Analysis of Greater Sage-grouse Lek Data:
Trends in Peak Male Counts
1965-2015

Prepared for:

Western Association of Fish and Wildlife Agencies

522 Notre Dame Court, Cheyenne, WY 82009

Prepared by:

Ryan M. Nielson, Lyman L. McDonald, Jason Mitchell, Shay Howlin, and Chad LeBeau

Western EcoSystems Technology (WEST), Inc.

415 West 17th St., Suite 200, Cheyenne, WY 82001

September 30, 2015

WEST Inc. Environmental & Statistical Consultants

NATURAL RESOURCES ⬩ SCIENTIFIC SOLUTIONS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUGGESTED CITATION

Nielson, R. M., L. L. McDonald, J. Mitchell, S. Howlin, and C. LeBeau. 2015. Analysis of greater sage-grouse lek data: Trends in peak male counts 1965-2015. Western EcoSystems Technology, Inc., Cheyenne, Wyoming, USA.

ABSTRACT

Trends in greater sage-grouse breeding populations are typically indexed by determining the peak number of males attending a lek in a lekking season. Numerous studies have estimated negative trends in sage-grouse breeding populations over time via data collected for the last 50 years. However, the inherent bias in data collection and unknown relationship between lek counts and population size limits the utility of using counts to evaluate range-wide population trends. This study estimated trends in the male segment of greater sage-grouse breeding populations within core and periphery areas in seven habitat management zones during two time periods, 1965-2015 and 2005-2015. In addition, we compared analysis methods used in this study to previous studies, and provided recommendations on future data collection. We developed a hierarchical model that followed individual leks through time and allowed trends at individual leks to inform estimates of regional trends. We fit overdispersed Poisson models using a Bayesian hierarchical framework and Markov-chain Monte Carlo (MCMC) methods. The average range-wide decline, weighted across management zones, was 2.10% per year, for an average total decline of 66% from 1965-2015. Estimates of trend over 2005-2015 for individual management zones, in both core and periphery areas, indicated that recent annual declines were more severe compared to the average declines over the entire analysis period 1965-2015. The declines estimated in this study were similar to other studies; however, review of the literature reveals numerous issues surrounding the historical data, the on-going monitoring and sampling scheme, and utilization of various statistical methods, all of which limit our inference on population trends. We believe the overdispersed Poisson regression model is the most appropriate analysis method for these and future data, regardless of whether the focus remains on

peak male counts or total counts of observed sage-grouse based on a more spatially balanced sample of monitoring sites that are randomly selected.

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is an important species both politically and ecologically throughout the sagebrush-steppe habitats of North America. The species was recently a candidate for listing under the federal Endangered Species Act, in part due to continued contraction of their historical range and estimated declines in population abundance (Schroeder et al. 2004, Connelly and Braun 1997, Connelly et al. 2004, Garton et al. 2011). The common approach to monitoring trends in sage-grouse abundance has been to count the number of males attending strutting grounds (leks) in the spring (Connelly et al. 2003). The number of males attending leks has decreased throughout much of the range of sage-grouse over the past few decades (Connelly and Braun 1997, Connelly et al. 2004, Garton et al. 2011). This decline has largely been attributed to anthropogenic influences (Naugle et al. 2011, Johnson et al. 2011, Kirol et al. 2015) or landscape changes associated with large wildfires (Blomberg et al. 2012). Declines in the number of males attending leks could be related to several causes, including low male juvenile recruitment, poor survival, and low productivity as a result of decreased habitat suitability (Holloran et al. 2010, Taylor et al. 2011).

Trends in sage-grouse breeding populations are typically monitored through an index based on the peak count of males attending leks during a given lekking season; however, the inherent bias in data collection and unknown relationship between lek counts and population sizes limits the utility of using lek counts to evaluate range-wide population trends (Beck and Braun 1980, Connelly and Braun 1997, Walsh et al. 2004, GTC 2008). The potential biases in these trend estimates are unknown, which makes comparisons among areas and time periods difficult. Many of the leks consistently monitored over the last 50 years were a judgment or convenience sample, not part of a probability-based sample of leks; additionally, survey effort at many individual leks has been inconsistent over time (GTC 2008). Despite problems associated with the collection and analysis of lek count data, these datasets represent the only long-term data available for analyzing trends in sage-grouse populations.

Numerous analyses have been conducted to estimate trends in sage-grouse breeding populations and the findings generally support a conclusion of overall range-wide declines (e.g., Connelly and Braun 1997, Garton et al. 2011). These analyses utilized different methods to estimate trends in breeding populations. Some have focused on estimating trends in the average peak (maximum) number of males attending leks within a season (Connelly and Braun 1997), instantaneous rates of change (Connelly et al. 2004), linear mixed-effects models (GTC 2008, WAFWA 2015a), finite rates of change and population reconstruction models (Garton et al. 2011 and 2015), and Bayesian hierarchical models (WAFWA 2015b).

Our objective was to provide an independent analysis of the peak male lek attendance data collected across the range of sage-grouse. The Western Association of Fish and Wildlife Associations (WAFWA) contracted with Western Ecosystems Technology, Inc. (WEST) to develop an independent trend analysis of all available historical peak-male sage-grouse count data. Our analysis included data collected on leks from 1965-2015, followed trends in individual leks over time, and was designed to rely on as few assumptions as possible. In addition, we conducted a comparative review of previous analyses conducted presented in Garton et al. (2015) and WAFWA (2015a) that outlines the pros and cons of each method.

METHODS

WAFWA provided WEST with a lek database compiled from individual state agency data sources from the 11 western states within various sage-grouse WAFWA management zones that itemized the number of peak males observed on monitored leks from 1965-2015 (Fig. 1). As used here, “peak” means the maximum number of male sage-grouse observed on a particular lek in a particular year. The individual leks in this database represented a wide range of monitoring efforts, both over time (e.g., single year versus multiple years) and within a single lekking season (i.e., number of site visits by an experienced biologist). Few leks have been monitored consistently since 1965, since expanding survey efforts over time have led to the monitoring of additional leks. Finally, data from some leks are temporally sporadic, due to issues of survey effort, land access, and weather.

For this analysis, we defined a lek as a point-based display site with fixed geographic latitudinal and longitudinal coordinates, at which 2 or more males were counted in 2 or more years in 1965-2015 between 15 March and 15 May in early morning (Connelly et al. 2011). In addition, data from larger leks and potentially spatially related satellite leks or activity centers were combined using a spatial clustering analysis that separated leks and activity centers > 1.2 km apart to be separate, and counts within the resulting 1.2-km lek clusters were combined into lek complexes (WAFWA 2015b). This and other data filtering, standardization, and quality control and assurance was conducted by WAFWA prior to our analysis WAFWA (2015a and b).

There were many zero values for peak male counts at individual leks in the data provided to WAFWA by individual states, and those zeros could represent a multitude of scenarios which were impossible to distinguish. For example, a zero value for peak number of males may have indicated that a lek was not surveyed in that year (i.e., a missing value). In other cases, a zero could have been an artifact of a lek being surveyed only once in a season, and the timing or conditions of that visit were not ideal. Another scenario could have involved multiple visits to a lek within a season, but no males were ever detected during those visits.

We reduced strings of consecutive zero values collected over subsequent years from the database because the cause and interpretation of those zero values was ambiguous (WAFWA 2015b). We did not remove the first zero at a lek following a count of male attendance in an attempt to avoid the confounding factors mentioned above. This approach minimizes the potential of mixing various sources of zero values mentioned above.

Long-term trends in sage-grouse breeding populations were estimated within the core area, the periphery (i.e., outside the core area), as well as the combined area (core + periphery = management zone; Fig. 1) within each management zone (Fig. 1). Core areas were defined as high population density areas that contained 75% of the average peak count from leks monitored between 2010 and 2014 (Doherty et al. 2010).

Modeling Trends in Peak Male Lek Attendance

Trends in actual peak number of males at a lek may vary over time and space. For example, localized areas may support stable sage-grouse populations, while a larger geographic extent of sage-grouse may experience population declines or increases. Hierarchical models allow for modeling of trends at various scales simultaneously. We developed a hierarchical model that both followed individual leks through time and allowed trends at individual leks to inform estimates of trends within encompassing management zones and states. This approach reduced the potential bias that could have resulted if larger leks (larger lek = more males) were monitored earlier in time and many smaller leks were only recently included in monitoring efforts (WAFWA 2015b). This hierarchical modeling approach included both fixed and random effects and was similar to approaches used to estimate trends of different species in Breeding Bird Survey data (Sauer and Link 2002, 2011; Thogmartin et al. 2004; Nielson et al. 2008) and data from large-scale monitoring efforts like the western-wide golden eagle survey (Millsap et al. 2013, Nielson et al. 2014).

