pinedale lek count analysis.
- The areal disturbance metric in each year was the percent decline due to areal disturbance at the population level predicted by the Pinedale lek count analysis (assuming no movement).
- The sex ratio is 1:1; each female of age-2 and older produces between 4 and 8 hatchlings annually at low density in average quality habitat; and males recruit to the adult population (and are counted) at age-2.

During the Wyoming population dynamics data preparation it was assumed that:

- The population abundance in each working group in each year was the mean average number of males per lek.

- The abundance in each working group in each year was only reliable if at least five separate leks were counted at least once (unreliable values were excluded).
- The Pinedale Planning Area lek count and population dynamics analyses utilized detailed surface disturbance data on well pads, pipelines, and roads associated with oil and gas development (Ramey and Ivey 2014), whereas the working group population dynamics analysis was based upon a proportion of areal disturbance from well pads only, relative the potential habitat available to sage grouse within each working group (i.e. that available prior to oil and gas disturbance). It should be noted that because the calculated areal disturbances are based solely on well pads they represent a metric of relative disturbance as opposed to an absolute measure.

For the Pinedale and Wyoming population dynamics models:

- The proportion surface area disturbance was chosen as the oil and gas metric (instead of whether the proportion surface area disturbance was greater than 3% or the lek was within 6.44 km of a developing, producing or injecting well) as it was a continuous response.
- For our Wyoming population dynamics analysis, we used the boundaries of the Upper Green River Working Group, rather than Pinedale Planning Area. Although these have very similar boundaries, by using the Upper Green River Working Group boundaries in our population dynamics analysis were consistent with the State of Wyoming working group designations and allowed us to include hunting harvest composition data to refine our model.
- The limited number of lek counts that met our analysis requirements from the South-Central and Southwest working groups prevented their inclusion in our Wyoming population dynamics analysis (i.e. working groups had to have at least five or surveys for each year, and associated data range to be included).
- A relative habitat quality index for each working group was calculated as the proportion of potential sage grouse habitat with >25% sagebrush cover. A 1.5km moving window was used for sagebrush cover classification based on the 2012 Landfire Existing Vegetation Type (EVT) and Biophysical Setting (BpS) datasets. Potential sage grouse habitat was delineated as those areas remaining after all obvious non-habitat was excluded, including: open water, barren ground, alpine, subalpine, forests, woodlands, ruderal grassland and shrubland, agriculture, and development. In order to isolate oil and gas disturbance from other forms of development, and thus test its effects on greater sage-grouse, the cumulative oil and gas pad disturbances from 1918-1990 were replaced with the co-located pre-European settlement vegetation types, using the BpS dataset. This requires "cutting out" the oil and gas pad footprints, filling them in with the pre-European (BpS) vegetation values for sagebrush and potential sage grouse habitat (as defined above), and finally merging them into the habitat and sagebrush datasets derived from the EVT dataset. This composite dataset comprised of elements of both the EVT and BpS datasets, provides a reproducible measure of habitat quality and greater sage-grouse range, minus the pre-1990 effects of oil and gas pads, for each working group.

Statistical Analysis

Hierarchical Bayesian models were fitted to the count data using R version 3.1.2 (Team, R Core 2013) and JAGS 3.4.0 (Plummer 2012) which interfaced with each other via jaggernaut 2.2.8 (Thorley 2013). For additional information on hierarchical Bayesian modelling in the BUGS language, of which JAGS uses a dialect, the reader is referred to Kéry and Schaub (2011, pp. 41-44).

Unless specified, the models assumed vague (low information) prior distributions (Kéry and Schaub 2011, pp. 36). The posterior distributions were estimated from a minimum of 1,000 Markov Chain Monte Carlo (MCMC) samples thinned from the second halves of three chains (Kéry and Schaub 2011, pp. 38-40). Model convergence was confirmed by visual examination of the traceplots and by ensuring that Rhat (Kéry and Schaub 2011, pp. 40) was less than 1.1 for each of the parameters in the model (Kéry and Schaub 2011, pp. 61). Model adequacy was confirmed by examination of residual plots.

The posterior distributions of the *fixed* (Kéry and Schaub 2011, pp. 75) parameters are summarised in terms of a *point* estimate (mean), *lower* and *upper* 95% credible limits (2.5th and 97.5th percentiles), the standard deviation (*SD*), percent relative *error* (half the 95% credible interval as a percent of the point estimate) and *significance* (Kéry and Schaub 2011, pp. 37, 42).

Variable selection was achieved by dropping *insignificant* (Kéry and Schaub 2011, pp. 37, 420), fixed (Kéry and Schaub 2011, pp. 77-82) variables and *uninformative* random variables. A fixed variables was considered to be insignificant if its significance was $\geq$ 0.05 while a random variable was considered to be uninformative if its percent relative error was $\geq$ 80%.

The results are displayed graphically by plotting the modeled relationships between particular variables and the response with 95% credible intervals (CRIs) with the remaining variables held constant. In general, continuous and discrete fixed variables are held constant at their mean and first level values respectively while random variables are held constant at their typical values (expected values of the underlying hyperdistributions) (Kéry and Schaub 2011, pp. 77-82). Where informative the influence of particular variables is expressed in terms of the *effect size* (i.e., percent change in the response variable) with 95% CRIs (Bradford, Korman, and Higgins 2005).

Pinedale Lek Counts

To account for spatial autocorrelation in oil and gas disturbance the Pinedale Planning Area was divided into 7 blocks.

The male lek count data were analyzed using an overdispersed Poisson mixed effects model. Key assumptions of the Pinedale lek count model include:

- The male lek count varies by year.
- The male lek count varies randomly by block, lek and lek within year.
- The male lek count varies with the proportion surface area disturbance within 6.44 km (4.0 mi).

- The male counts are Poisson-gamma distributed.

Proportion surface area disturbance as a second-order polynomial was not a significant predictor of the male active lek count.

Through the use of random effects the model was able to estimate the abundance at each lek in each year whether or not it was surveyed in that year.

The abundance in each year was estimated by averaging the predicted male abundance at all leks for that year.

Results

Table 1. Proportion of variation explained (R^2) by inclusion or removal of key variables in the Pinedale population dynamics model.

model_id	**R^2**
PDO + ArealDisturbance	80
PDO	78
Areal Disturbance	8
-Null	1

Table 2. Proportion of variation explained (R^2) by the Wyoming population dynamics analysis model with different explanatory variables.

model_id	**R^2**
PDO +ArealDisturbance(Survival) +ArealDisturbance(Productivity)	69
ArealDisturbance(Survival) +ArealDisturbance(Productivity)	6
PDO	67
Null	5
PDO + ArealDisturbance(Survival)	68
PDO +ArealDisturbance(Productivity)	68

Table 3a-c. The posterior distributions for the *fixed* (Kery and Schaub 2011, p. 75) parameters in each model are summarized below.

3a. Pinedale lek counts model.

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bArealDisturbance	-0.42990	-0.55600	-0.30620	0.06610	29	0.001
sBlockYear	0.16690	0.10270	0.24040	0.03410	41	0.001
sDispersion	0.50062	0.47873	0.52221	0.01130	4	0.001
sMalesLek	1.01200	0.86830	1.17700	0.07840	15	0.001
sMalesLekYear	0.43555	0.39355	0.47971	0.02218	10	0.001

Convergence	Iterations
1.05	1e+05

3b. Pinedale population dynamics model.

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bChicksPerAdult	2.9680	2.0470	3.9520	0.5970	32	0.0010
bSurvival	-0.1474	-0.3602	0.1118	0.1433	160	0.4097
bSurvivalArealDisturbance	0.0443	-0.0383	0.1285	0.0414	190	0.2725
bSurvivalPDO	0.4997	0.3154	0.6999	0.0993	38	0.0010
sAbundance	5.1530	3.3890	8.0980	1.1990	46	0.0010

Convergence	Iterations
1.01	20000

cc. Wyoming population dynamics model.

Parameter	Estimate	Lower	Upper	SD	Error	Significance
bChickCarryingCapacity	4.8310	4.4060	5.4220	0.2580	11	0.0010
bChicksPerAdult	2.8790	2.0960	3.9090	0.4980	31	0.0010
bProductivityArealDisturbance	-0.1002	-0.2761	0.0588	0.0835	170	0.2116
bProductivityHabitatQuality	0.1861	0.1045	0.2808	0.0446	47	0.0010
bProductivityPDO	0.2764	0.1660	0.3848	0.0566	40	0.0010
bSurvival	0.1665	0.0426	0.2777	0.0600	71	0.0040
bSurvivalArealDisturbance	0.0886	-0.0142	0.2137	0.0553	130	0.0999
bSurvivalPDO	0.3747	0.2816	0.4707	0.0469	25	0.0010
sAbundance	4.4440	3.7300	5.2520	0.3900	17	0.0010
sOverDispersion	0.4383	0.3445	0.5559	0.0541	24	0.0010

Convergence	Iterations
1.07	10000

Figures

Pinedale Lek Counts

Figure 1. Mean number of males observed at leks surveyed in the Pinedale Planning Area by longitude, latitude, and year.

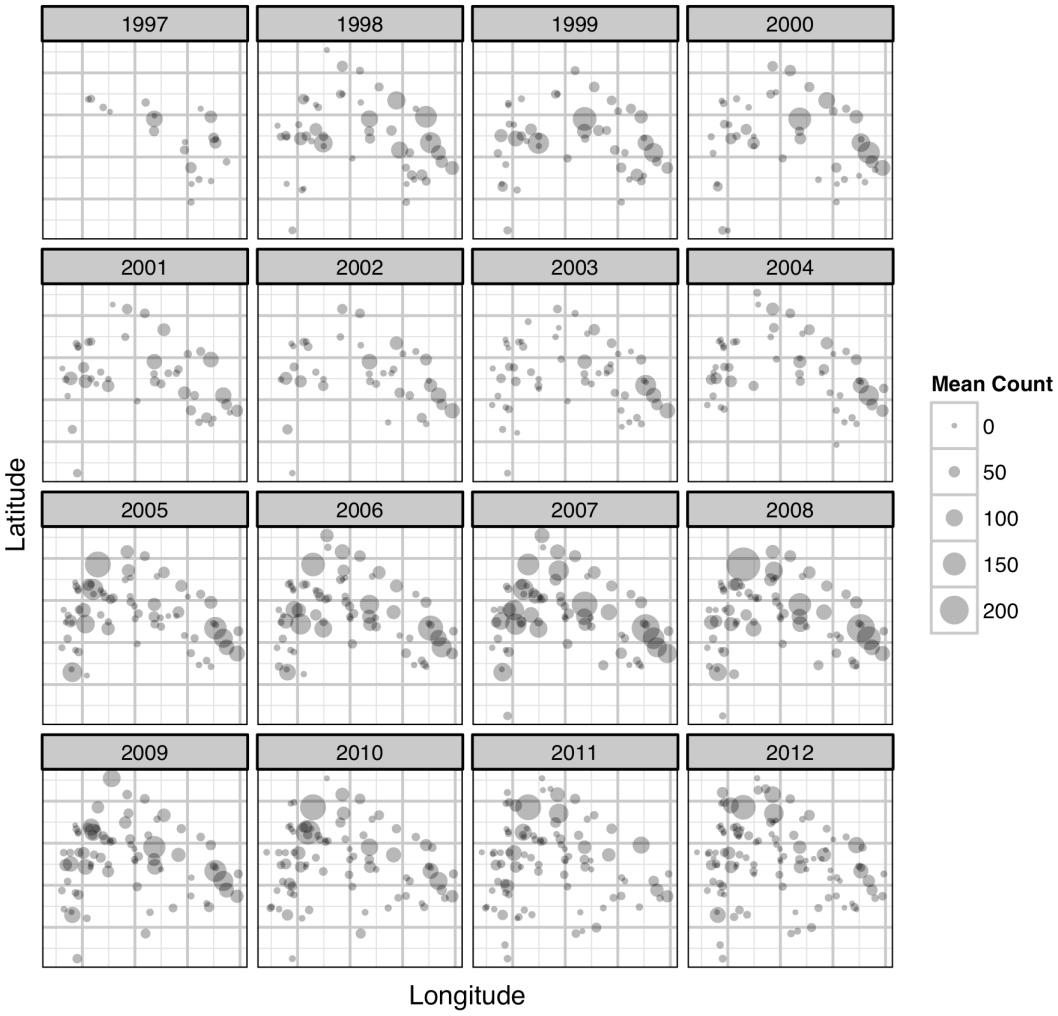


Figure 2. Estimated percent change in male count at an active lek by proportion surface area disturbance within 6.44 km (with 95% confidence intervals). The lek count model assumed that males did not move among leks. Although biologically unrealistic (as sage grouse can move between leks) this provides a conservative test of areal disturbance effects on lek attendance at a local level.

