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Research Article

The Importance of Within-Year Repeated Counts and the Influence of Scale on Long-Term Monitoring of Sage-Grouse

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ABSTRACT Long-term population monitoring is the cornerstone of animal conservation and management. The accuracy and precision of models developed using monitoring data can be influenced by the protocols guiding data collection. The greater sage-grouse (*Centrocercus urophasianus*) is a species of concern that has been monitored over decades, primarily, by counting the number of males that attend lek (breeding) sites. These lek count data have been used to assess long-term population trends and for multiple mechanistic studies. However, some studies have questioned the efficacy of lek counts to accurately identify population trends. In response, monitoring protocols were changed to have a goal of counting lek sites multiple times within a season. We assessed the influence of this change in monitoring protocols on model accuracy and precision applying generalized additive models to describe trends over time. We found that at large spatial scales including >50 leks, the absence of repeated counts within a year did not significantly alter population trend estimates or interpretation. Increasing sample size decreased the model confidence intervals. We developed a population trend model for Wyoming greater sage-grouse from 1965 to 2008, identifying significant changes in the population indices and capturing the cyclic nature of this species. Most sage-grouse declines in Wyoming occurred between 1965 and the 1990s and lek count numbers generally increased from the mid-1990s to 2008. Our results validate the combination of monitoring data collected under different protocols in past and future studies—provided those studies are addressing large-scale questions. We suggest that a larger sample of individual leks is preferable to multiple counts of a smaller sample of leks. © 2011 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, generalized additive models, greater sage-grouse, lek, monitoring, population trends, Wyoming.

Accurate assessment of population trends is fundamental to population biology and important for effective animal conservation and management. Population monitoring is essential to understand population trends and is a cornerstone in the management of wildlife resources (Williams et al. 2002).

Data generated through monitoring serve 2 primary purposes. First, data are used to provide descriptions of population trends over time. Second, data are used in mechanistic studies to examine relationships between the species monitoring data and a suite of covariates suspected to influence patterns in the monitoring data. Examples of mechanistic use of monitoring data include studies addressing the influence of climate (Pellet et al. 2006, Yamamura et al. 2006, Grosbois et al. 2008), habitat change (Seoane and Carrascal 2008, Hewson and Noble 2009), and population viability analysis (Morris et al. 2002, Lindenmayer and McCarthy 2006, Wakamiya and Roy 2009). The time-series descriptions are simple models that describe species response over time. If y represents the animal abundance index, then generally, the time-series descriptions are $y =$ time. Mechanistic models are more complex with many additional covariates potentially affecting the animal index (y). The accuracy and precision of both time-series and mechanistic analyses are largely determined by the methods used to collect the monitoring data which serve as the response variable.

Greater sage-grouse (*Centrocercus urophasianus* hereafter sage-grouse) have been the focus of extensive monitoring for decades (Connelly et al. 2004). The monitoring results have led to concern and interest in sage-grouse for several reasons. The historical range of sage-grouse has contracted substantially (Schroeder et al. 1999, Schroeder et al. 2004) and estimates in 1997 suggested a decline of 33% for breeding populations range-wide (Connelly and Braun 1997). Populations are threatened by anthropogenic factors that alter sagebrush ecosystems, including agricultural conversion (Connelly et al. 2004), exotic plant invasions (Wisdom et al. 2002, Knick et al. 2003), and energy exploration and extrac-

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tion (Lyon and Anderson 2003, Holloran et al. 2005, Aldridge and Boyce 2007, Walker et al. 2007, Doherty et al. 2008, and others). The species is currently designated as a candidate for listing under the United States Endangered Species Act by the United States Fish and Wildlife Service. Thus, accurate assessment of trends over time and long-term mechanistic studies are critical to proper status assessments for the species, range-wide, and for individual populations.