We fit overdispersed Poisson regression models to peak male attendance data for each individual lek, within each management zone and state. Management zones 2 and 7 were combined due to their proximity; additionally, zone 7 included very little empirical lek data. Within a management zone or state, counts $Y_{i,j,t}$ (*i* for management zone/state, *j* for lek, and *t* for year) were assumed to be independent Poisson random variables with means $\lambda_{i,j,t}$. The means were log-linear with respect to explanatory variables, i.e.,

$$\ln(\lambda_{i,j,t}) = \mu_i + a_j + (\beta_i + b_j)(t - t^*) + \varepsilon_{i,j,t}. \tag{1}$$

Explanatory variables included in equation (1) include a_j and b_j, a random intercept and slope for individual leks j, respectively, while parameters μ_i and β_i represent fixed effects for the overall intercept and slope, respectively, for the individual management zone or state i. Additionally, *t* represents year, while t^* represents the baseline year of 1990; the difference $t - t^*$ centered the model at the median year 1990. Finally, $\varepsilon_{i,j,t}$ represents overdispersed error terms specific to the t^{th} year, i^{th} lek, and j^{th} management zone/state.

We fit the overdispersed Poisson models using Bayesian hierarchical framework and Markov-chain Monte Carlo (MCMC) methods (Gelman et al. 2007, Gelman and Hill 2007). MCMC methods require specification of random effects and priors, respectively. For each individual management-zone or state model, we set μ_i and β_i, to originate from a multivariate normal:

$$\begin{bmatrix}\mu_i\\ \beta_i\end{bmatrix} \sim MVN \begin{bmatrix}\sigma_\mu & \rho\sigma_\mu\sigma_\beta\\ \rho\sigma_\mu\sigma_\beta & \sigma_\beta\end{bmatrix}, \tag{2}$$

with intercept and slope standard-deviation priors, σ_μ and σ_β , respectively, each initially set to follow a Uniform(0, 100), and their correlation (ρ) prior initially set to follow a Uniform(-1, 1). The overdispersed error term ($\varepsilon_{i,j,t}$) was sampled from a mean-zero normal distribution with a tolerance prior of Gamma(0.001, 0.001), where tolerance equaled the inverse of the variance.

We estimated posterior distributions via the MCMC methodology and utilized WinBUGS for all models. We used a burn-in of 76,000 initial samples, after which another 4,000 samples formed the simulation sample from which posterior distributions were obtained. We did not thin (i.e., discard) any of the 4,000 follow-up samples; in this way, all replicates following burn-in contributed to estimation of posterior distributions. Following model runs for all management zones, we calculated range-wide estimates of trends using a weighted average of the individual estimates of trends from each management zone model. Weights were based on the proportion of leks monitored in each zone. Ninety percent credible intervals (CRIs) – essentially the Bayesian form of a confidence interval – were calculated for all estimates of trend. If a 90% CRI did not include 0.0, then we concluded there was evidence of trend in the data.

Given the tendency of sage-grouse peak-male count data to exhibit large-scale periodicities over time, we also investigated how analysis of data from different time periods could affect estimates of trends using the results from the Bayesian hierarchical model (equation [1]). We focused on estimating recent trends (2005-2015) for the core, periphery, and the combined areas (range-wide) within each of the management zones. The objective of our analysis was to estimate overall trends in peak male lek attendance by following individual leks through time. We examined model fit by plotting estimated trends and empirical counts of peak male lek attendance for individual leks.

RESULTS

Modeling Trends in Peak Male Lek Attendance

Based on the overdispersed Poisson model, the number of peak males per lek declined within the core, periphery, and the combined areas within each management zone from 1965-2015 (Table 1; Figs. 2-7). Declines within management zones for the core and periphery combined varied from 1.29% per year in management zone 3 to 4.24% per year in management zone 1 (Table 1; Figs. 2-7). The 90% CRIs for all of these estimates did not contain 0.0, indicating statistical significance of estimated declines (Table 1). Based on weighted averages of these individual trend estimates for each management zone, overall range-wide declines were also statistically significant (Table 1, Figure 8). The weighted average decline across the management zones was 2.10% per year (90% CRI: -2.22% to -1.98%). The average decline for each management zone was 15 to 67% lower within the core areas and 23 to 171% larger in the periphery areas compared to trend estimates within each management zone – i.e., declines in the periphery were larger than declines in the management zones, which in turn were larger than estimated declines with the core. Plots of estimated trends for a random sample of leks suggested there was an acceptable level of goodness-of-fit of the models to the empirical data (Figs. 9-12).

Estimated trends for each state varied from a decline of 0.56% per year in California to a decline of 6.98% per year in South Dakota (Table 1). Ninety percent credible intervals for estimated declines in individual states did not include 0.0, indicating statistical significance of estimates, with exception of the estimated decline in California (90% CRI from -1.52 to 0.41). Estimates of trend over 2005-2015 for the individual management zones, core and periphery areas indicated that recent annual declines were more severe compared to the average declines over the entire analysis period 1965-2015 (Table 2; Fig. 13), and all negative trends were statistically significant.

Comparison of Analysis Methods

We have compared the analysis presented in this report to the analyses of Garton et al. (2015) and WAFWA (2015a). Our aim was not to suggest other analyses were incorrect, but to identify the differences in assumptions and implications of variation in modelling approaches.

Analysis of the long-term sage-grouse male lek count database was not an easy task. The problems in the collection and management of the data could not be solved with any amount of data preparation or any one summarization technique. The collection of these data did not involve sampling in the classical sense, in that a probabilistic sampling of existing or potential leks was not conducted. Many of the assumptions made in this and previous reports attempted to correct for data not obtained through a random sample of the population of leks. Like any dataset predominantly obtained through opportunistic observations, the analyses require multiple assumptions confounded with undefined biases.

Garton et al. (2015)

The goals of the Garton et al. (2015) analysis were to model changes in the sage-grouse population, develop population projections, and estimate probability of species persistence. For this analysis, and the preceding analysis outlined in Garton et al. (2011), the authors developed a model to estimate minimum breeding male population size for each WAFWA management zone and Sage-Grouse Management Zone (SMZ) based on monitored leks within each zone. Garton et al. (2015, 2011) first "reconstructed an index of population abundance for each population," and then estimated rate of change between any two years for each population based on data from leks with 3 or more surveys at each lek. A population estimate was built from the 2013 observed number of peak males and the observed finite growth rate for each successive pair of years going back in time (e.g., 2012 to 2013, 2011 to 2012, 2010 to 2011, etc.). Estimating the rate of change between two successive years only involved combining data from all leks within a population that were visited at least 3 times in both years. Thus, the finite rate of change between did not treat the lek as the primary sampling unit, but instead clustered leks by population. Population trends were estimated for the reconstructed population with a stochastic density dependent growth model with zero-, one-, or two-year time lags and changing carrying capacities through time.

The assumptions of the Garton et al. (2015) analysis include: (1) the 2013 lek count data constituted an unbiased sample of all leks, and the combined sample of leks providing pair-wise estimates of population change provided unbiased estimate of rate of change across all leks within the population, (2) the growth rate of the population was density dependent, sigmoidal in form, and normally distributed, and (3) trends in males were representative of trends in the population as a whole.

Compared with the analysis methods presented in this report, the Garton et al. (2015) analysis differed in several ways. Though both analyses used data arising from state lek count surveys, the two analyses utilized slightly different data. The Garton et al. (2015) analysis covered 1965 to 2013 and did not include recent Colorado data. Data filtering and summarization originally described by Garton et al. (2011), and repeated for the Garton et al. (2015) analysis, resulted in the removal of data that were included in the dataset used in this analysis. The analysis presented in this report used data provided by WAFWA, and covered years 1965-2015, including all 11 states, and did not remove individual lek data with fewer than 3 visits in a year or one monitoring year between 2 years of no monitoring effort.

Though based on the same type of survey data, the Garton et al. (2015) analysis and the one presented here treated the inherent problems in the data differently. Two inherent problems with any analysis of survey data include changes in survey effort through time and poor standardization of data collection and reporting. Garton et al. (2015) approached the problem of unequal sampling effort, i.e., varying effort by year and lek, by developing a model to estimate minimum breeding male population size for each population, which in turn, was based on observed finite rates of change at certain monitored leks. The reconstructed minimum breeding male population size was based on the count of peak males in 2013. Although not all leks were visited in 2013, effort expended in 2013 became the base effort for the reconstructed population size. While this population reconstruction provided a way for Garton et al. (2015) to deal with unequal survey effort and the resulting biases, it did assume that the sample of leks surveyed in 2013 was unbiased.

The modelling conducted by Garton et al. (2015) can be viewed as reconstructing population sizes, and then fitting a model to the reconstructed data with estimating equations defined by population growth, with the assumptions made about the process evaluated with models fit to the existing data. Garton et al. (2015) and the analysis presented here both aimed to estimate temporal trends in sage-grouse populations, but we did not attempt to forecast abundance and estimate the probability of extinction as Garton et al. (2015). Our approach can be viewed as a design-based analysis where standard statistical models were fit to estimate assumed exponential trends. Both approaches are valid modelling paradigms in the ecological sciences, and each approach has some appeal.

The analysis of Garton et al. (2015) was based on a stochastic exponential growth model, which was fit to the reconstructed univariate dataset via maximum likelihood estimation. Most notably, this approach assumed a sigmoidal form of the growth (or decline) was the correct model, with nonlinear dependence of demographic rates on population abundance. Trend estimates presented by Garton et al. (2015) were interpreted as trends in carrying capacity and were not accompanied by estimates of variability. It is unclear whether these estimates were not obtained or not presented in the report, though Garton et al. (2011) notes that standard error estimates were “large.” Without an estimate of variance, the estimate of trend is difficult to interpret.