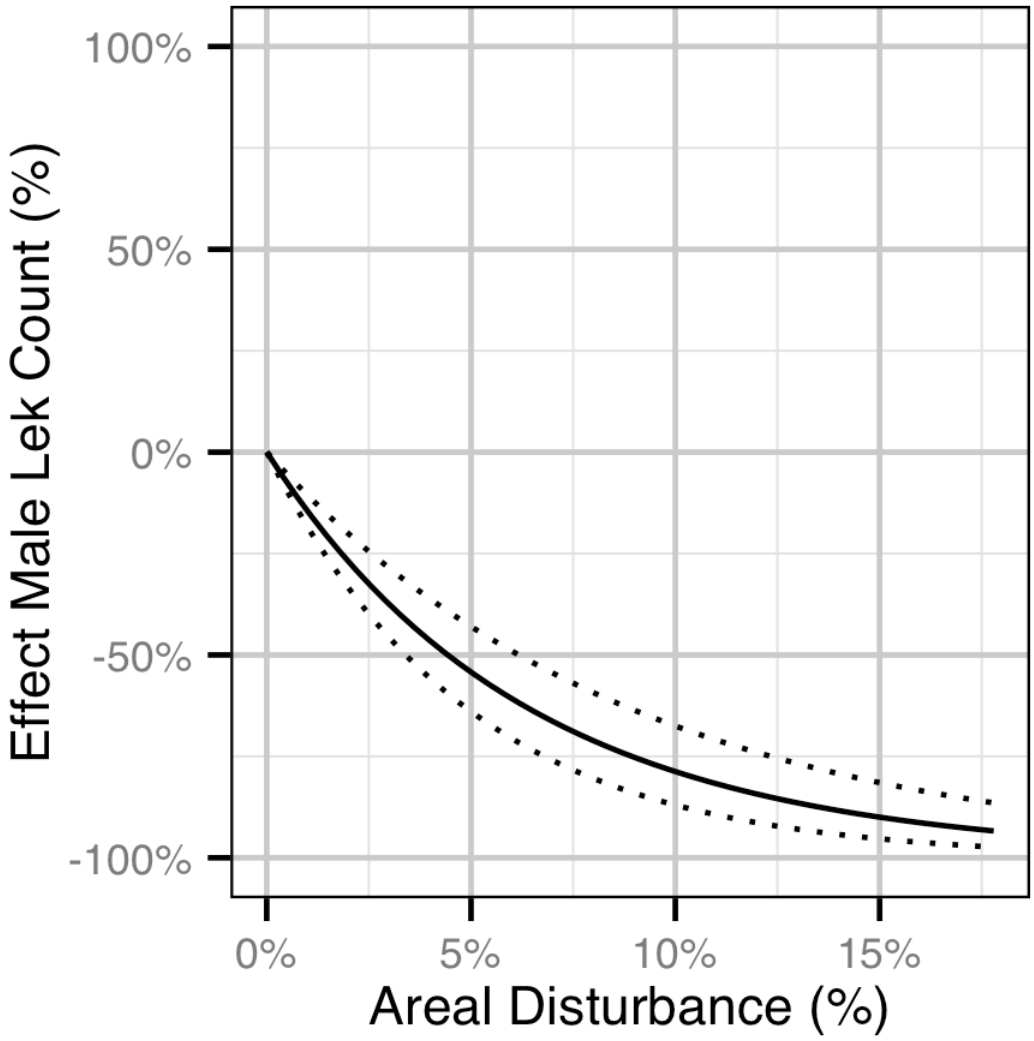


Figure 3. Estimated abundance (mean males per lek) in the Pinedale Planning Area by year (with 95% CRIs).

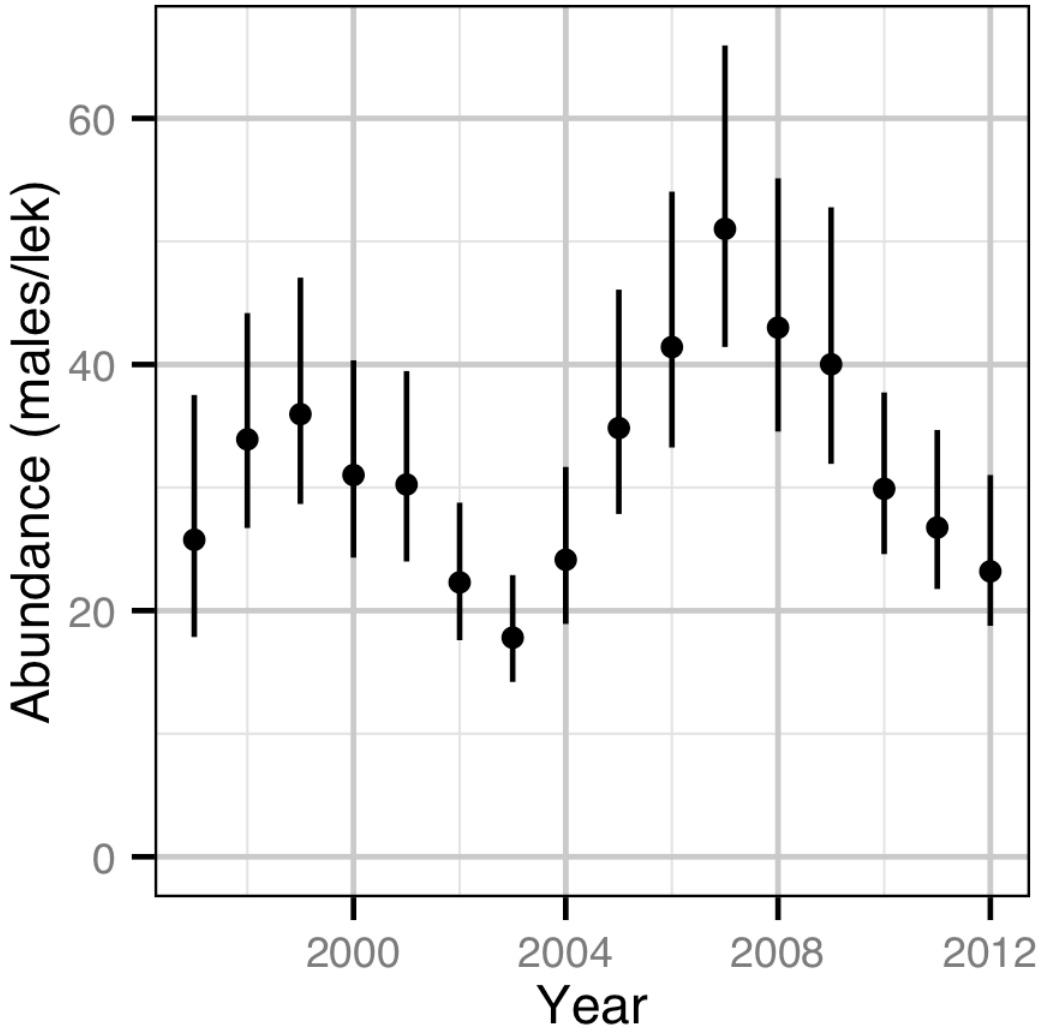
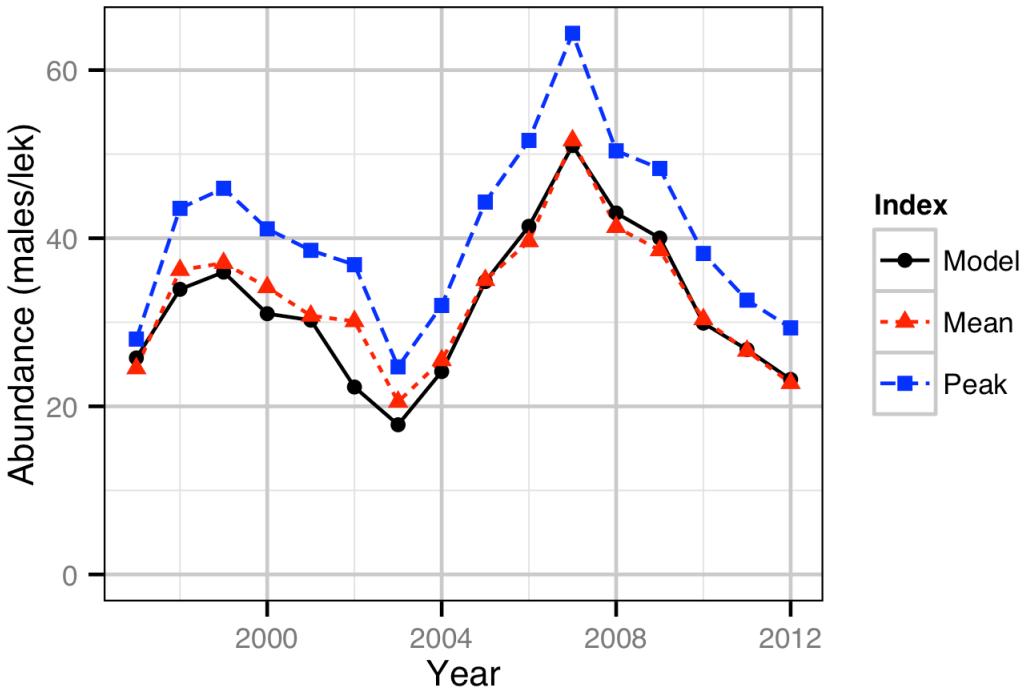


Figure 4. Males per lek by index and year. The indices are the model's prediction (Model), the mean average number (Mean) and the mean peak number (Peak). Mean peak number is the traditionally reported summary statistic used for estimating population trends from lek count data. Use of the mean average number of males per lek, however, provides an estimate that is not biased by the number of counts at each lek.



Pinedale Population Dynamics Analysis

Figure 5. Observed abundance (mean males per lek in blue) in the Pinedale Planning Area versus predicted value (in black with 95% CRIs).

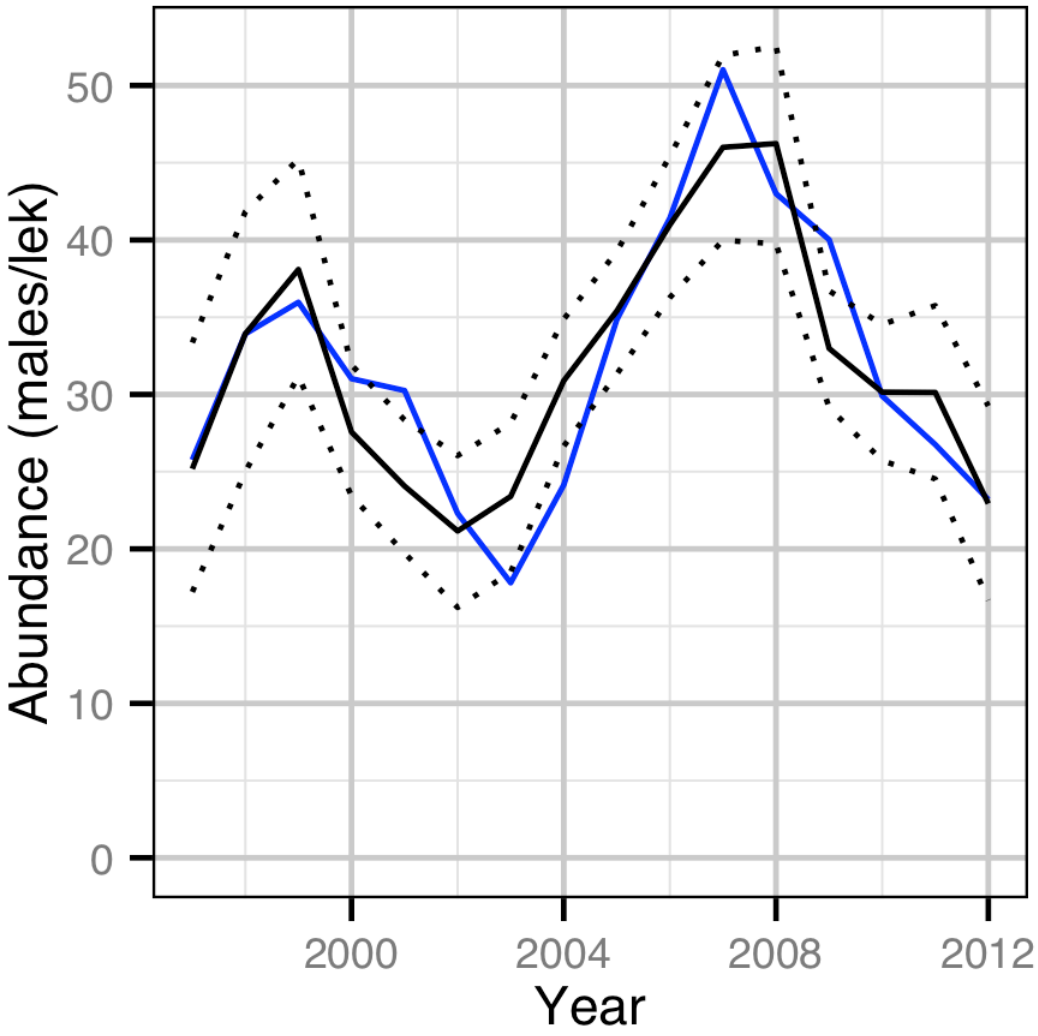


Figure 6. Pacific Decadal Oscillation Index by year. Positive numbers indicate a warm phase and negative numbers a cool phase.