Sage-grouse have a lek mating system, in which males congregate at display grounds during the breeding season. Counts of males attending leks in the spring are one of the primary methods of monitoring sage-grouse populations. Male lek count data have been used extensively in multiple leking species and appear useful for assessing change, particularly at broad scales, and correlate with annual abundance estimates for adult males in some areas (Connelly et al. 2004, Alonso et al. 2005, Warren and Baines 2008, Fedy and Doherty 2011, Broms et al. 2010). Lek counts have also been used in many mechanistic studies including population viability analysis (LaMontagne et al. 2003, Garton et al. in press), response to stressors (Connelly et al. 2003, Walker et al. 2007), geographic variation in population cycles (Williams et al. 2004), or environmental and habitat conditions (Niemuth and Boyce 2004, Kolzsch et al. 2007). Despite the wide spread use of lek counts to infer trends and examine potential mechanistic influences, several authors have raised concerns regarding the efficacy of lek counts to assess population change (Beck and Braun 1980, Walsh et al. 2004).

In response to concerns regarding lek counts, and based on the recommendations of many experts the monitoring standard for sage-grouse was revised to recommend ≥ 3 within-year repeated measures at each lek site (Patterson 1952, Braun et al. 1977, Jenni and Hartzler 1978, Connelly et al. 2000, Connelly et al. 2004). The maximum or peak count of males is then typically used as the population index. However, there are concerns with using the peak count. Male sage-grouse occasionally visit >1 lek within a breeding season (Dalke et al. 1963, Emmons and Braun 1984, Schroeder et al. 1999). Therefore, there is potential to count an individual male multiple times and inflate the abundance index if nearby leks are not surveyed at the same time. Nevertheless, 3 counts are standard for many sage-grouse monitoring programs.

Despite the implementation of the 3-count standard, many leks were counted only 1 or 2 times within a year. Given the current standard of 3 counts per lek per year, we are left with the question: is it appropriate to use leks that were counted only once within a given year when modeling long-term trends? Many studies have used leks counts and there is general agreement on the 3-count standard, but does that mean researchers should not use data in analyses from leks that have only been counted once, or is the effect on overall estimation minimal? How are the accuracy and precision of models built using lek count data affected by the inclusion or exclusion of leks counted under different monitoring protocols? To investigate these questions, we analyzed the effect of 1 count or 3 (or more) count protocols on a simple time-series model. We used these results to describe historical trends in Wyoming male lek counts from 1965 to 2008, including identification of significant changes in the rate of increase or decrease, and compared the percentage change in male lek counts between key years.

STUDY AREA

We analyzed sage-grouse data from across the state of Wyoming; a state with a large expanse of sagebrush habitat (approx. 38% of the state; Connelly et al. 2004) and which was predicted to remain one of the few strongholds for sage-grouse populations (Knick et al. 2003). Furthermore, Wyoming had one of the longest-running lek monitoring programs with data collected as early as 1948 (Connelly et al. 2004). These data were collected by several agencies and collated and managed by the Wyoming Game and Fish Department (WGFD). Male attendance at leks in Wyoming and other parts of the species' range follows an approximately normal distribution from early March to early May (Schroeder et al. 1999).

METHODS

The National Oceanic and Atmospheric Administration (NOAA) divided Wyoming into 10 unique climate divisions (Fig. 1). Climate variation could affect the patterns of population trends in grouse (June 1963, Gill 1966, Schroeder et al. 1999, Aldridge and Boyce 2008) and may influence population trends of sage-grouse in Wyoming. Therefore, we examined trends within each unique climate division, as well as across Wyoming. Grouping lek count data by climate divisions resulted in considerable variation in sample size among the regions both in number of years surveyed and the number of lek sites surveyed each year. We did not investigate climatic factors as predictive covariates for the trends. The purpose of grouping by climatic division was to account for spatial clustering of samples and to facilitate the examination of variation in sample size. We required continuous inter-annual observations within a climate division; that is, ≥ 1 lek surveyed each year within the climate division. There were too few leks counted within NOAA climate divisions 1 or 2 to estimate trends (division 1 range: 4–10 leks, $\bar{x} = 6.6$/yr; division 2 range: 2–10 leks, $\bar{x} = 5.6$/yr). Therefore, we did not include data from these climate divisions; all other divisions met our criteria.