It is possible that the modelling approach of Garton et al. (2015) attempted to extract too many population growth characteristics using one unreplicated time series for each population or management zone. It is likely this approach experienced estimation difficulties for a portion of the 26 models fit to each reconstructed index of abundance, though the text doesn’t report the extent of this. Model results were not presented for many populations and management zones, indicating possible estimation failure of the models for these areas. Dennis et al. (2006) note that four-parameter models of this type often don’t converge on acceptable estimates under some criteria. The Garton et al. (2015) approach also assumes there is density dependence in the population size, a modelling form requiring sufficient data to estimate (Boyce 1992).

The exponential growth models employed by Garton et al. (2015) are limited to a univariate time series for the observation equation. Population sizes estimated with the reconstruction model have unknown statistical properties. There was no indication in Garton et al. (2011) or Garton et al. (2015) that the approach taken to reduce the dataset across hundreds of leks down to one time series (for a management zone) has been adequately peer reviewed or has been recommended by the research community that promotes growth models of this type.

WAFWA (2015a)

The goal of the WAFWA (2015a) analysis was to assess trends in peak-male counts at leks range-wide, within each management zone, and separately within each state. The analysis identified two time periods of interest: 1965-1989 and 1990-2014. Data preparation was similar to that used for the data analyzed in our analysis presented here. The trend model fit for the WAFWA (2015a) analysis required a data transformation, which complicated interpretation. The assumptions of the WAFWA (2015a) analysis included: (1) log-transformed peak-male count data, plus one, were normally distributed, (2) detection probabilities for males on each lek did not change through time, and (3) trends in the peak number of males found at leks were representative of trends in the population as a whole. Our analysis presented here also makes the latter two assumptions.

When compared with the analysis methods presented in this report, the WAFWA (2015a) analysis differed in several ways. The preparation of the data was conducted by WAFWA for both analyses, so the data analyzed were similar with the exception of the time series duration. The WAFWA (2015a) analysis covered the period from 1965-2014, while the analysis presented here covered the period from 1965-2015. In addition, the analysis presented here was conducted on subsets of the data in the core and periphery areas. In addition, we did not transform the data prior to analysis, which simplified interpretation and modeling assumptions.

The trend analysis of WAFWA (2015a) was based on a linear mixed effects model with a log-transformed response. While this approach to the estimation of population trends was similar to our analysis presented in this report, in that they are both linear statistical models, the WAFWA (2015a) model assumed a normal distribution of the count data after adding 1. Prior to the analysis, the count data was log-transformed, with the addition of 1 to each observed count. It is unlikely the transformation of the count data satisfied the assumption of normality. It is well known that generalized linear models are better suited to accommodate count data (McCullagh and Nelder 1989) and the selection of the constant when log-transforming zero counts has implications in both model fit and interpretation of model output (O'Hara and Kotz 2010).

DISCUSSION AND CONCLUSIONS

We detected declines in sage-grouse breeding populations across the current range of sage-grouse, similar to other sage-grouse studies (e.g., Garton et al. 2015, WAFWA 2015a). Declines in lek counts range-wide were more severe over the last 10 years compared to the last 50 years. However, leks located within the core areas are experiencing less of a decline compared to leks located in periphery areas. The first comprehensive analysis of sage-grouse breeding population trends compared long-term averages in the total number of males per lek through 1984 to averages after 1985 (Connelly and Braun 1997). More recently, Connelly et al. (2004) estimated an overall rate of decline of 2% per year in the average peak number of males attending leks from 1965 to 2003. Garton et al. (2011) predicted that at least 13% of sage-grouse populations may decline below effective population sizes of 50 within the next 30 years. Also, Garton et al. (2011) projected that 75% of populations and 2 of the seven management zones in the U.S. are likely to decline below effective population sizes of 500 within 100 years if current conditions and trends persist. Garton et al. (2015) updated their previous analysis from 2011 by adding additional years of lek count data, and estimated a 56% decline in breeding males between 2007 and 2013 range-wide. Lastly, WAFWA (2015b) estimated a yearly 0.83% decline in the average number of peak males per lek per year range-wide during 1965-2015.

We did not analyze how changes in monitoring effort from state-to-state or over time could impact estimates of trends. We did not attempt to assess whether the number of leks has decreased over time. Such an analysis was not possible, as the leks monitored in 1965-2015 were not developed from a probabilistic-based sample of all potential lek sites. Our analysis of trends is likely biased due to the opportunistic-based sample of leks that has been monitored. This is confounded by the possibility that larger leks have a longer monitoring history and are generally easier to identify. In addition, many smaller leks may have entered monitoring programs more recently due to increased effort, use of aerial surveys, and increased access to both public and private land. Our analysis was designed to follow individual leks through time and may have reduced the potential effect that increasing sampling effort and including more smaller leks had on the trend analysis.

Has the number of sage-grouse decreased over time? This may or may not be evident in analyses that estimate changes in the peak number of males observed on a lek. Although analyses may claim that number of peak males on a lek is a good index, or proxy, for population abundance, differences in sampling effort between states and over time makes it difficult to say that the state databases of lek counts accurately represent the true trends in abundance of the species. To complicate matters, WEST has seen abundance of another lekking species (lesser prairie-chicken, McDonald et al. 2015) expand, while average cluster-size of birds observed has declined. In the scenario of monitoring sage-grouse leks, if average cluster, or lek size decreases, so will male attendance, which may not be reflective of actual changes in the breeding population.

There were additional underlying issues associated with the lek count data that likely influence the results from population trend analyses that use lek count data. The WAFWA (2015b) report contains various summary statistics that clarify changes in survey effort during the analysis period, and potential conflicting approaches to records in the monitoring data. For example, there were reports of some leks in the same location in the same year, but those records were associated with different lek names. Missing values (no survey effort) were occasionally recorded with a 0.0 count for the number of males, which is confusing when the same value of 0.0 can be recorded when a lek was visited but no males were observed. Obviously, a peak count of 0.0 males at a lek could be recorded in many situations: 1) the lek had been abandoned, 2) no sage-grouse were observed, 3) males were present but none were detected, and 4) males were not present at the time(s) the lek was visited but could have been present at another time.

We investigated whether models could even be fit to the database containing all zeros from the variety of sources mentioned above. We compared analysis of the data only containing the first zero, i.e., the analysis contained here, to an analysis containing all zeros. The results of the analysis containing all zeros in the data resulted in estimates of larger declines during the analysis period (1965-2015), but those results are not presented here, as the inclusion of superfluous zeros artificially exacerbates already decreasing trends.

The analysis presented here is a deviation from the analysis presented in WAFWA (2015b) in that it uses the estimates of trend from equation (1) for overall trend within each management zone, core or periphery area, and state. The analysis presented in WAFWA (2015b) took those estimates a step further based on methods presented in Sauer and Link (2002, 2011) and Millspaugh et al. (2013). This additional step involved predicting actual average peak male lek attendance within an area in 1965 and 2015 (first and last years in the analysis period), and then calculating the average rate of change based on the ratio of the two estimates. Further investigation into this method of estimating annual rate of change revealed those estimates for the lek data were often understated. Estimates of trend based on two predicted numbers (first year and final year) can misrepresent an overall negative or positive trend when the final year's prediction (2015) is relatively high or low compared to the prediction for the first year (1965), but does not follow the overall trend during the analysis period. For example, if there was an overall negative trend from 1965 to 2013 but a sudden increase in predictions for 2014 and 2015, that could have resulted in an overall positive trend based on population estimates for only the first and final year of the analysis period. This approach can be sensitive to cycles in the data and aberrant or anomalous predictions.

We did not correlate estimates of trends to habitat characteristics or drought indices, nor attempt to identify a cyclical pattern in the data, as suggested by (Garton et al. 2015). Cyclical patterns in sage-grouse abundance and productivity likely exist, but patterns are likely variable across the range of sage-grouse. Previous analyses have not identified a unifying pattern that could be easily incorporated into a trend analysis similar to the one presented here.

While acknowledging that our analysis does not ameliorate every problem inherent to this dataset for estimating trends, we advocate the implementation of an alternate range-wide sampling protocol to estimate trends in the sage-grouse population. We recommend that future monitoring for management of sage-grouse depend on a probabilistic sample of potential habitat units to detect changes in total abundance of the species. If the number of males is of interest, then tracking the number of males on both currently known and unknown leks should be a priority. The search procedures employed in future monitoring should have the chance of detecting all males. Monitoring programs using a spatially balanced sample of transects like the western-wide golden eagle survey (Nielson et al. 2014), the lesser prairie-chicken survey (McDonald et al. 2015), and the breeding bird survey (Sauer and Link 2011) provide examples of large-scale monitoring programs that aim to evaluate total changes in abundance, rather than indices to abundance that may contain bias and require more assumptions. If agencies continue to only count the number of males at known, then random sampling of units of land containing existing and previously unknown leks needs to be included. Clearly, sampling effort (e.g., number of visits per season) and data recording should be standardized. We believe the overdispersed Poisson regression model is the most appropriate analysis method for this and future data, regardless of whether the focus remains on peak male counts or total counts of sage-grouse observed along a random sample of transects or in a random sample of land units.

LITERATURE CITED

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3:55.