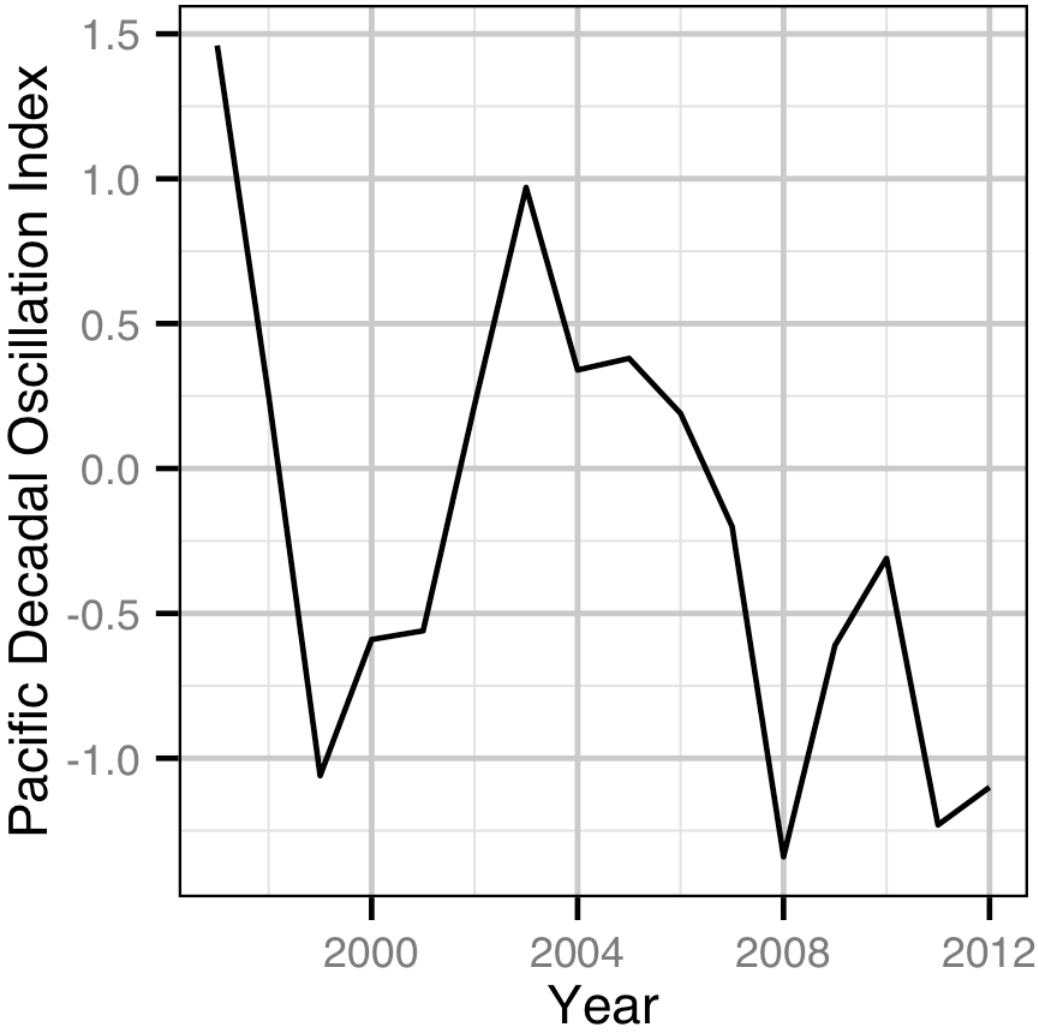


Figure 7. Estimated relationship between annual survival and areal disturbance with a PDO of zero in the Pinedale Planning Area (with 95% CRIs). The relationship is not significant.

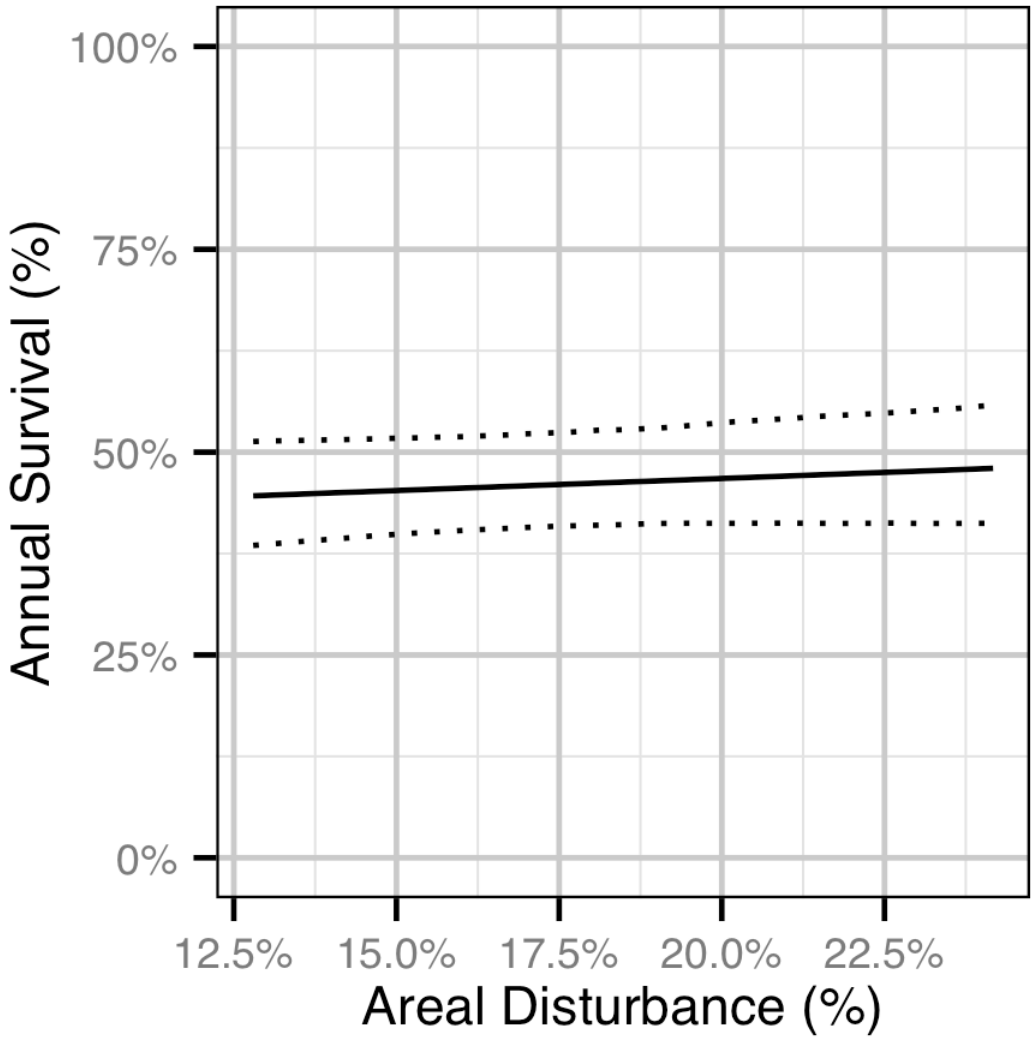


Figure 8. Estimated relationship between annual survival in the Pinedale Planning Area and the Pacific Decadal Oscillation index with an areal disturbance of 20% within 6.44km of leks in the Pinedale Planning Area (with 95% CRIs).

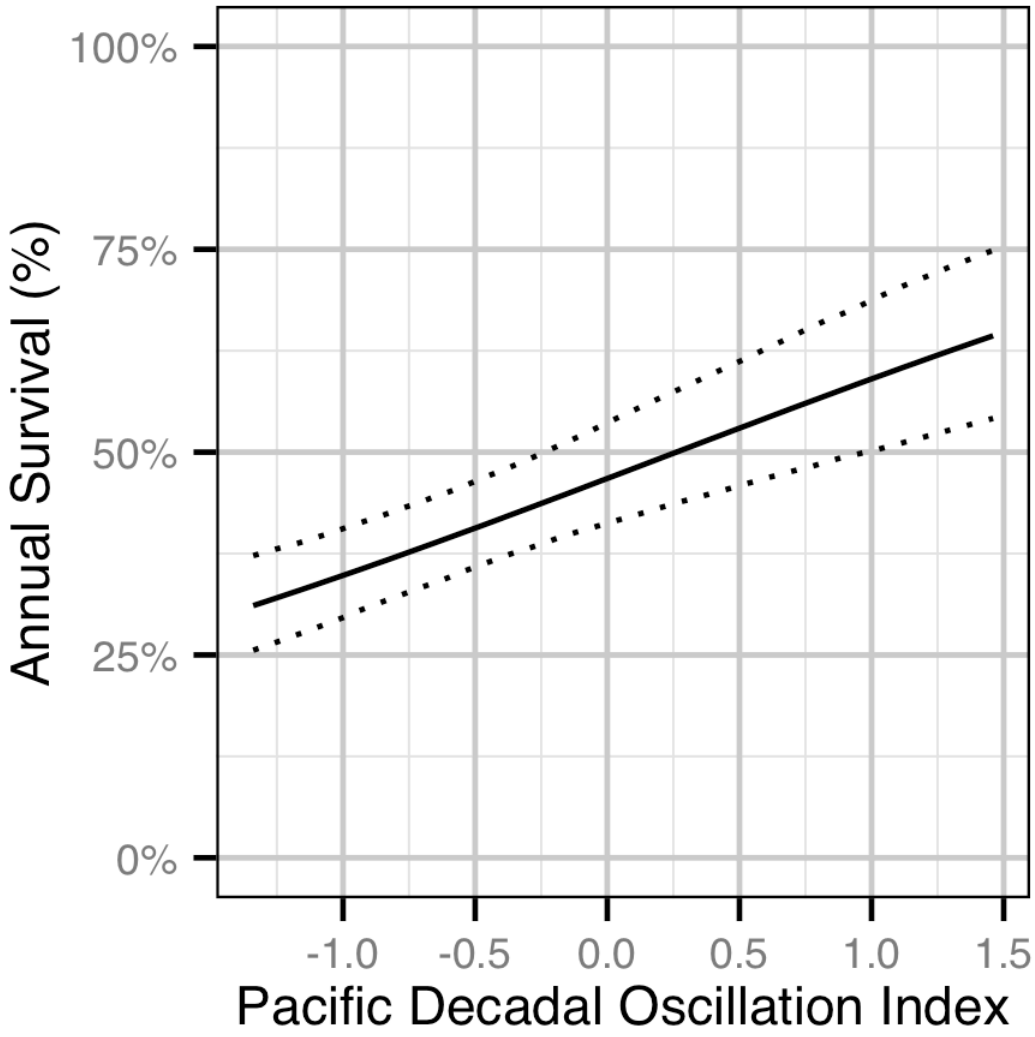
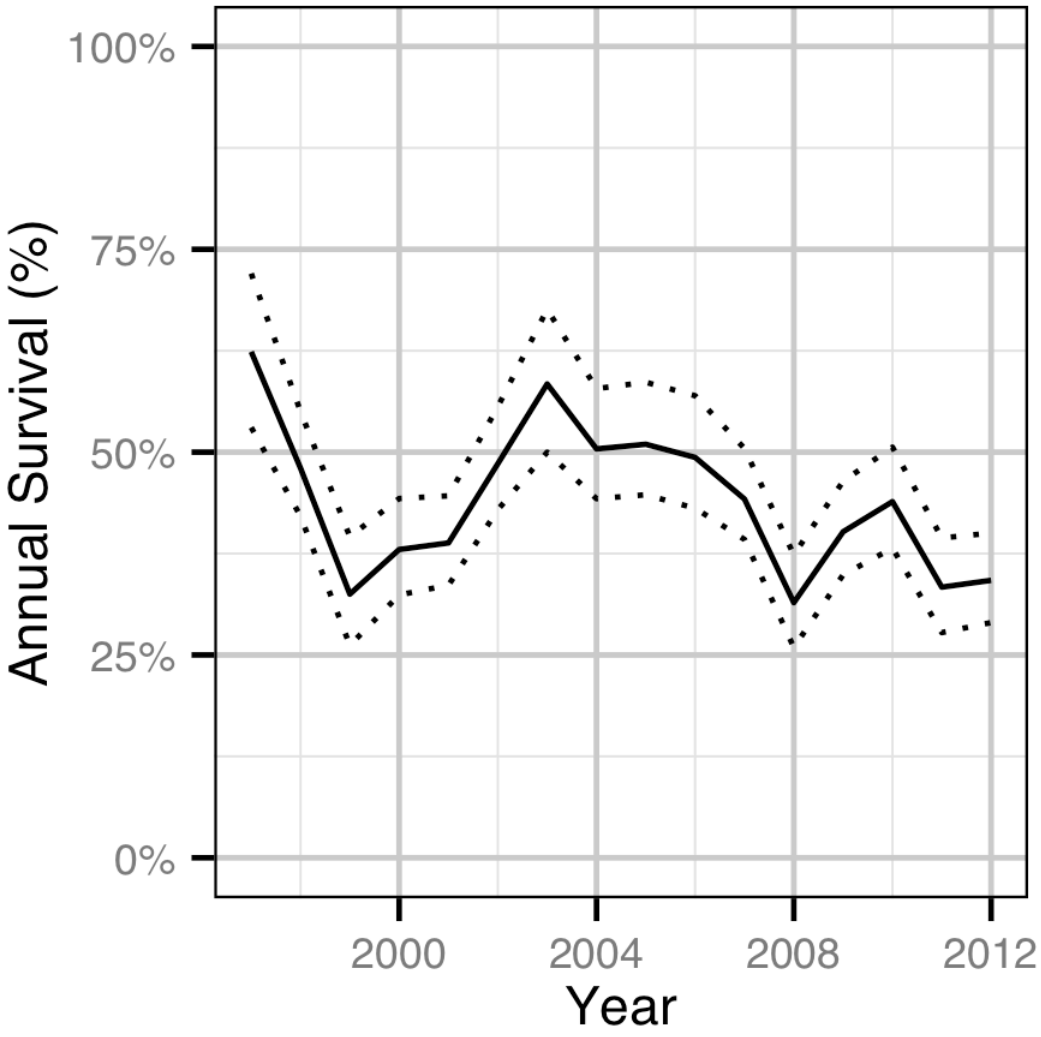