There are several popular methods for analyzing long-term population monitoring data. For example, linear route regression (Geissler and Noon 1981, Sauer and Geissler 1990, Thomas 1996), linear mixed-effects models (Sage- and Columbian Sharp-tailed Grouse Technical Committee, unpublished report), and the Mountford method (1982, 1985). However, these approaches are not particularly well suited to the investigation of long-term, nonlinear, trends in population numbers (Fewster et al. 2000). Structural time-series analyses in combination with the Kalman filter have successfully described nonlinear trends (Visser 2004, Soldaat et al. 2007). However, Soldaat et al. (2007:S355) noted that data included in the analysis should not contain "too many" zero values.

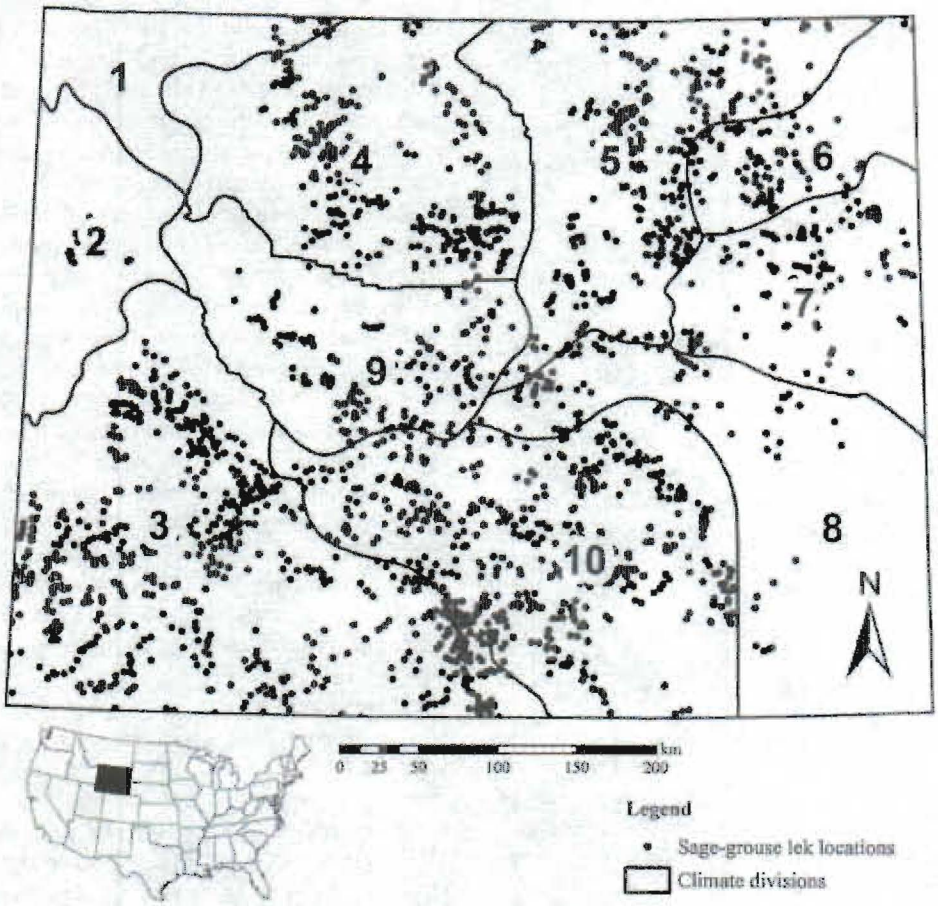

Figure 1. Current distribution of greater sage-grouse in Wyoming with the 10 National Oceanic and Atmospheric Administration's climate divisions numbered on the map. Map also shows the distribution of known leks that were surveyed (1965–2008).

Generalized additive models (GAM; Hastie and Tibshirani 1990, Wood 2006) are, globally, among the most widely used methods to smooth time-series data allowing for appropriate characterization of nonlinearities and examination of population trends. For example, GAMs are used for the analysis of monitoring data in the Breeding Bird Scheme (Fewster et al. 2000), Wetland Bird Survey (Atkinson et al. 2006), and the British Butterfly Monitoring Scheme in the United Kingdom (Rothery and Roy 2001) and many others. Generalized additive models allow the analyst to choose the level of smoothing as a balance between linearity and capturing every fluctuation within a population. Generalized additive models do not make any assumptions regarding the shape of the relationship between predictor and response variables, making them well suited to the analysis of trends for species in which populations are known to cycle (e.g., voles *Microtus agrestis*, grouse *Tetrioninae*, rabbits *Sylvilagus* sp.; Chitty 1960, Moss and Watson 2001, Fedy and Doherty 2011).