Boyce, M.S., 1992. Population Viability Analysis. Annu. Rev. Ecol. Syst. 23:481-506.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. University of Idaho College of Natural Resources Experiment Station Bulletin, Bulletin 80. University of Idaho, Moscow, ID.

Connelly J. W., E. T. Rinkes, and C. E. Braun. 2011. Characteristics of greater sage-grouse habitats. Pages 69–83 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

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

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

Doherty, K. E., J. D. Tack, J. S. Evans, and D. E. Naugle. 2010. Mapping breeding densities of greater sage-grouse: A tool for range-wide conservation planning. BLM Completion

Report: Inter Agency Agreement # L10PG0911. Bureau of Land Management, Washington, D.C. 29 pp.

Garton, E. O, A. G. Wells, J. A. Baumgardt, and J. W. Connelly. 2015. Greater sage-grouse population dynamics and probability of persistence. Final Report to Pew Charitable Trusts.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293-383 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2007. Bayesian Data Analysis. CRC Press, New York, NY, third edition.

Gelman, A., and J. Hill. 2007. Data Analysis Using Regression and Multi-level/Hierarchical Models. Cambridge, New York, NY.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. J. Amundson, and S. T. Knick. 2011. Influence of environmental and anthropogenic features on greater sage-grouse populations, 1997–2007. Pages 407–450 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Kirol, C. P., J. L. Beck, S. V. Huzurbazar, M. J. Holloran, and S. N. Miller. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:968–990.

McCullagh, P. and J.A. Nelder. 1989. Generalized linear models. Chapman and Hall, London.

McDonald, L., K. Adachi, T. Rintz, and G. Gardner. 2015 Range-wide Abundance of the Lesser Prairie-chicken: 2012, 2013, 2014, and 2015. Western EcoSystems Technology, Inc, 200 South 2nd Street, Suite B, Laramie, WY, 82070.

Millsap, B. A., G. S. Zimmerman, J. R. Sauer, R. M. Nielson, M. Otto, E. Bjerre, and R. Murphy. 2013. Golden eagle population trends in the western United States: 1968–2010. Journal of Wildlife Management 77:1436–1448.

Naugle, D. E., K. E. Doherty, B. L. Walker, M. J. Holloran, and H. E. Copeland. 2011. Energy development and greater sage-grouse. Pages 489–503 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series. Volume 38. University of California Press, Berkeley, California, USA.

Nielson, R. M., L. McManus, T. Rintz, L. L. McDonald, R. K. Murphy, W. H. Howe, and R. E. Good. 2014. Monitoring abundance of golden eagles in the western United States. Journal of Wildlife Management, 78:721-730.

Nielson, R. M., L. L. McDonald, J. P. Sullivan, C. Burgess, D. S. Johnson, D. H. Johnson, S. Bucholtz, S. Hyberg, and S. Howlin. 2008. Estimating the response of Ring-necked pheasants (*Phasianus colchicus)* to the conservation reserve program. The Auk 125:434–444.

O'Hara, R. B. and D. J. Kotze. 2010. Do not log-transform count data. Methods in Ecology and Evolution 1 (2): 118–122.

Sage- and Columbian Sharp-Tailed Grouse Technical Committee (GTC). 2008. Greater Sage-Grouse Population Trends: An Analysis of Lek Count Databases 1965-2007. Provided to K. E. Mayer, Chair, Bird Committee, Western Association of Fish and Wildlife Agencies. Prepared by the Sage- and Columbian Sharp-tailed Grouse Technical Committee, Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming. July 2008.

Sauer, J. R. and W. A. Link. 2002. Hierarchical modeling of population stability and species group attributes from survey data. Ecology, 86:1743-1751.

Sauer, J. R. and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. The Auk 128:87-98.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–373.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2011. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Thogmartin, W. E., J. R. Sauer, and M. G. Knutson. 2004. A Hierarchical spatial model of avian abundance with application to Cerulean warblers. Ecological Applications 14:1766–1779.

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

Western Association of Fish and Wildlife Agencies (WAFWA). 2015a. Greater sage-grouse population trends: An analysis of lek count databases 1965-2014. Report to Sage and Columbian Sharp-tailed Grouse Technical Committee, Western Association of Fish and Wildlife Agencies, Laramie, WY, May 2014.

Western Association of Fish and Wildlife Agencies (WAFWA). 2015b. Greater sage-grouse population trends: An analysis of lek count databases 1965-2015. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

TABLES

Table 1. Sample sizes (*N*; number of leks) and estimates of trend (percent change per year) with 90% credible intervals for peak number of male sage-grouse on leks 1965-2015 for individual WAFWA management zones and U.S. States. Analyses based on management zones focused on all leks in the 75% core areas; periphery areas (non-core); and all leks, regardless of location within each zone. In addition, a weighted average of trends across management zones was calculated for an estimate of range-wide trends. Positive numbers indicate increases, while negative numbers indicate declines. Any 90% credible interval excluding 0.0 is evidence of a statistically significant trend.

		Core		Periphery		All Combined	
Partition	Region	*N*	Estimated Annual % Change (90% Credible Interval)	*N*	Estimated Annual % Change (90% Credible Interval)	*N*	Estimated Annual % Change (90% Credible Interval)
Management Zone	1	877	-3.45 (-3.77 to -3.14)	657	-5.40 (-5.89 to -4.94)	1,534	-4.24 (-4.50 to -3.99)
	2 & 7	1,327	-0.60 (-0.82 to -0.37)	730	-2.83 (-3.19 to -2.49)	2,057	-1.38 (-1.57 to -1.18)
	3	464	-0.43 (-0.79 to -0.09)	189	-3.49 (-4.12 to -2.86)	653	-1.29 (-1.63 to -0.96)
	4	1,284	-1.10 (-1.34 to -0.85)	668	-3.70 (-4.07 to -3.34)	1,952	-1.94 (-2.14 to -1.74)
	5	358	-1.42 (-2.00 to -0.84)	152	-3.48 (-4.46 to -2.53)	510	-2.15 (-2.68 to -1.63)
	6	31	-2.71 (-4.46 to -1.01)	15	-3.90 (-6.14 to -1.31)	46	-3.17 (-4.53 to -1.80)
Range-wide		4,341	-1.30 (-1.43 to -1.17)	2,411	-3.62 (-3.83 to -3.42)	6,752	-2.10 (-2.22 to -1.98)
State	CA					99	-0.56 (-1.52 to 0.41)
	CO					384	-1.34 (-1.77 to -0.90)
	ID					1,243	-1.94 (-2.20 to -1.70)
	MT					1,126	-4.27 (-4.58 to -3.94)
	ND					39	-3.99 (-5.16 to -2.83)
	NV					946	-1.51 (-1.84 to -1.20)
	OR					490	-2.99 (-3.51 to -2.46)
	SD					43	-6.98 (-9.48 to -4.64)
	UT					395	-1.40 (-1.76 to -1.05)
	WA					46	-3.09 (-4.63 to -1.57)
	WY					1,941	-2.05 (-2.28 to -1.82)

Table 2. Sample sizes (*N*; number of leks) and estimates of trend (percent change per year) with 90% credible intervals for peak number of male sage-grouse on leks 2005-2015 for individual WAFWA management zones. Analyses based on management zones focused on all leks in the 75% core areas; periphery areas (non-core); and all leks, regardless of location within each zone. In addition, a weighted average of trends across management zones was calculated for an estimate of range-wide trends. Positive numbers indicate increases, while negative numbers indicate declines. Any 90% credible interval excluding 0.0 is evidence of a statistically significant trend.

		Core		Periphery		All Combined	
Partition	Region	*N*	Estimated Annual % Change (90% Credible Interval)	*N*	Estimated Annual % Change (90% Credible Interval)	*N*	Estimated Annual % Change (90% Credible Interval)
Management Zone	1	812	-12.45 (-13.39 to -11.48)	489	-18.01 (-20.13 to -15.88)	1,301	-15.15 (-16.02 to -14.26)
	2 & 7	1,211	-6.99 (-7.74 to -6.24)	531	-10.12 (-11.67 to -8.63)	1,742	-8.19 (-8.89 to -7.48)
	3	427	-1.19 (-2.60 to 0.24)	125	-5.85 (-9.58 to -1.94)	552	-2.15 (-3.52 to -0.77)
	4	1,186	-3.23 (-4.27 to -2.20)	553	-11.15 (-13.14 to -9.32)	1,739	-5.89 (-6.81 to -4.98)
	5	323	-8.30 (-10.13 to -6.42)	115	-7.77 (-12.07 to -3.23)	438	-8.57 (-10.17 to -6.92)
	6	29	-5.30 (-10.86 to 0.13)	6	-0.60 (-23.53 to 31.28)	35	-4.98 (-10.47 to 0.44)
Range-wide		3,988	-6.40 (-6.86 to -5.93)	1,819	-11.32 (-12.33 to -10.34)	5,807	-8.20 (-8.64 to -7.76)