Figure 9. Annual survival by year in the Pinedale Planning Area (with 95% CRIs).



Wyoming Population Dynamics Analysis

Figure 10. Wyoming local sage grouse working groups. These were used a proxies for populations in the Wyoming population dynamics analysis.

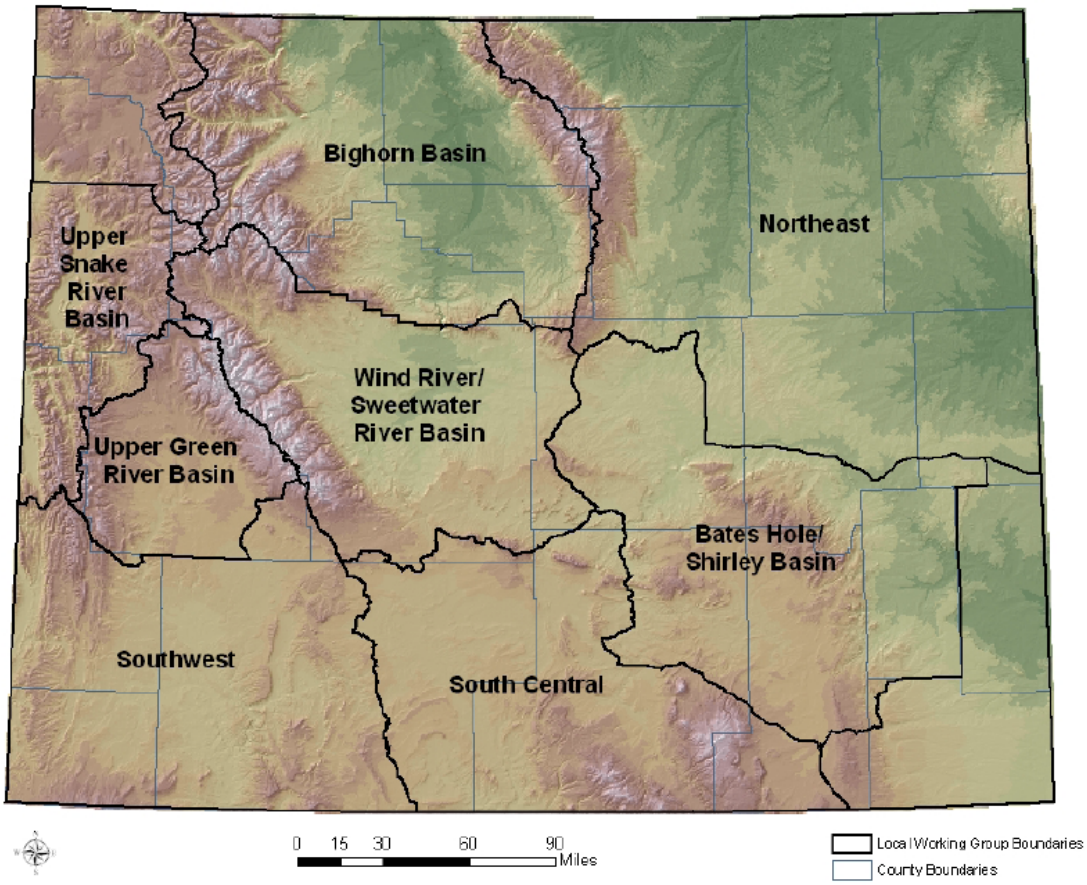


Figure 11. Average mean males per lek where five or more leks were counted at least once.

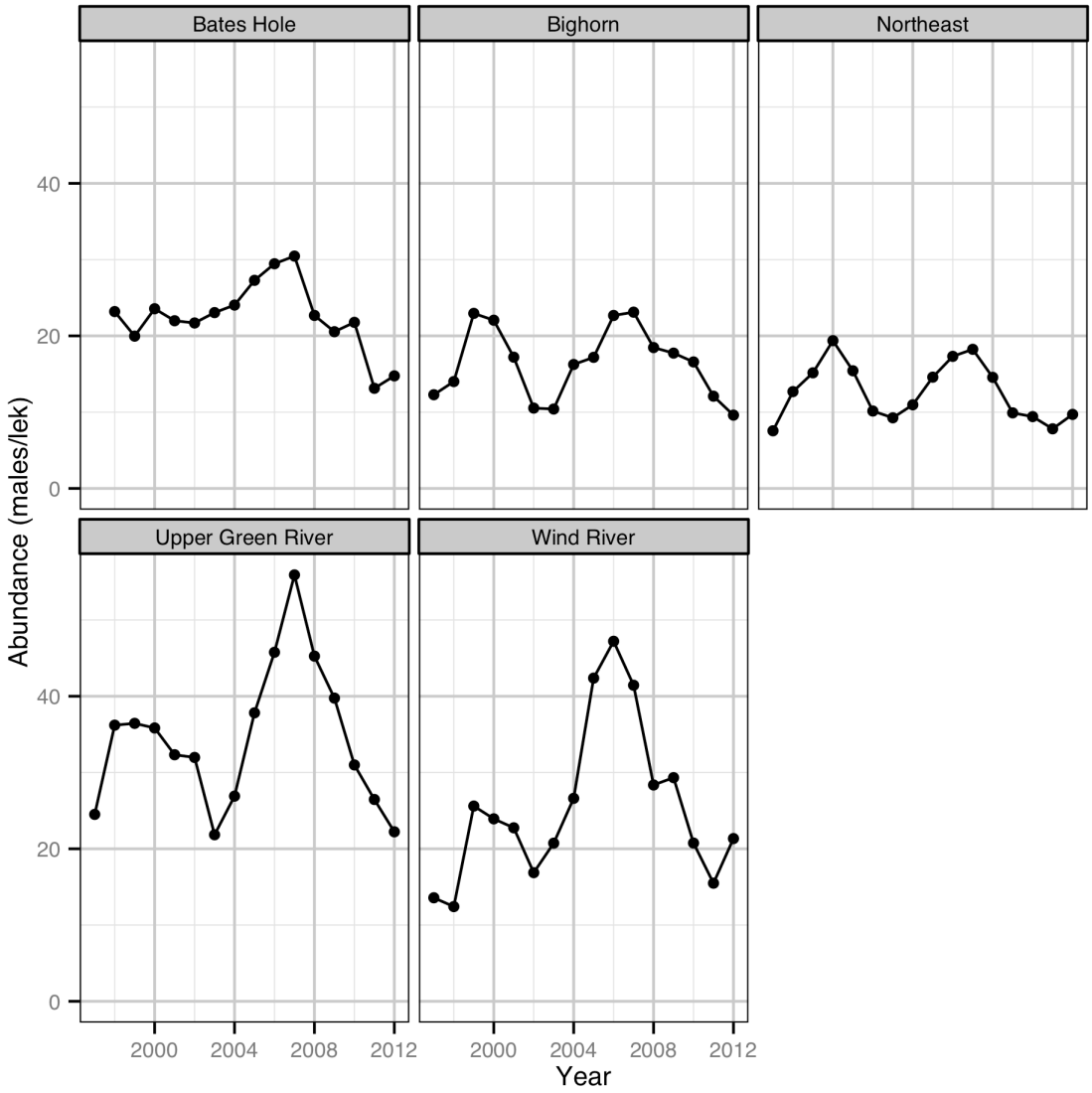


Figure 12. Calculated mean males per lek (in blue) versus predicted males per lek (in black with 95% CRIs) by working group and year.

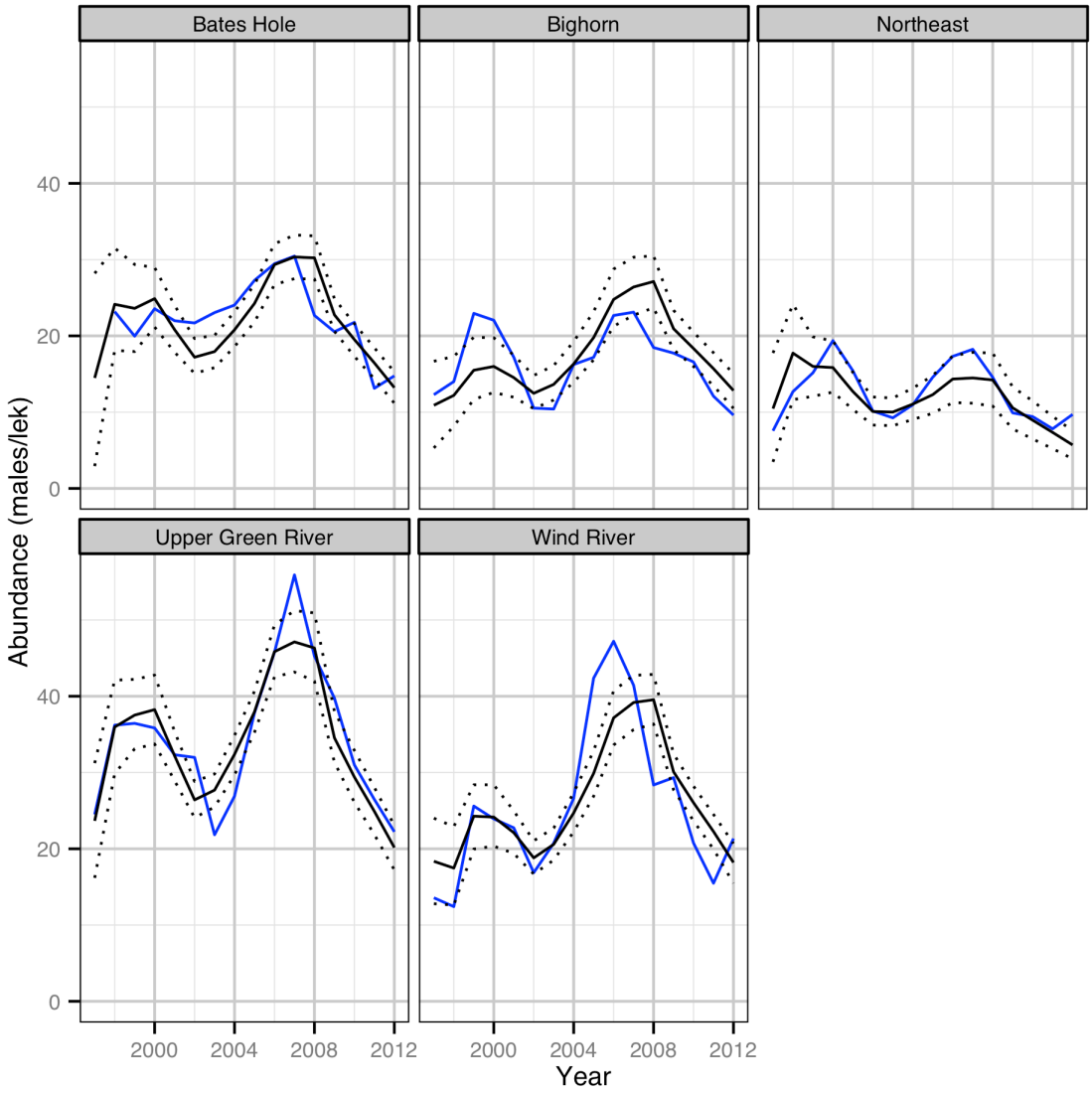


Figure 13. Areal disturbance by working group and year. The two working groups with the highest areal disturbance are Northeastern and Upper Green River.