We compiled male lek count time-series (hereafter lek count) data for sage-grouse in Wyoming. The time-series consisted of annual spring counts of male sage-grouse on leks from 1965 to 2008. We estimated missing data through GAMs. We assumed data to be missing at random, which generally means the chance of a predictor value missing (i.e., the site not surveyed) was not a function of the response for that observation (i.e., the number of males attending the lek; Hastie and Tibshirani 1990). This assumption was reasonable for the lek count data. Furthermore, recent research has illustrated that GAM approaches applied to long-term survey data were unaffected by up to 50% missing data (Atkinson et al. 2006). Counts were missing from our dataset for approximately 40% of site-by-year observations between 1965 and 2008 (i.e., we had counts at each site for 6 of every 10 yr). The duration (number of continuous years) of missing data per site had a Poisson distribution and a median value of 2 (yr). Therefore, most data were not missing in long continuous sections of years, and the level of missing data should not affect large-scale conclusions.

Statistical Analyses

We investigated indices of male sage-grouse population trends using an abundance index (Fewster et al. 2000) based on GAMs (Hastie and Tibshirani 1990). We modeled the expected peak male lek counts in each year using an abundance index (Fewster et al. 2000) within each NOAA climate divisions by applying a GAM with Poisson error distribution

and logarithmic link function (Fewster et al. 2000)

$$\log(\mu_{it}) = \alpha_i + s(t)$$

This model assumes the observation y_{it} is from a Poisson distribution with mean μ_{it}, and all counts are independent, where α_i is the lek effect for lek i and $s(t)$ represents the smoothing function of time and summarizes the smoothed quantities in year t. We fit the model by finding estimates for $\hat{\alpha}_i$ and $\hat{s}_t$ which we used to estimate count μ_{it} for each lek i and year t.

Fewster et al. (2000) defined the abundance index for year t relative to an arbitrarily chosen base year. Population monitoring efforts for sage-grouse increased by 737% range-wide (including Wyoming) between 1965 and 2003 and have remained high since 2003 (Connelly et al. 2004). Therefore, lek count data were more complete in recent years, with a greater number of leks surveyed, and we chose 2008 as our base year. We defined the annual abundance index curve for year t as

$$I(t) = \frac{\text{total predicted count for year } t}{\text{total predicted count for 2008}} = \frac{\exp(\hat{s}(t))}{\exp(\hat{s}(2008))}$$

This index measures relative abundance with respect to the last year (2008) in each count series. We modeled trends as a nonlinear function of time by estimating the components of the index using GAMs. We conducted all of our analyses using polynomial regression smoothing; however, other options exist (Hastie and Tibshirani 1990).

We specified the amount of smoothing applied to a GAM by the degrees of freedom selected using $0.3T$ (rounded to the nearest integer) degrees of freedom, where T is the number of years for which count data are available (Fewster et al. 2000). This provided a smoothed estimate of the population index over time to avoid sensitivity to short-term fluctuations that could mask the underlying trend (Mazzetta et al. 2007). Furthermore, $0.3T$ has become a convention when applying these models to wildlife time-series data and thus provides potential for comparison with other species (Robinson et al. 2005, Spinola and Gates 2008, Fonseca et al. 2009, Hewson and Noble 2009, Wright et al. 2009). We fit models using the gam function of the mgcv R-package (Woods 2008, R Version 2.7.2, www.r-project.org, accessed 1 Aug 2008).

We estimated variances using bootstrap methods (Fewster et al. 2000). This approach involves simulation-based analysis that does not rely on parametric model assumptions and therefore results in more robust variance estimates. The approach involves re-sampling K leks with replacement from the K leks within a region and re-estimating a regional index, which produces variance about the regional estimate. We did not sample variance estimates on individual observations because bootstrapping methods assume independence of samples; lek was the sampling unit, not individual observations at leks.