FIGURES

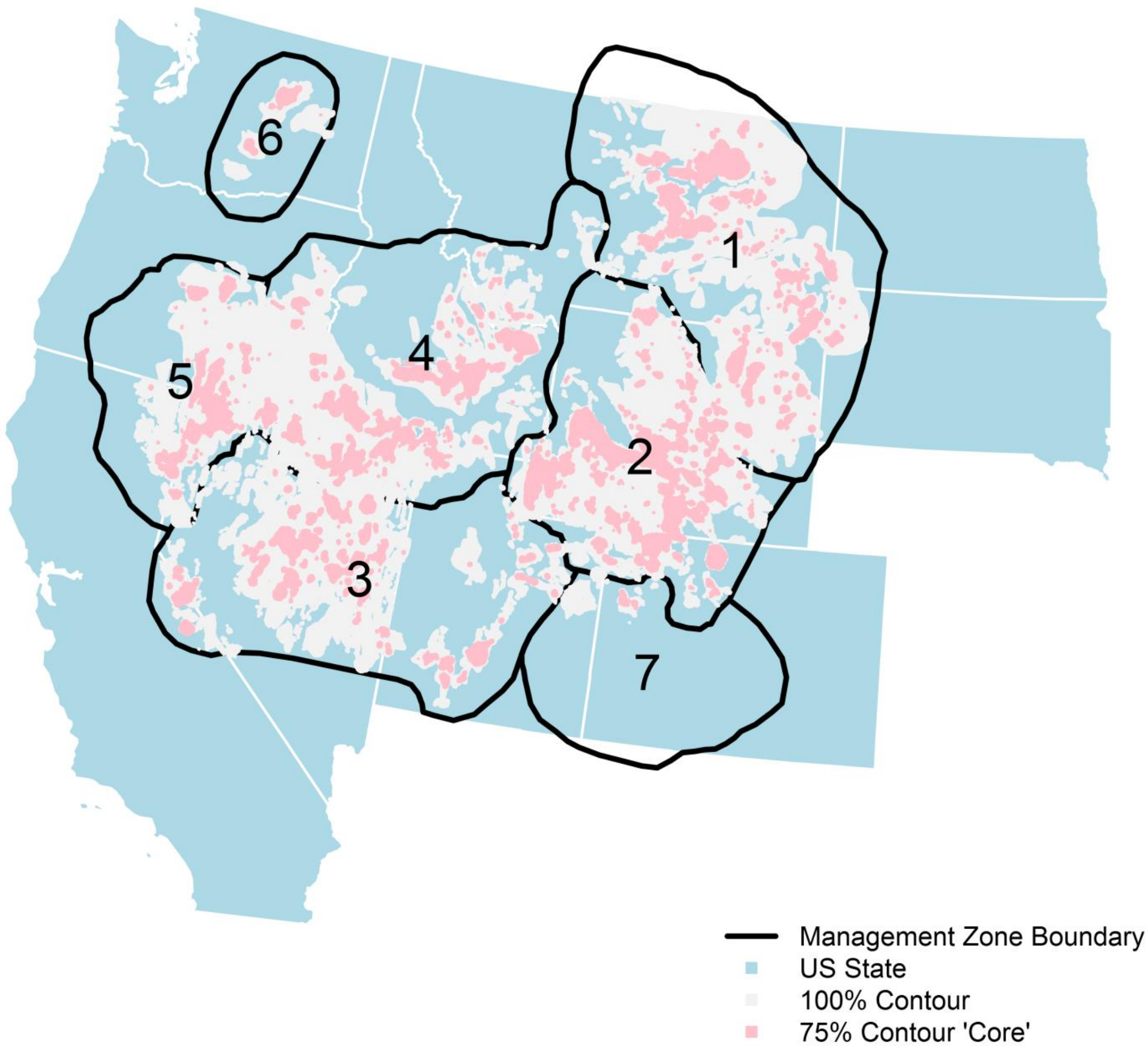

Figure 1. WAFWA sage-grouse management zones I (Great Plains), II (Wyoming Basins), III (Southern Great Basin), IV (Snake River Plain), V (Northern Great Basin), VI (Columbia Basin), and VII (Colorado Plateau) and 75% core areas.

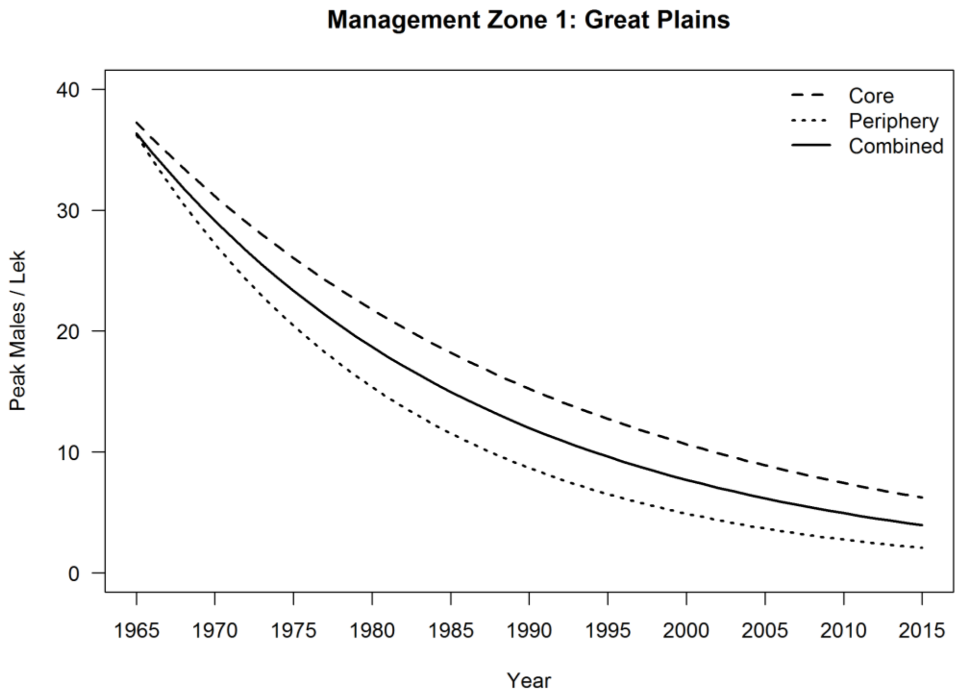

Figure 2. Estimated changes in the average peak number of male sage-grouse on leks in Management Zone 1 in the 75% core area, periphery, and combined.

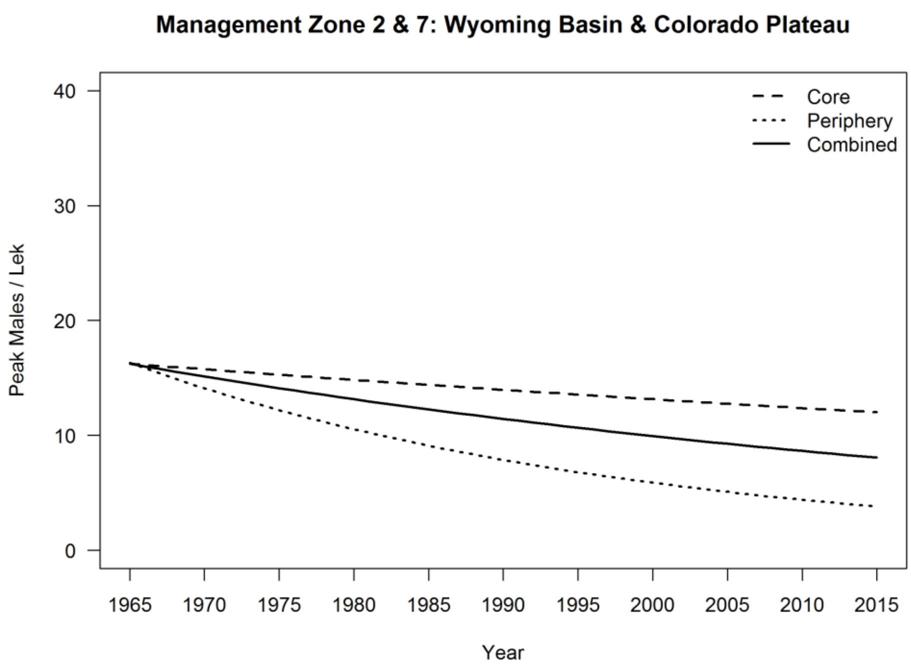

Figure 3. Estimated changes in the average peak number of male sage-grouse on leks in Management Zones 2 & 7 in the 75% core area, periphery, and combined.