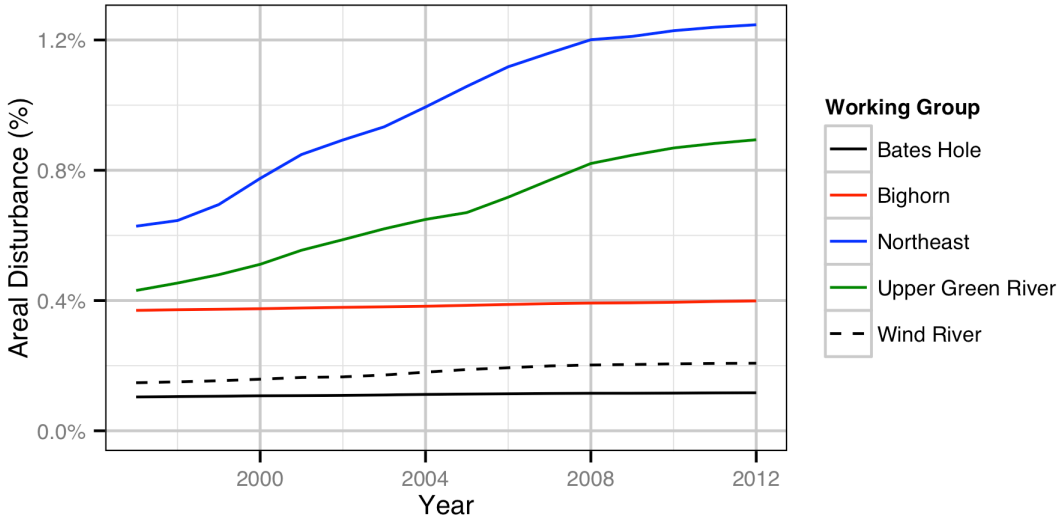


Figure 14. Estimated effect of Pacific Decadal Oscillation Index on chick productivity in Wyoming working groups with no areal disturbance, a habitat quality of 75% and an abundance of 30 males per lek (with 95% CRIs).

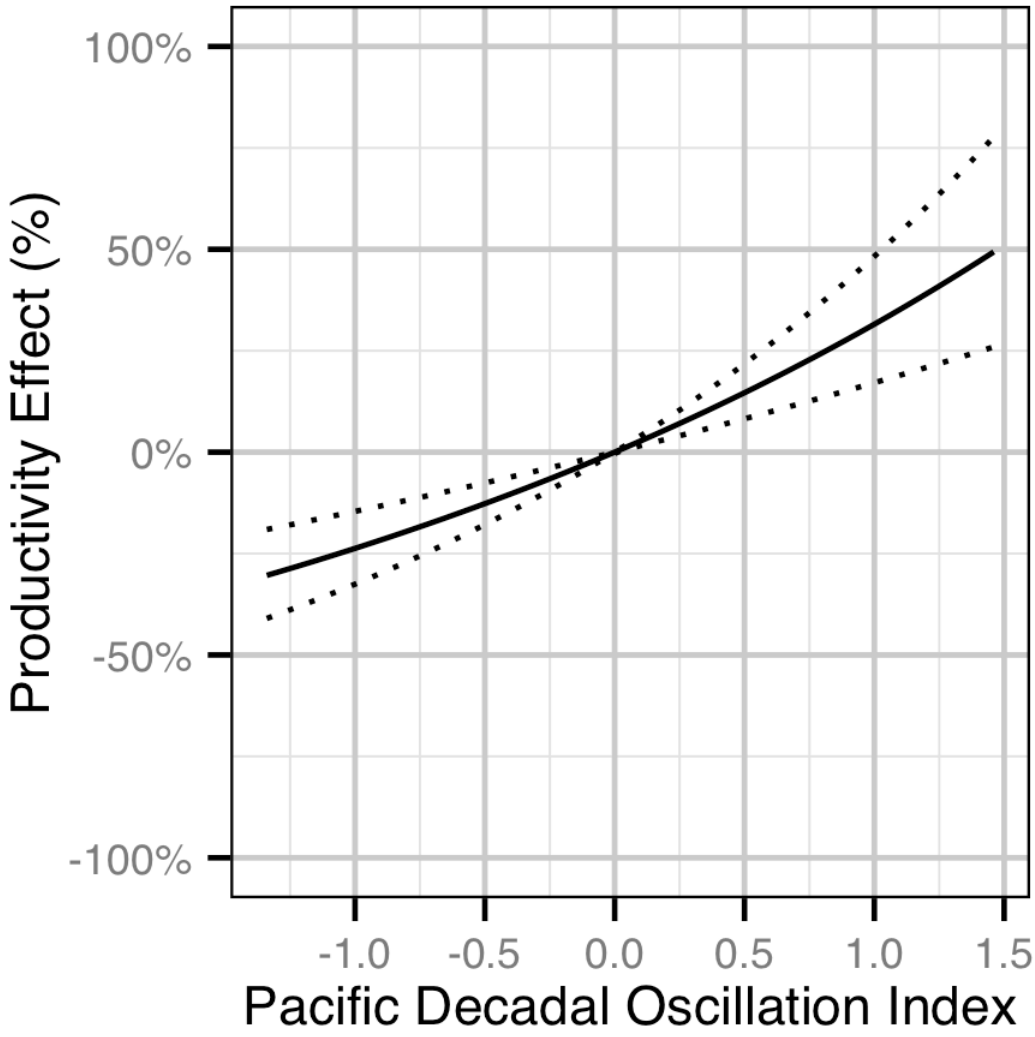


Figure 15. Estimated effect of habitat quality on chick productivity in Wyoming working groups, with a Pacific Decadal Oscillation Index of 0, no areal disturbance, and an abundance of 30 males per lek (with 95% CRIs).

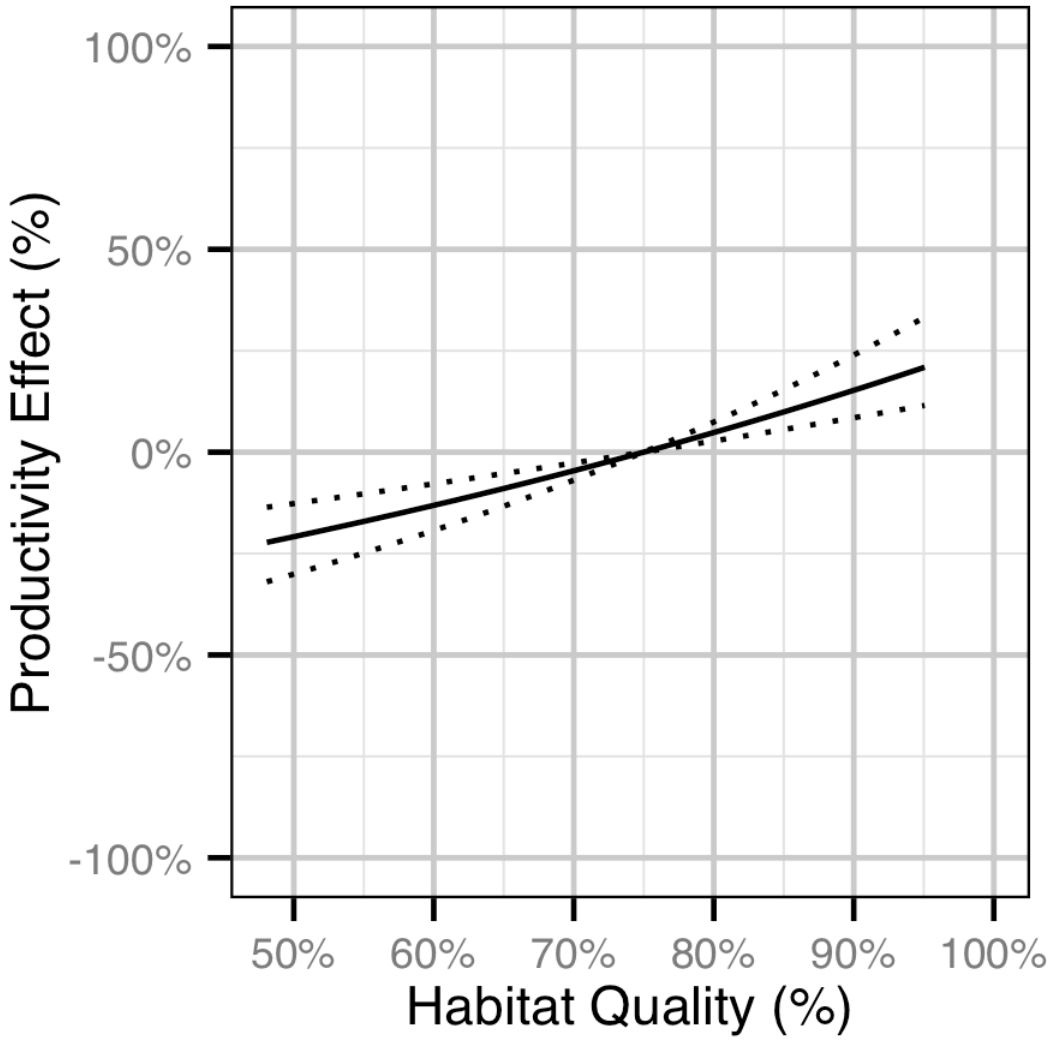


Figure 16. Estimated effect of areal disturbance on chick productivity in Wyoming working groups with a Pacific Decadal Oscillation Index of 0, a habitat quality index of 0.75 and an abundance of 30 males per lek (with 95% CRIs).

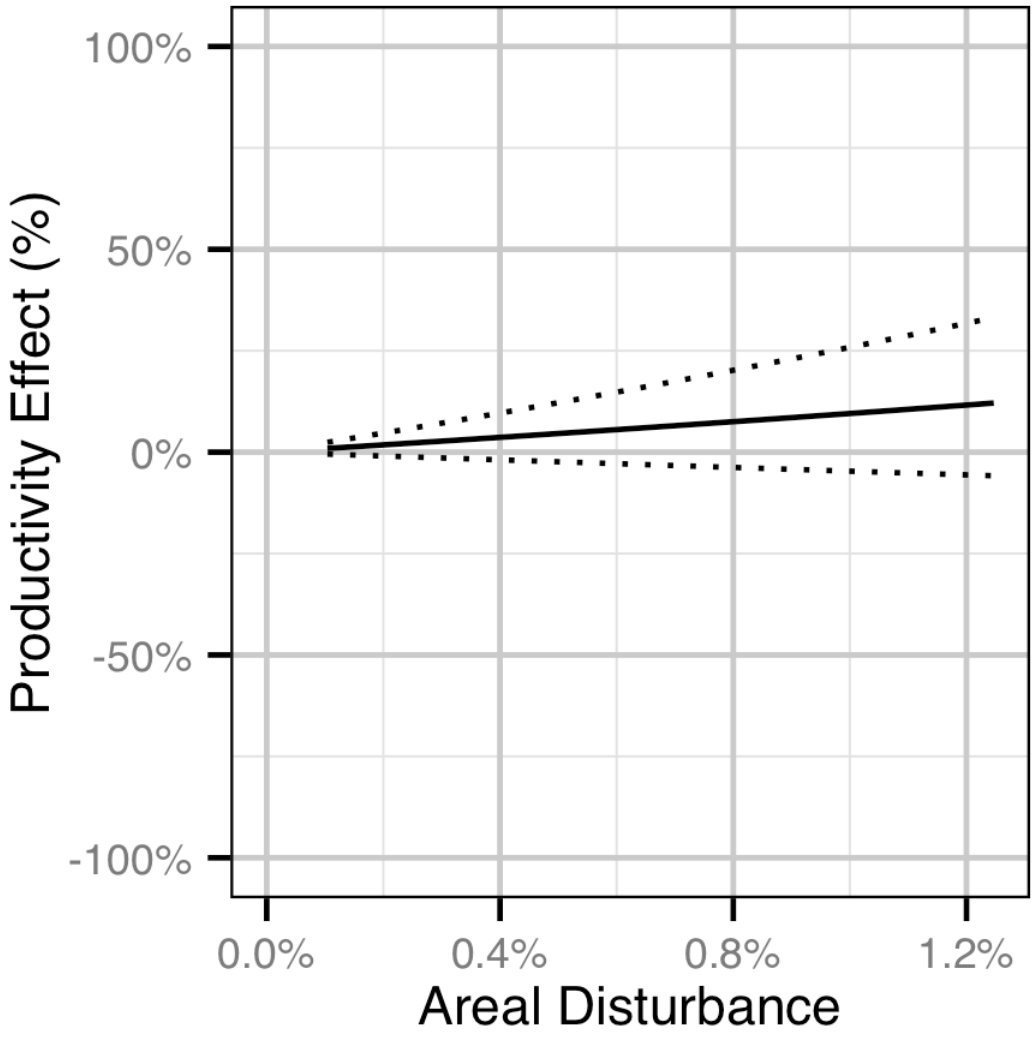


Figure 17. Estimated relationship between annual survival and the Pacific Decadal Oscillation Index (with 95% CRIs) in Wyoming working groups

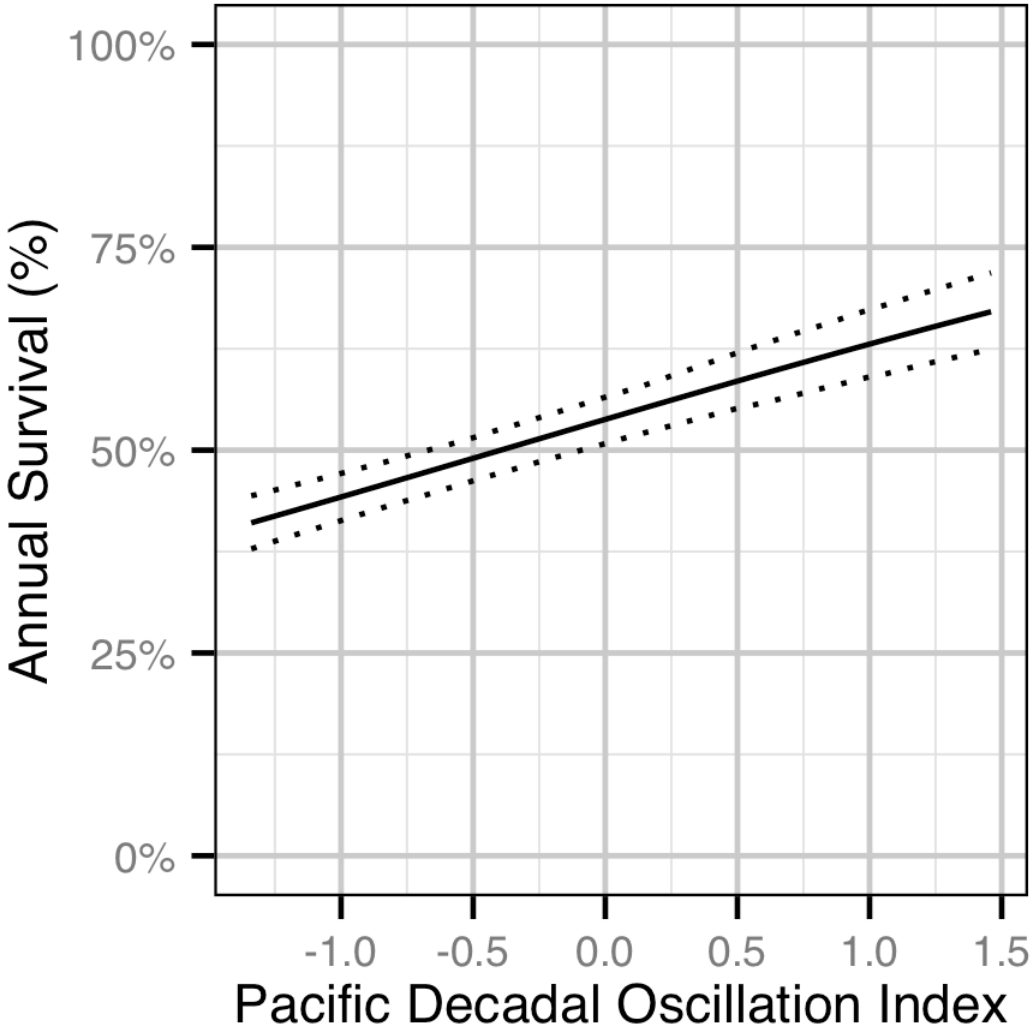
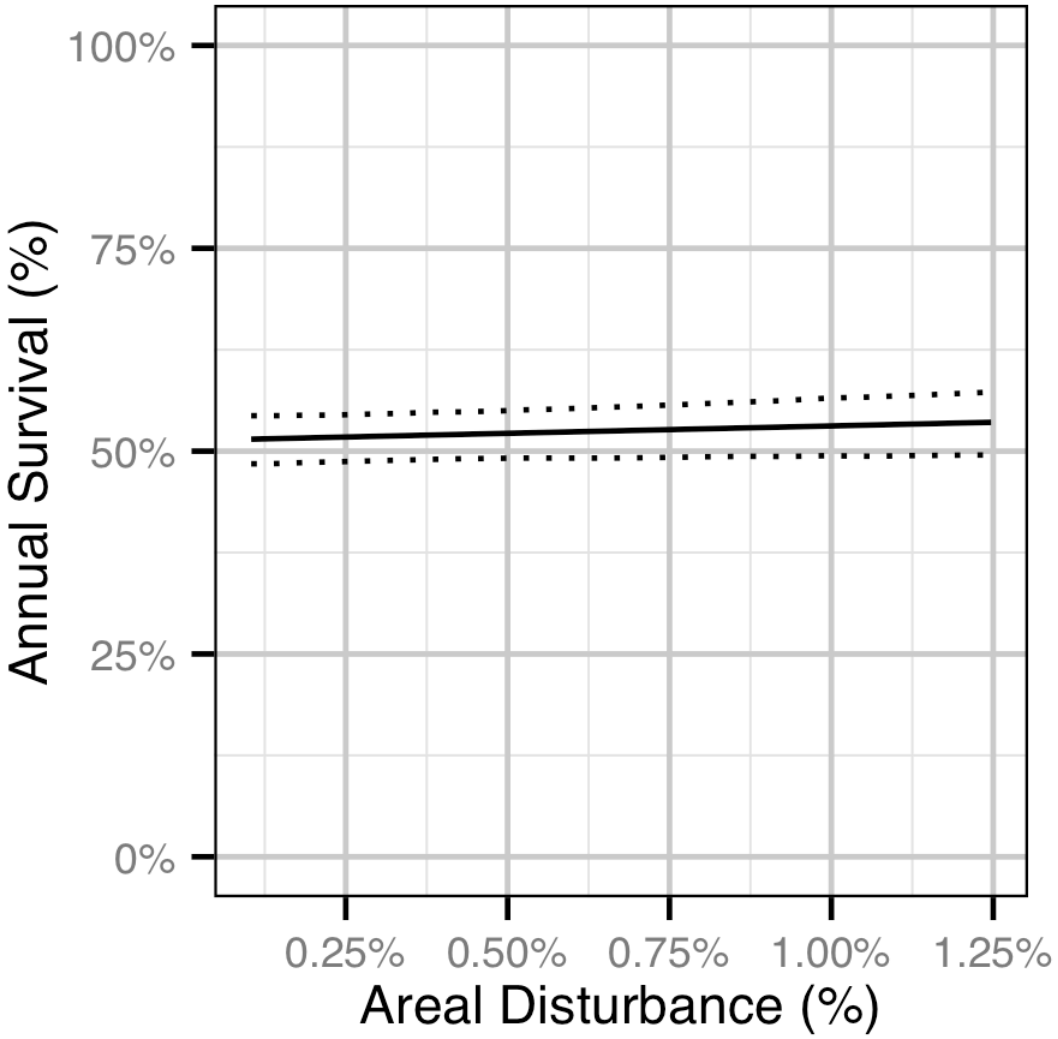


Figure 18. Estimated relationship between annual survival and areal disturbance (with 95% CRIs) in Wyoming working groups.



Appendix A.

Wyoming Lek Counts

Model Code

The JAGS model code, which uses a series of naming conventions, is presented below.

Pinedale Lek Counts

Variable/Parameter	Description
`ArealDisturbance[i]`	Proportion surface area disturbance within 6.44 km of lek on `i`th visit
`bArealDisturbance`	Effect of `ArealDisturbance` on `bYear`
`bArealDisturbance2`	Quadratic effect of `ArealDisturbance` on `bYear`
`Block[i]`	Block on `i`th visit
`bType[i]`	Effect of `Type` on bYear
`bYear[i]`	Intercept for `log(eMales)` in `i`th `Year`
`eMales[i]`	Expected male count on `i`th visit
`Lek[i]`	Lek on `i`th visit
`Males[i]`	Male count on `i`th visit
`sBlockYear`	SD of effect of `Block` within `Year` on `bYear`
`sDispersion`	SD of overdispersion term
`sMalesLek`	SD of effect of `Lek` on `bYear`
`sMalesLekYear`	SD of effect of `Lek` within `Year` on `bYear`
`Type[i]`	Type (count or survey) on `i`th visit
`Year[i]`	Year of `i`th visit

Pinedale Lek Counts - Model1

```
model{

  for(i in 1:nYear){
    bYear[i] ~ dnorm(2, 5^-2)
  }

  bArealDisturbance ~ dnorm(0, 5^-2)

  sBlockYear ~ dunif(0, 5)
  for(i in 1:nBlock){
    for(j in 1:nYear){
```

```
      bBlockYear[i,j] ~ dnorm(0, sBlockYear^-2)
    }
  }

  sMalesLek ~ dunif(0, 5)
  sMalesLekYear ~ dunif(0, 5)
  for(i in 1:nLek){
    bLek[i] ~ dnorm(0, sMalesLek^-2)
    for(j in 1:nYear){
      bLekYear[i,j] ~ dnorm(0, sMalesLekYear^-2)
    }
  }

  sDispersion ~ dunif(0, 5)
  for(i in 1:length(Males)) {
    log(eMales[i]) <- bYear[Year[i]] + bArealDisturbance *
ArealDisturbance[i] + bBlockYear[Block[i], Year[i]] + bLek[Lek[i]] +
bLekYear[Lek[i],Year[i]]
    eDispersion[i] ~ dgamma(1 / sDispersion^2, 1 / sDispersion^2)
    Males[i] ~ dpois(eMales[i] * eDispersion[i])
  }

}
```

Pinedale Lek Counts - Model2

```
model{

  for(i in 1:nYear){
    bYear[i] ~ dnorm(2, 5^-2)
  }

  bArealDisturbance ~ dnorm(0, 5^-2)
  bArealDisturbance2 ~ dnorm(0, 5^-2)

  sBlockYear ~ dunif(0, 5)
  for(i in 1:nBlock){
    for(j in 1:nYear){
      bBlockYear[i,j] ~ dnorm(0, sBlockYear^-2)
    }
  }

  sMalesLek ~ dunif(0, 5)
  sMalesLekYear ~ dunif(0, 5)
  for(i in 1:nLek){
    bLek[i] ~ dnorm(0, sMalesLek^-2)
    for(j in 1:nYear){
      bLekYear[i,j] ~ dnorm(0, sMalesLekYear^-2)
    }
  }
```

```
  sDispersion ~ dunif(0, 5)
  for(i in 1:length(Males)) {
    log(eMales[i]) <- bYear[Year[i]] + bArealDisturbance *
ArealDisturbance[i] + bArealDisturbance2 * ArealDisturbance[i]^2 +
bBlockYear[Block[i], Year[i]] + bLek[Lek[i]] + bLekYear[Lek[i],Year[i]]
    eDispersion[i] ~ dgamma(1 / sDispersion^2, 1 / sDispersion^2)
    Males[i] ~ dpois(eMales[i] * eDispersion[i])
  }

}
```