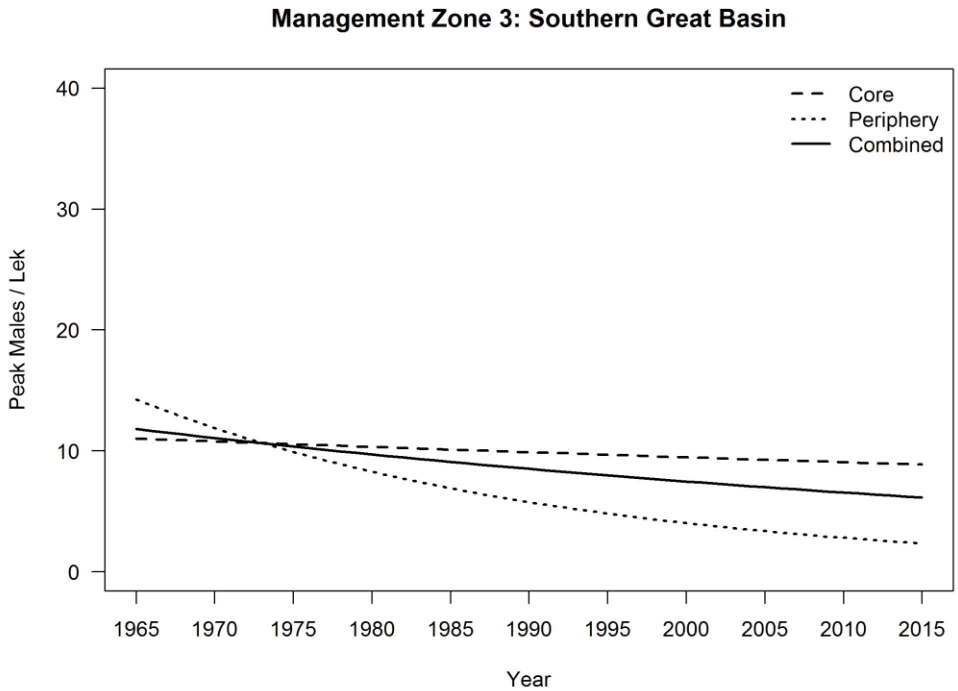

Figure 4. Estimated changes in the average peak number of male sage-grouse on leks in Management Zone 3 in the 75% core area, periphery, and combined.

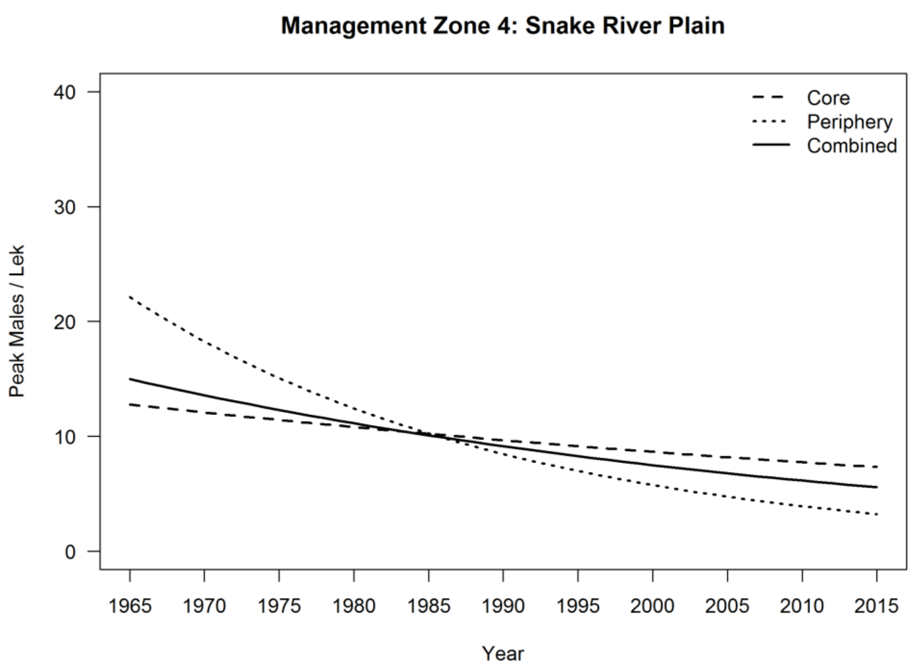

Figure 5. Estimated changes in the average peak number of male sage-grouse on leks in Management Zone 4 in the 75% core area, periphery, and combined.

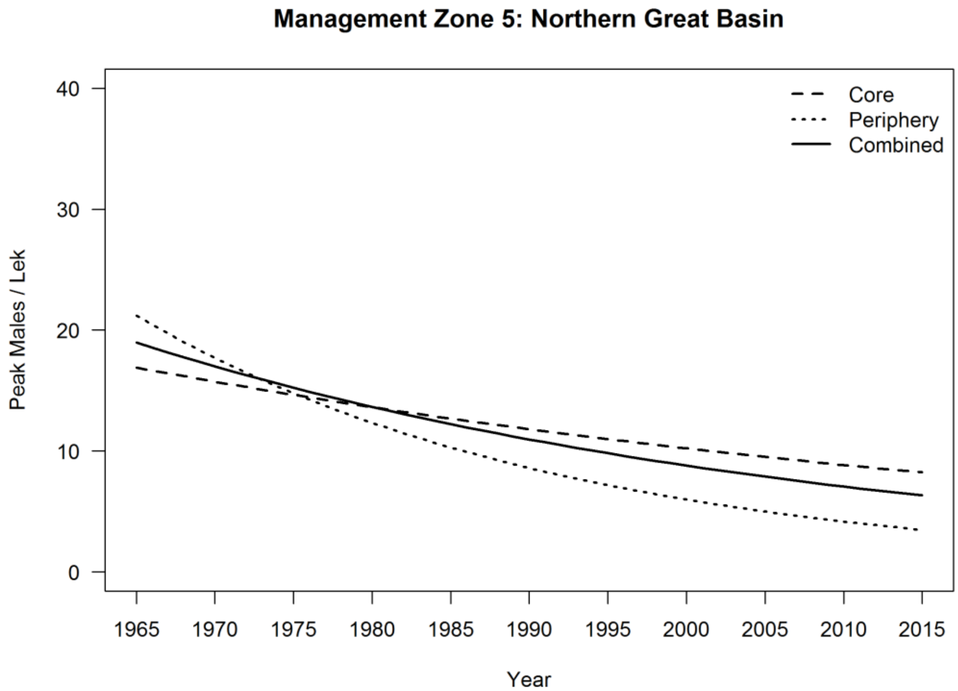

Figure 6. Estimated changes in the average peak number of male sage-grouse on leks in Management Zone 5 in the 75% core area, periphery, and combined.

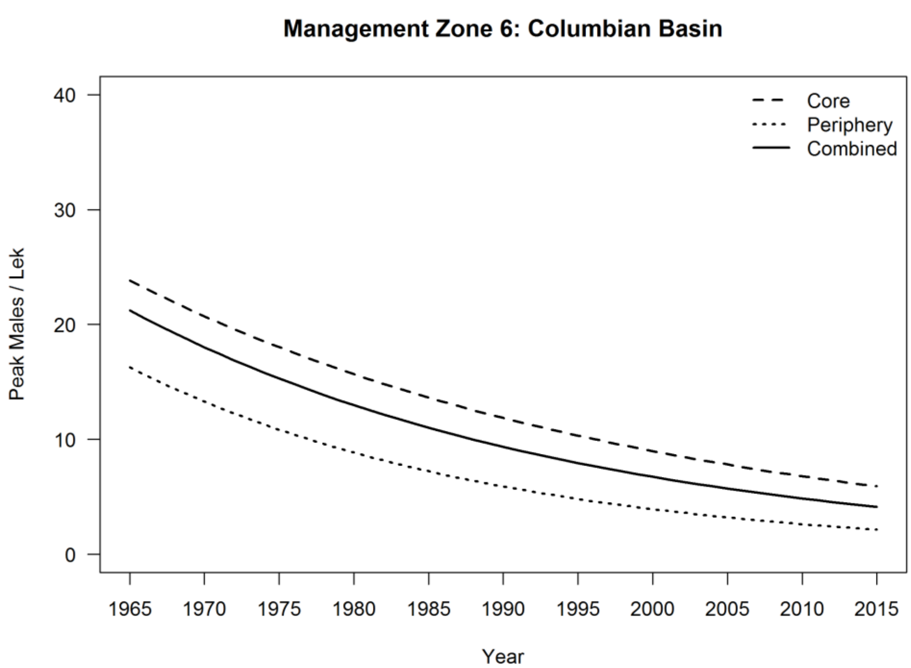

Figure 7. Estimated changes in the average peak number of male sage-grouse on leks in Management Zone 6 in the 75% core area, periphery, and combined.

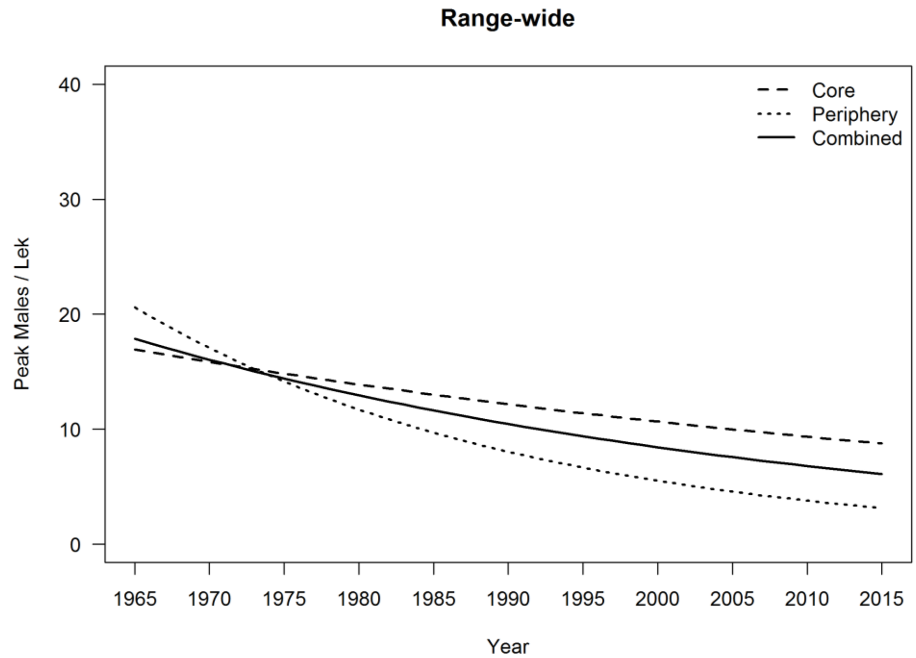

Figure 8. Trends in peak males per lek in core areas (containing 75% of males), periphery areas, and combined, range-wide 1965-2015.