Pinedale Lek Counts - Model3

```
model{

  for(i in 1:nYear){
    bYear[i] ~ dnorm(2, 5^-2)
  }

  sMalesLek ~ dunif(0, 5)
  sMalesLekYear ~ dunif(0, 5)
  for(i in 1:nLek){
    bLek[i] ~ dnorm(0, sMalesLek^-2)
    for(j in 1:nYear){
      bLekYear[i,j] ~ dnorm(0, sMalesLekYear^-2)
    }
  }

  sDispersion ~ dunif(0, 5)
  for(i in 1:length(Males)) {
    log(eMales[i]) <- bYear[Year[i]] + bLek[Lek[i]] +
bLekYear[Lek[i],Year[i]]
    eDispersion[i] ~ dgamma(1 / sDispersion^2, 1 / sDispersion^2)
    Males[i] ~ dpois(eMales[i] * eDispersion[i])
  }

}
```

Pinedale Lek Counts - Model4

```
model{

  for(i in 1:nYear){
    bYear[i] ~ dnorm(2, 5^-2)
  }

  sMalesLek ~ dunif(0, 5)
  sMalesLekYear ~ dunif(0, 5)
  for(i in 1:nLek){
```

```
    bLek[i] ~ dnorm(0, sMalesLek^-2)
    for(j in 1:nYear){
      bLekYear[i,j] ~ dnorm(0, sMalesLekYear^-2)
    }
  }

  sDispersion ~ dunif(0, 5)
  for(i in 1:length(Males)) {
    log(eMales[i]) <- bYear[Year[i]] + bLek[Lek[i]] +
bLekYear[Lek[i],Year[i]]
    eDispersion[i] ~ dgamma(1 / sDispersion^2, 1 / sDispersion^2)
    Males[i] ~ dpois(eMales[i] * eDispersion[i])
  }

}
```

Pinedale Lek Counts - Model5

```
model{

  for(i in 1:nYear){
    bYear[i] ~ dnorm(2, 5^-2)
  }

  bArealDisturbance ~ dnorm(0, 5^-2)

  bType[1] <- 0
  for(i in 2:nType) {
    bType[i] ~ dnorm(0, 5^-2)
  }

  sBlockYear ~ dunif(0, 5)
  for(i in 1:nBlock){
    for(j in 1:nYear){
      bBlockYear[i,j] ~ dnorm(0, sBlockYear^-2)
    }
  }

  sMalesLek ~ dunif(0, 5)
  sMalesLekYear ~ dunif(0, 5)
  for(i in 1:nLek){
    bLek[i] ~ dnorm(0, sMalesLek^-2)
    for(j in 1:nYear){
      bLekYear[i,j] ~ dnorm(0, sMalesLekYear^-2)
    }
  }

  sDispersion ~ dunif(0, 5)
  for(i in 1:length(Males)) {
```

```
    log(eMales[i]) <- bYear[Year[i]] + bArealDisturbance *
ArealDisturbance[i] + bType[Type[i]] + bBlockYear[Block[i], Year[i]] +
bLek[Lek[i]] + bLekYear[Lek[i],Year[i]]
    eDispersion[i] ~ dgamma(1 / sDispersion^2, 1 / sDispersion^2)
    Males[i] ~ dpois(eMales[i] * eDispersion[i])
  }

}
```

Pinedale Population Dynamics

Variable/Parameter	Description
`Abundance[i]`	Number of males per lek in `i`th year
`ArealDisturbance[i]`	Percent decline in population abundance in `i`th year from lek count model
`bAdults[i]`	Expected abundance of adults in `i`th Year
`bChicks[i]`	Expected abundance of chicks in `i`th Year
`bChicksPerAdult`	Number of chicks per adult
`bSurvival`	Intercept for `logit(eSurvival)`
`bSurvivalArealDisturbance`	Effect of `ArealDisturbance` on `bSurvival`
`bSurvivalPDO`	Effect of `PDO` on `bSurvival`
`bYearling[i]`	Expected abundance of yearlings in `i`th Year
`eSurvival[i]`	Expected annual survival in `i`th Year
`PDO[i]`	Pacific Decadal Oscillation Index in `i`th year
`sAbundance`	SD of residual variation in `Abundance`

Pinedale Population Dynamics - Model1

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalPDO ~ dnorm(0, 2^-2)
  bSurvivalArealDisturbance ~ dnorm(0, 2^-2)
  for(i in 1:nYear) {
    logit(eSurvival[i]) <-bSurvival + bSurvivalPDO * PDO[i] +
bSurvivalArealDisturbance * ArealDisturbance[i]
  }

  bAdults[1] ~ dunif(0, 100)
  bYearlings[1] ~ dunif(0, 100)
  bChicks[1] <- bChicksPerAdult * bAdults[1]
  for(i in 2:nYear){
    bAdults[i] <- (bYearlings[i-1] + bAdults[i-1]) * eSurvival[i-1]
    bYearlings[i] <- bChicks[i-1] * eSurvival[i-1]
```

```
    bChicks[i] <- bChicksPerAdult * bAdults[i]
  }

  sAbundance ~ dunif(0, 10)
  for(i in 1:nYear) {
    Abundance[i] ~ dnorm(bAdults[i] / 2, sAbundance^-2)
  }
}
```

Pinedale Population Dynamics - Model2

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalPDO ~ dnorm(0, 2^-2)
  for(i in 1:nYear) {
    logit(eSurvival[i]) <-bSurvival + bSurvivalPDO * PDO[i]
  }

  bAdults[1] ~ dunif(0, 100)
  bYearlings[1] ~ dunif(0, 100)
  bChicks[1] <- bChicksPerAdult * bAdults[1]
  for(i in 2:nYear){
    bAdults[i] <- (bYearlings[i-1] + bAdults[i-1]) * eSurvival[i-1]
    bYearlings[i] <- bChicks[i-1] * eSurvival[i-1]
    bChicks[i] <- bChicksPerAdult * bAdults[i]
  }

  sAbundance ~ dunif(0, 10)
  for(i in 1:nYear) {
    Abundance[i] ~ dnorm(bAdults[i] / 2, sAbundance^-2)
  }
}
```

Pinedale Population Dynamics - Model3

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalArealDisturbance ~ dnorm(0, 2^-2)
  for(i in 1:nYear) {
    logit(eSurvival[i]) <-bSurvival + bSurvivalArealDisturbance *
ArealDisturbance[i]
  }

  bAdults[1] ~ dunif(0, 100)
```

```
  bYearlings[1] ~ dunif(0, 100)
  bChicks[1] <- bChicksPerAdult * bAdults[1]
  for(i in 2:nYear){
    bAdults[i] <- (bYearlings[i-1] + bAdults[i-1]) * eSurvival[i-1]
    bYearlings[i] <- bChicks[i-1] * eSurvival[i-1]
    bChicks[i] <- bChicksPerAdult * bAdults[i]
  }

  sAbundance ~ dunif(0, 10)
  for(i in 1:nYear) {
    Abundance[i] ~ dnorm(bAdults[i] / 2, sAbundance^-2)
  }
}
```

Pinedale Population Dynamics - Model4

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bSurvival ~ dnorm(0, 2^-2)
  for(i in 1:nYear) {
    logit(eSurvival[i]) <-bSurvival
  }

  bAdults[1] ~ dunif(0, 100)
  bYearlings[1] ~ dunif(0, 100)
  bChicks[1] <- bChicksPerAdult * bAdults[1]
  for(i in 2:nYear){
    bAdults[i] <- (bYearlings[i-1] + bAdults[i-1]) * eSurvival[i-1]
    bYearlings[i] <- bChicks[i-1] * eSurvival[i-1]
    bChicks[i] <- bChicksPerAdult * bAdults[i]
  }

  sAbundance ~ dunif(0, 10)
  for(i in 1:nYear) {
    Abundance[i] ~ dnorm(bAdults[i] / 2, sAbundance^-2)
  }
}
```

Wyoming Population Dynamics

Variable/Parameter	Description
`bAdults[i]`	Expected adult abundance in `i`th `Year`
`bChickCarryingCapacity`	Intercept for `log(eChickCarryingCapacity)`
`bChicks[i]`	Expected chick abundance in `i`th `Year`
`bChicksPerAdult`	Expected chicks per adult at low abundance
`bProductivityArealDisturbance`	Effect of `ArealDisturbance` on `log(bChicks)`

bProductivityHabitatQuality	Effect of HabitatQuality on log(bChicks)
bProductivityPDO	Effect of PDO on log(bChicks)
bSurvival	Intercept for logit(eSurvival)
bSurvivalArealDisturbance	Effect of ArealDisturbance on log(bChicks)
bSurvivalPDO	Effect of PDO on bSurvival
bYearling[i]	Expected yearling abundance in i^{th} Year
ChickWings[i,j]	Number of chick SD of residual variation in Abundance
eChickCarryingCapacity	Expected carrying capacity (chicks per adult)
eSurvival[i]	Expected yearling and adult survival from i^{th} to $i+1^{th}$ Year
sAbundance	SD of residual variation in Abundance
sDispersion	SD of extra-bionmial variation in ChickWings

Wyoming Population Dynamics - Model1

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bChickCarryingCapacity ~ dnorm(0, 5^-2)

  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      log(eChickCarryingCapacity[i,j]) <- bChickCarryingCapacity
    }
  }

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalPDO ~ dnorm(0, 2^-2)
  bSurvivalArealDisturbance ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      logit(eSurvival[i,j]) <- bSurvival + bSurvivalPDO * PDO[i,j] +
bSurvivalArealDisturbance * ArealDisturbance[i,j]
    }
  }

  bProductivityPDO ~ dnorm(0, 2^-2)
  bProductivityArealDisturbance ~ dnorm(0, 2^-2)
  bProductivityHabitatQuality ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    bAdults[i,1] ~ dunif(0, 100)
    bYearlings[i,1] ~ dunif(0, 100)
    log(bChicks[i,1]) <- log(bChicksPerAdult * bAdults[i,1] / (1 +
```

```
bAdults[i,1] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,1])) +
bProductivityArealDisturbance * ArealDisturbance[i,1] +
bProductivityHabitatQuality * HabitatQuality[i,1]
    for(j in 2:nYear){
      log(bChicks[i,j]) <- log(bChicksPerAdult * bAdults[i,j] / (1 +
bAdults[i,j] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,j])) +
bProductivityPDO * PDO[i,j-1] + bProductivityArealDisturbance *
ArealDisturbance[i,j] + bProductivityHabitatQuality *
HabitatQuality[i,j]
      bYearlings[i,j] <- bChicks[i,j-1] * eSurvival[i,j-1]
      bAdults[i,j] <- (bYearlings[i,j-1] + bAdults[i,j-1]) *
eSurvival[i,j-1]
    }
  }

  sOverDispersion ~ dunif(0, 2)
  sAbundance ~ dunif(0, 10)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      eWeightedAbundance[i,j] <- bChicks[i,j] + bYearlings[i,j] +
bAdults[i,j]

      eOverDispersion[i,j] ~ dnorm(0, sOverDispersion^-2)

      logit(eProportionChicks[i,j]) <- logit(bChicks[i,j] /
eWeightedAbundance[i,j]) + eOverDispersion[i,j]

      ChickWings[i,j] ~ dbin(eProportionChicks[i,j],
NumberOfWings[i,j])

      eAbundance[i,j] <- bAdults[i,j] / 2
      Abundance[i,j] ~ dnorm(eAbundance[i,j], sAbundance^-2)
    }
  }
}
```

Wyoming Population Dynamics - Model2

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bChickCarryingCapacity ~ dnorm(0, 5^-2)

  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      log(eChickCarryingCapacity[i,j]) <- bChickCarryingCapacity
    }
  }
```

```
  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalArealDisturbance ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      logit(eSurvival[i,j]) <- bSurvival + bSurvivalArealDisturbance *
ArealDisturbance[i,j]
    }
  }

  bProductivityArealDisturbance ~ dnorm(0, 2^-2)
  bProductivityHabitatQuality ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    bAdults[i,1] ~ dunif(0, 100)
    bYearlings[i,1] ~ dunif(0, 100)
    log(bChicks[i,1]) <- log(bChicksPerAdult * bAdults[i,1] / (1 +
bAdults[i,1] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,1])) +
bProductivityArealDisturbance * ArealDisturbance[i,1] +
bProductivityHabitatQuality * HabitatQuality[i,1]
    for(j in 2:nYear){
      log(bChicks[i,j]) <- log(bChicksPerAdult * bAdults[i,j] / (1 +
bAdults[i,j] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,j])) +
bProductivityArealDisturbance * ArealDisturbance[i,j] +
bProductivityHabitatQuality * HabitatQuality[i,j]
      bYearlings[i,j] <- bChicks[i,j-1] * eSurvival[i,j-1]
      bAdults[i,j] <- (bYearlings[i,j-1] + bAdults[i,j-1]) *
eSurvival[i,j-1]
    }
  }

  sOverDispersion ~ dunif(0, 2)
  sAbundance ~ dunif(0, 10)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      eWeightedAbundance[i,j] <- bChicks[i,j] + bYearlings[i,j] +
bAdults[i,j]

      eOverDispersion[i,j] ~ dnorm(0, sOverDispersion^-2)

      logit(eProportionChicks[i,j]) <- logit(bChicks[i,j] /
eWeightedAbundance[i,j]) + eOverDispersion[i,j]

      ChickWings[i,j] ~ dbin(eProportionChicks[i,j],
NumberOfWings[i,j])

      eAbundance[i,j] <- bAdults[i,j] / 2
      Abundance[i,j] ~ dnorm(eAbundance[i,j], sAbundance^-2)
    }
```

```
  }
}
```