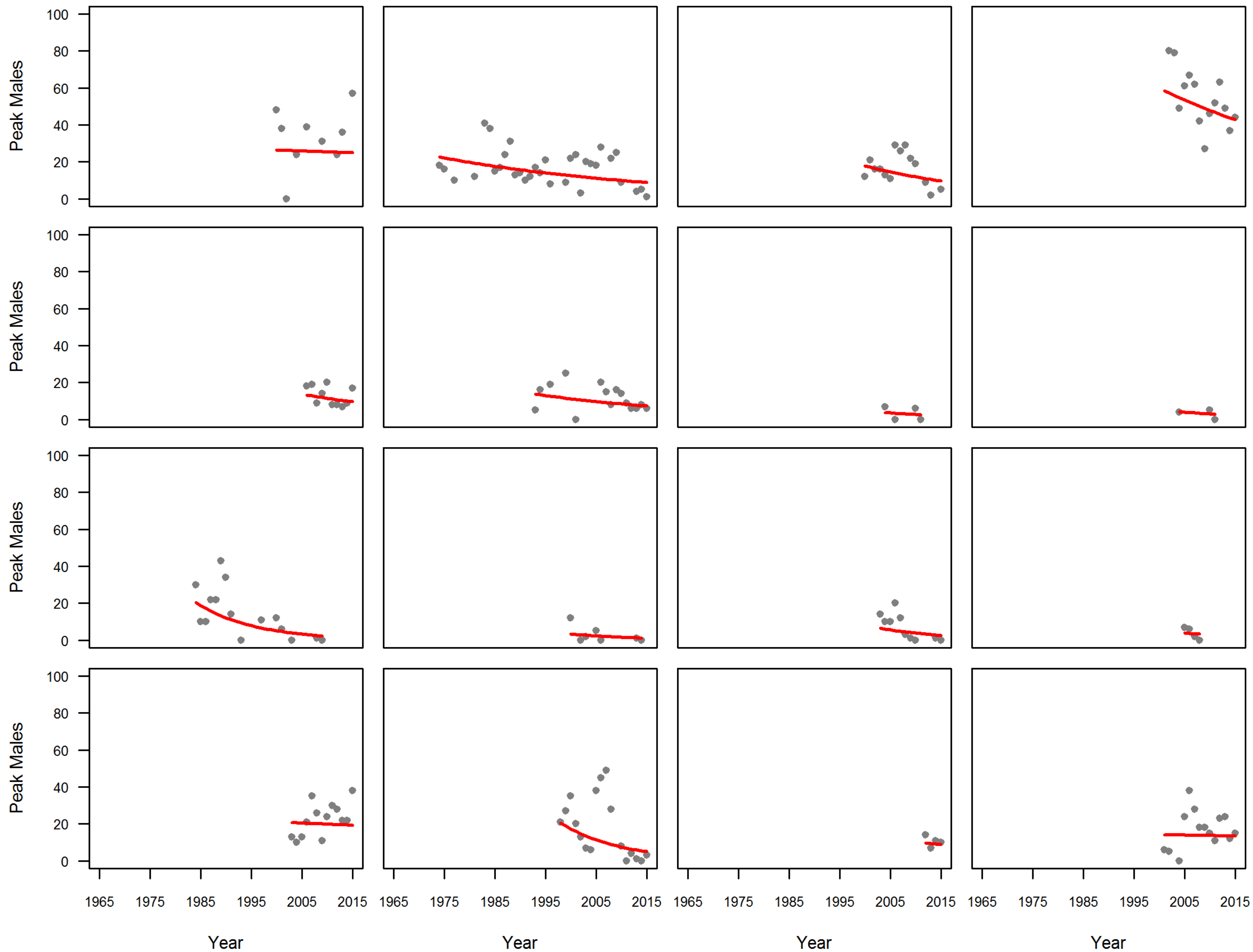

Figure 9. Estimated trends and empirical counts of peak male sage-grouse for a random sample of individual leks 1965-2015.

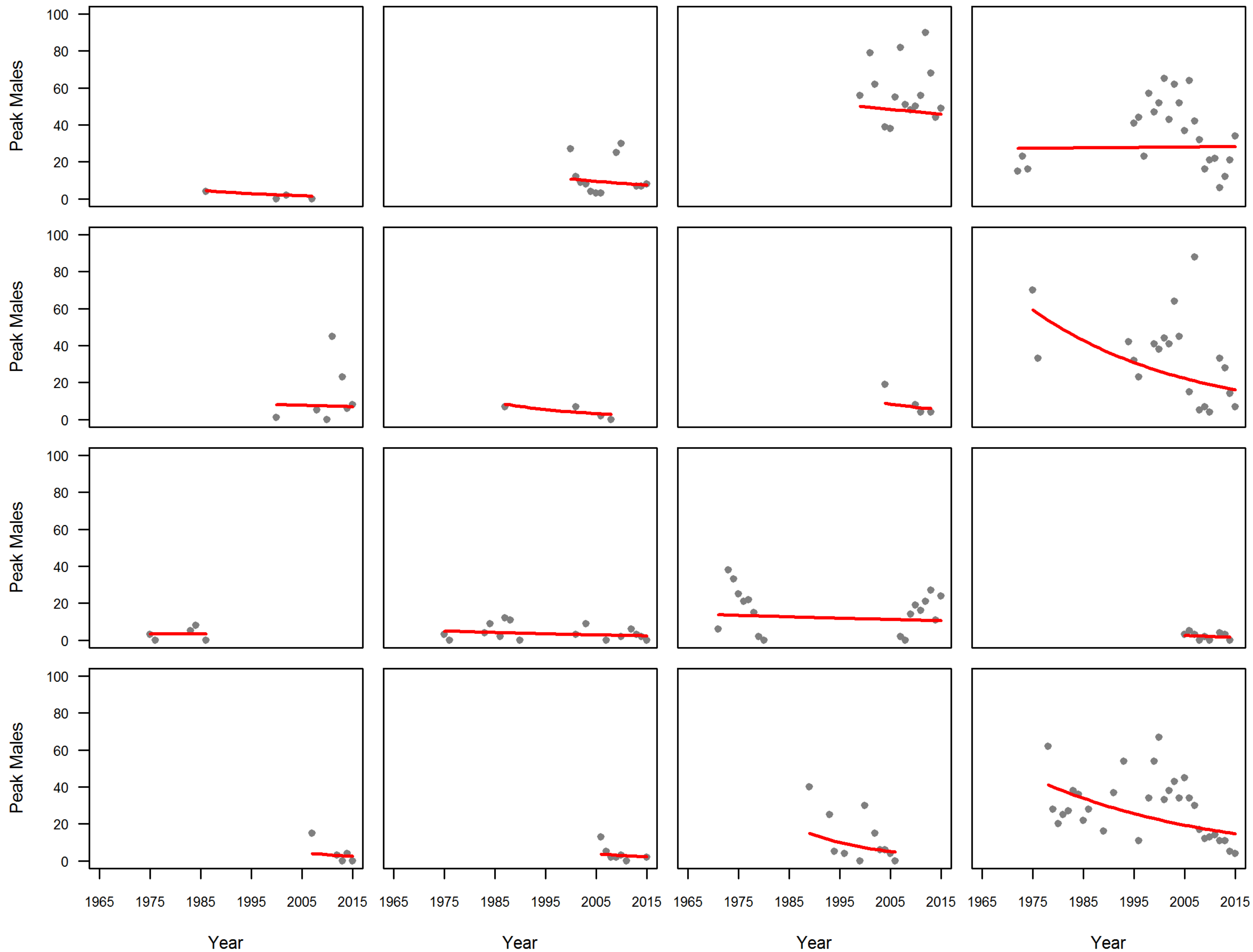

Figure 10. Estimated trends and empirical counts of peak male sage-grouse for a random sample of individual leks 1965-2015.

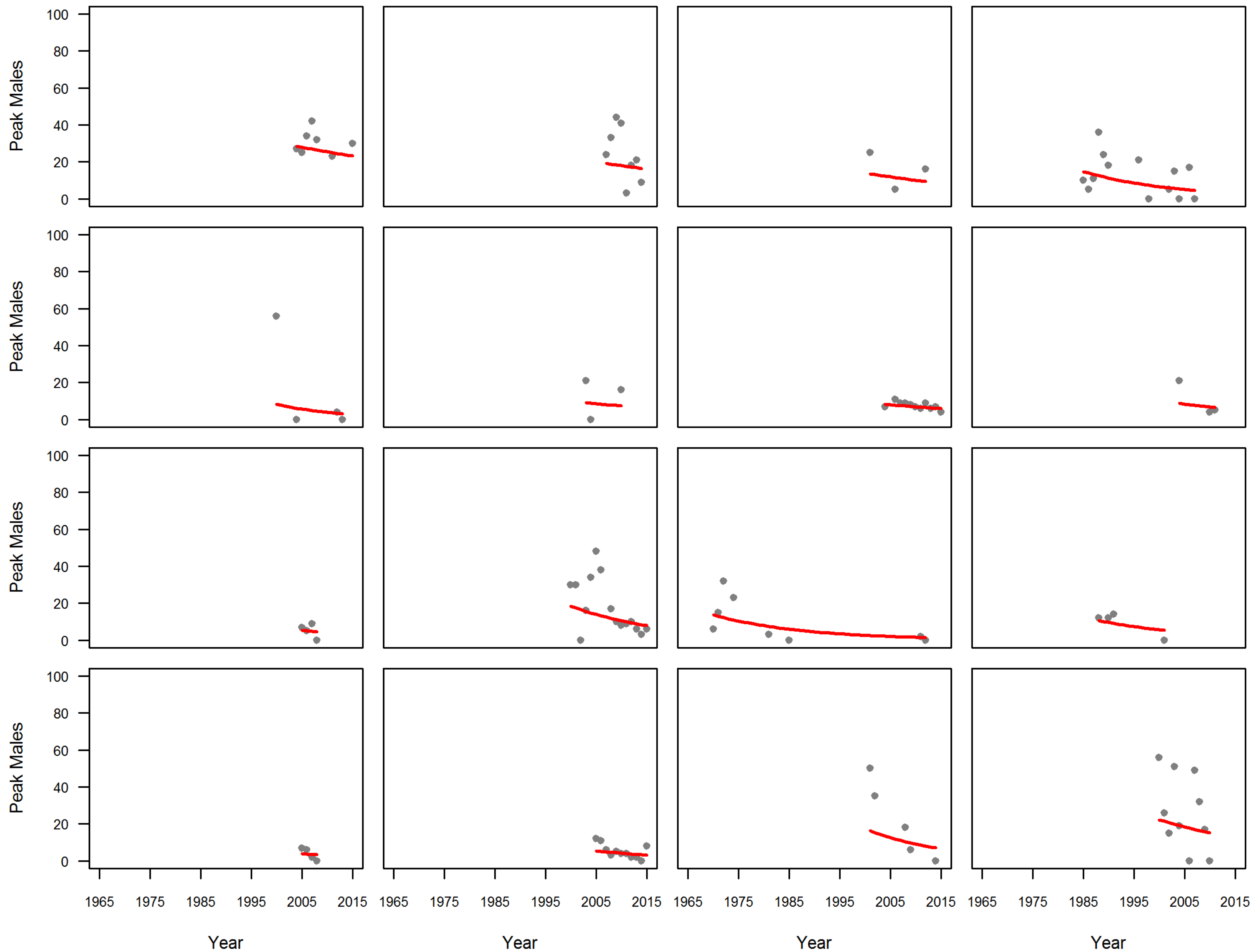

Figure 11. Estimated trends and empirical counts of peak male sage-grouse for a random sample of individual leks 1965-2015.

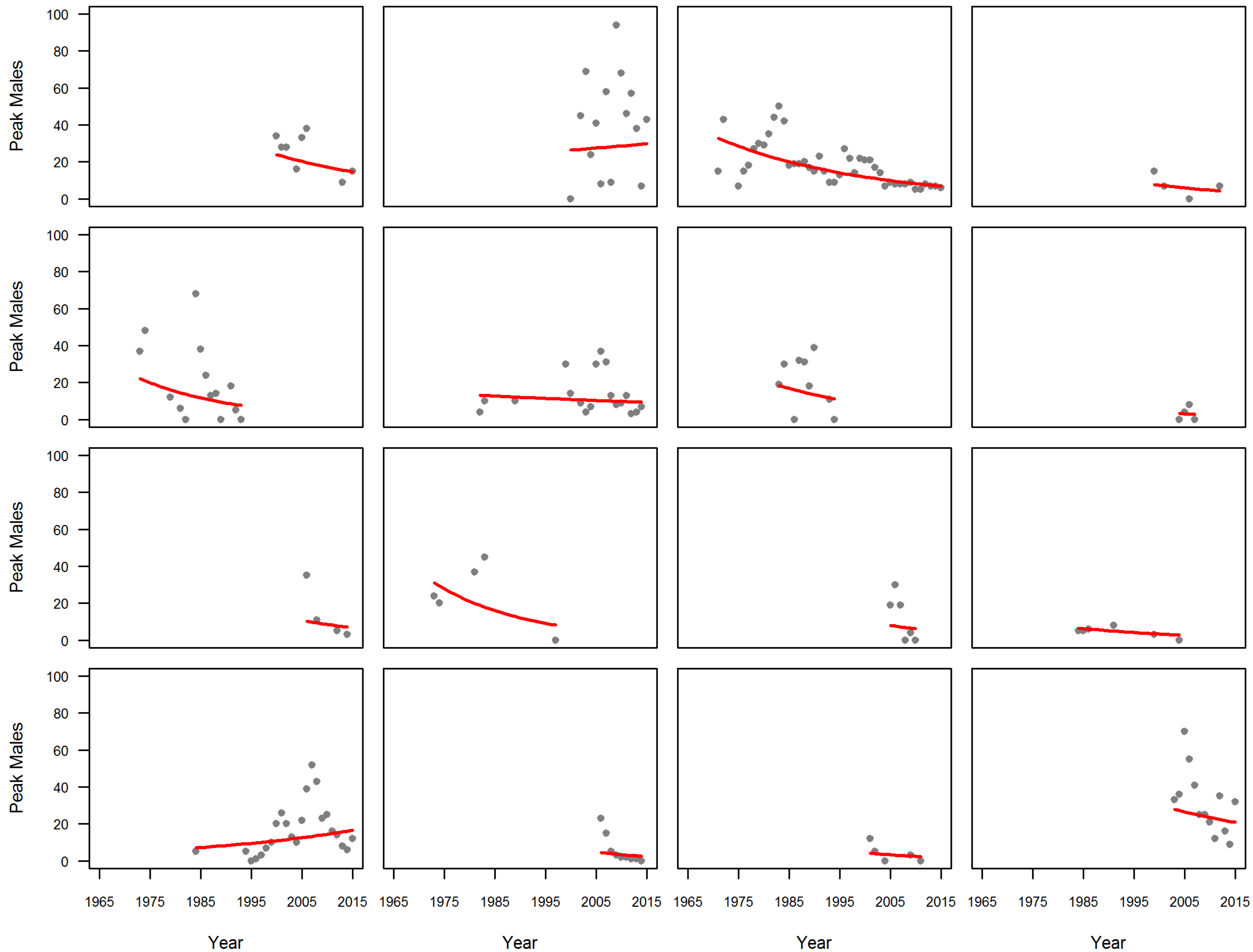

Figure 12. Estimated trends and empirical counts of peak male sage-grouse 1965-2015 for a random sample of individual leks.

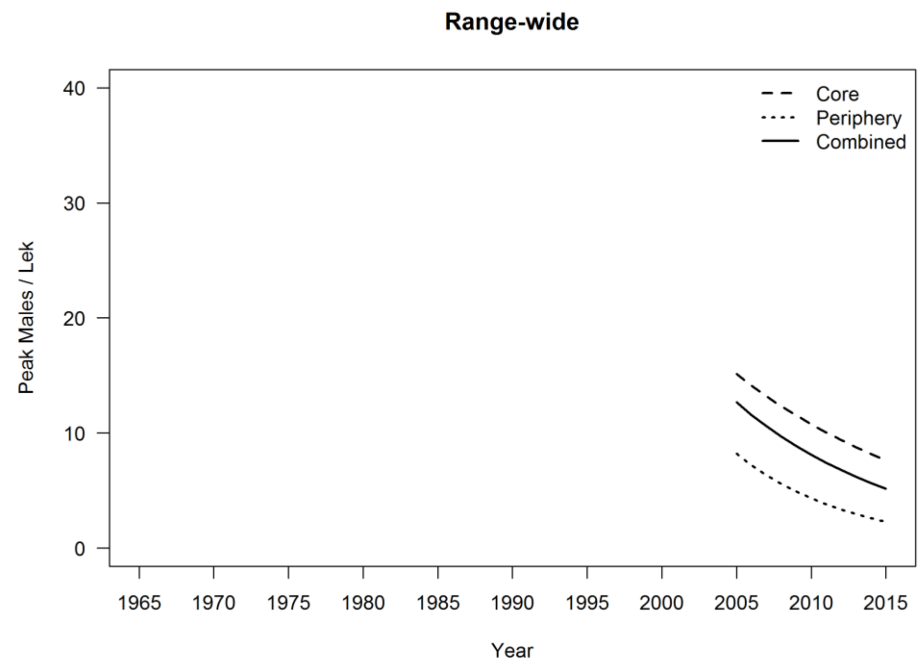

Figure 13. Trends in peak males per lek in core areas (containing 75% of males), periphery areas, and combined, range-wide 1965-2015.