Wyoming Population Dynamics - Model3

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bChickCarryingCapacity ~ dnorm(0, 5^-2)

  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      log(eChickCarryingCapacity[i,j]) <- bChickCarryingCapacity
    }
  }

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalPDO ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      logit(eSurvival[i,j]) <- bSurvival + bSurvivalPDO * PDO[i,j]
    }
  }

  bProductivityPDO ~ dnorm(0, 2^-2)
  bProductivityHabitatQuality ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    bAdults[i,1] ~ dunif(0, 100)
    bYearlings[i,1] ~ dunif(0, 100)
    log(bChicks[i,1]) <- log(bChicksPerAdult * bAdults[i,1] / (1 +
bAdults[i,1] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,1])) +
bProductivityHabitatQuality * HabitatQuality[i,1]
    for(j in 2:nYear){
      log(bChicks[i,j]) <- log(bChicksPerAdult * bAdults[i,j] / (1 +
bAdults[i,j] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,j])) +
bProductivityPDO * PDO[i,j-1] + bProductivityHabitatQuality *
HabitatQuality[i,j]
      bYearlings[i,j] <- bChicks[i,j-1] * eSurvival[i,j-1]
      bAdults[i,j] <- (bYearlings[i,j-1] + bAdults[i,j-1]) *
eSurvival[i,j-1]
    }
  }

  sOverDispersion ~ dunif(0, 2)
  sAbundance ~ dunif(0, 10)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      eWeightedAbundance[i,j] <- bChicks[i,j] + bYearlings[i,j] +
bAdults[i,j]
```

```
      eOverDispersion[i,j] ~ dnorm(0, sOverDispersion^-2)

      logit(eProportionChicks[i,j]) <- logit(bChicks[i,j] /
eWeightedAbundance[i,j]) + eOverDispersion[i,j]

      ChickWings[i,j] ~ dbin(eProportionChicks[i,j],
NumberOfWings[i,j])

      eAbundance[i,j] <- bAdults[i,j] / 2
      Abundance[i,j] ~ dnorm(eAbundance[i,j], sAbundance^-2)
    }
  }
}
```

Wyoming Population Dynamics - Model4

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bChickCarryingCapacity ~ dnorm(0, 5^-2)

  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      log(eChickCarryingCapacity[i,j]) <- bChickCarryingCapacity
    }
  }

  bSurvival ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      logit(eSurvival[i,j]) <- bSurvival
    }
  }

  bProductivityHabitatQuality ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    bAdults[i,1] ~ dunif(0, 100)
    bYearlings[i,1] ~ dunif(0, 100)
    log(bChicks[i,1]) <- log(bChicksPerAdult * bAdults[i,1] / (1 +
bAdults[i,1] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,1])) +
bProductivityHabitatQuality * HabitatQuality[i,1]
    for(j in 2:nYear){
      log(bChicks[i,j]) <- log(bChicksPerAdult * bAdults[i,j] / (1 +
bAdults[i,j] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,j])) +
bProductivityHabitatQuality * HabitatQuality[i,j]
      bYearlings[i,j] <- bChicks[i,j-1] * eSurvival[i,j-1]
      bAdults[i,j] <- (bYearlings[i,j-1] + bAdults[i,j-1]) *
```

```
eSurvival[i,j-1]
    }
  }

  sOverDispersion ~ dunif(0, 2)
  sAbundance ~ dunif(0, 20)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      eWeightedAbundance[i,j] <- bChicks[i,j] + bYearlings[i,j] +
bAdults[i,j]

      eOverDispersion[i,j] ~ dnorm(0, sOverDispersion^-2)

      logit(eProportionChicks[i,j]) <- logit(bChicks[i,j] /
eWeightedAbundance[i,j]) + eOverDispersion[i,j]

      ChickWings[i,j] ~ dbin(eProportionChicks[i,j],
NumberOfWings[i,j])

      eAbundance[i,j] <- bAdults[i,j] / 2
      Abundance[i,j] ~ dnorm(eAbundance[i,j], sAbundance^-2)
    }
  }
}
```

Wyoming Population Dynamics - Model5

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bChickCarryingCapacity ~ dnorm(0, 5^-2)

  for(i in 1:nWorkingGroup) {
  for(j in 1:nYear) {
  log(eChickCarryingCapacity[i,j]) <- bChickCarryingCapacity
  }
  }

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalPDO ~ dnorm(0, 2^-2)
  bSurvivalArealDisturbance ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
  for(j in 1:nYear) {
  logit(eSurvival[i,j]) <- bSurvival + bSurvivalPDO * PDO[i,j] +
bSurvivalArealDisturbance * ArealDisturbance[i,j]
  }
  }
```

```
  bProductivityPDO ~ dnorm(0, 2^-2)
  bProductivityHabitatQuality ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
  bAdults[i,1] ~ dunif(0, 100)
  bYearlings[i,1] ~ dunif(0, 100)
  log(bChicks[i,1]) <- log(bChicksPerAdult * bAdults[i,1] / (1 +
bAdults[i,1] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,1])) +
bProductivityHabitatQuality * HabitatQuality[i,1]
  for(j in 2:nYear){
  log(bChicks[i,j]) <- log(bChicksPerAdult * bAdults[i,j] / (1 +
bAdults[i,j] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,j])) +
bProductivityPDO * PDO[i,j-1] + bProductivityHabitatQuality *
HabitatQuality[i,j]
  bYearlings[i,j] <- bChicks[i,j-1] * eSurvival[i,j-1]
  bAdults[i,j] <- (bYearlings[i,j-1] + bAdults[i,j-1]) * eSurvival[i,j-
1]
  }
  }

  sOverDispersion ~ dunif(0, 2)
  sAbundance ~ dunif(0, 10)
  for(i in 1:nWorkingGroup) {
  for(j in 1:nYear) {
  eWeightedAbundance[i,j] <- bChicks[i,j] + bYearlings[i,j] +
bAdults[i,j]

  eOverDispersion[i,j] ~ dnorm(0, sOverDispersion^-2)

  logit(eProportionChicks[i,j]) <- logit(bChicks[i,j] /
eWeightedAbundance[i,j]) + eOverDispersion[i,j]

  ChickWings[i,j] ~ dbin(eProportionChicks[i,j], NumberOfWings[i,j])

  eAbundance[i,j] <- bAdults[i,j] / 2
  Abundance[i,j] ~ dnorm(eAbundance[i,j], sAbundance^-2)
  }
  }
  }
```

Wyoming Population Dynamics - Model6

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bChickCarryingCapacity ~ dnorm(0, 5^-2)

  for(i in 1:nWorkingGroup) {
  for(j in 1:nYear) {
```

```
  log(eChickCarryingCapacity[i,j]) <- bChickCarryingCapacity
  }
  }

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalPDO ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
  for(j in 1:nYear) {
  logit(eSurvival[i,j]) <- bSurvival + bSurvivalPDO * PDO[i,j]
  }
  }

  bProductivityPDO ~ dnorm(0, 2^-2)
  bProductivityArealDisturbance ~ dnorm(0, 2^-2)
  bProductivityHabitatQuality ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
  bAdults[i,1] ~ dunif(0, 100)
  bYearlings[i,1] ~ dunif(0, 100)
  log(bChicks[i,1]) <- log(bChicksPerAdult * bAdults[i,1] / (1 +
bAdults[i,1] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,1])) +
bProductivityArealDisturbance * ArealDisturbance[i,1] +
bProductivityHabitatQuality * HabitatQuality[i,1]
  for(j in 2:nYear){
  log(bChicks[i,j]) <- log(bChicksPerAdult * bAdults[i,j] / (1 +
bAdults[i,j] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,j])) +
bProductivityPDO * PDO[i,j-1] + bProductivityArealDisturbance *
ArealDisturbance[i,j] + bProductivityHabitatQuality *
HabitatQuality[i,j]
  bYearlings[i,j] <- bChicks[i,j-1] * eSurvival[i,j-1]
  bAdults[i,j] <- (bYearlings[i,j-1] + bAdults[i,j-1]) * eSurvival[i,j-
1]
  }
  }

  sOverDispersion ~ dunif(0, 2)
  sAbundance ~ dunif(0, 10)
  for(i in 1:nWorkingGroup) {
  for(j in 1:nYear) {
  eWeightedAbundance[i,j] <- bChicks[i,j] + bYearlings[i,j] +
bAdults[i,j]

  eOverDispersion[i,j] ~ dnorm(0, sOverDispersion^-2)

  logit(eProportionChicks[i,j]) <- logit(bChicks[i,j] /
eWeightedAbundance[i,j]) + eOverDispersion[i,j]

  ChickWings[i,j] ~ dbin(eProportionChicks[i,j], NumberOfWings[i,j])

  eAbundance[i,j] <- bAdults[i,j] / 2
```

```
  Abundance[i,j] ~ dnorm(eAbundance[i,j], sAbundance^-2)
  }
  }
  }
```

Wyoming Population Dynamics - Model7

```
model{

  bChicksPerAdult ~ dunif(2, 4)

  bChickCarryingCapacity ~ dnorm(0, 5^-2)

  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      log(eChickCarryingCapacity[i,j]) <- bChickCarryingCapacity
    }
  }

  bSurvival ~ dnorm(0, 2^-2)
  bSurvivalPDO ~ dnorm(0, 2^-2)
  bSurvivalHunterDays ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      logit(eSurvival[i,j]) <- bSurvival + bSurvivalPDO * PDO[i,j] +
bSurvivalHunterDays * HunterDays[i,j]
    }
  }

  bProductivityPDO ~ dnorm(0, 2^-2)
  bProductivityHabitatQuality ~ dnorm(0, 2^-2)
  for(i in 1:nWorkingGroup) {
    bAdults[i,1] ~ dunif(0, 100)
    bYearlings[i,1] ~ dunif(0, 100)
    log(bChicks[i,1]) <- log(bChicksPerAdult * bAdults[i,1] / (1 +
bAdults[i,1] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,1])) +
bProductivityHabitatQuality * HabitatQuality[i,1]
    for(j in 2:nYear){
      log(bChicks[i,j]) <- log(bChicksPerAdult * bAdults[i,j] / (1 +
bAdults[i,j] * (bChicksPerAdult - 1) / eChickCarryingCapacity[i,j])) +
bProductivityPDO * PDO[i,j-1] + bProductivityHabitatQuality *
HabitatQuality[i,j]
      bYearlings[i,j] <- bChicks[i,j-1] * eSurvival[i,j-1]
      bAdults[i,j] <- (bYearlings[i,j-1] + bAdults[i,j-1]) *
eSurvival[i,j-1]
    }
  }

  sOverDispersion ~ dunif(0, 2)
  sAbundance ~ dunif(0, 10)
```

```
  for(i in 1:nWorkingGroup) {
    for(j in 1:nYear) {
      HunterDays[i,j] ~ dunif(0, 1)

      eWeightedAbundance[i,j] <- bChicks[i,j] + bYearlings[i,j] +
bAdults[i,j]

      eOverDispersion[i,j] ~ dnorm(0, sOverDispersion^-2)

      logit(eProportionChicks[i,j]) <- logit(bChicks[i,j] /
eWeightedAbundance[i,j]) + eOverDispersion[i,j]

      ChickWings[i,j] ~ dbin(eProportionChicks[i,j],
NumberOfWings[i,j])

      eAbundance[i,j] <- bAdults[i,j] / 2
      Abundance[i,j] ~ dnorm(eAbundance[i,j], sAbundance^-2)
    }
  }
}
```