The Fewster et al. (2000) method allows investigation of population change points with a numerical analysis of second derivatives of the smoothed indices. Change points indicate a significant change in the rate of growth or decline of the abundance index. A second derivative value above zero indicates an increase in the rate of growth or a decrease in the rate of decline. Second derivative values that are negative indicate a decrease in growth rate or an increased rate of decline. We calculated change points based on the smallest possible window size of one year to obtain estimates of the second derivatives at maximum resolution. Therefore, change points in our study represent changes in the rate of the population trajectory from the previous year. We determined significance of the change points ($P < 0.05$) and the 95% confidence intervals by bootstrapping. We generated 399 bootstrap replicates for all climate division models. Exploratory analyses revealed that confidence interval estimates and the identification of change points did not differ substantially using either 199 or 399 bootstrap replicates (B. C. Fedy, Colorado State University, unpublished data). Both values have been used previously (Fewster et al. 2000, Siriwardena 2004). We used 199 bootstrap replicates to estimate the confidence intervals for the state-wide models because they were computationally very intensive.

Data Re-Sampling

We conducted an analysis in multiple steps to evaluate whether one count was sufficient in identifying long-term trends. First, we developed time-series models on data using identified peak values for leks that were counted ≥ 3 times. We selected only leks with ≥ 3 observations within a year (hereafter the reduced dataset). From those selected leks, we identified the maximum (peak) count of males counted for each lek within each given year. We estimated trends and confidence intervals based on these peak male counts using the GAM procedures outlined above. We assessed trends for each climate division and also state wide. We refer to these models as peak-sample models. These models represent time-series built on the best available and recommended data including only the peak counts from leks with ≥ 3 counts within a year.

Next, we simulated visiting a lek only once per year to see how this would affect model accuracy. To this end, we re-sampled the reduced dataset to generate 50 new datasets by randomly selecting any one of the 3 or more observations per lek, per year, repeated for each climate division and the state-wide analyses. Thus, when re-sampling the data we were not necessarily selecting the peak male count for each year. The re-sampled data could include the same value for a particular lek in a given year as the peak-sample models, but this clearly was not always the case. We then used the GAM procedures to estimate population trends based on each of these 50 re-sampled datasets for each climate division and state-wide analyses and compared the 50 re-sampled models to the peak-sample models. When we refer to the accuracy of the re-sampled data, we are comparing the results to the peak model to detect any biases introduced by sampling only once per year. The links between lek counts and true population size are not clearly established (as mentioned elsewhere) and therefore, we do not assume the peak model accurately represents true population size.

We quantified differences among the peak-sample models and the 50 randomly re-sampled models in several ways. First, we quantified the number of predicted trend points generated by the re-sampled GAMs that fell outside the 95% confidence intervals of the peak-sample models. Second, across each division, we assessed accuracy of the re-sampled models at recognizing the same change points identified from the peak sample models. We considered the change points recognized by the peak-sample models the true (i.e., the best estimated) change points and classified the points generated by the 50 re-sampled models in terms of Type I and Type II errors. For example, a Type I error occurred when the re-sampled data identified a significant change point and the peak-sample model did not (false positive). A Type II error occurred when the re-sampled models did not classify a significant change point that was identified by the peak-sample models (false negative).

We examined the relationship between sample size (varied across climate division analyses) and the accuracy of trend estimation by comparing the number of leks included in a given year and the associated confidence interval. We then regressed the spread of the confidence interval (width) in a given year against the number of leks sampled in that year. We tested multiple possible regression relationships (linear, exponential, logarithmic, polynomial, power) to determine the best shape of the relationship. We considered the relationship resulting in the highest coefficient of determination to be the best fit. We then used this best-fit regression model to estimate the relationship between the number of lek sampled and the percent of statistically detectable annual change in a population. We also tested the same possible regression relationships to examine the relationship between sample size and confidence interval at the state-wide level.

Overall State-Wide Population Trends

We used all available Wyoming lek count data to build an overall state-wide description of population trends using the same GAM approaches outlined above. However, for this model the rarefication of the data was informed by the previous analyses in this study. Therefore, we included in the analysis all leks with birds present that were surveyed between 1965 and 2008 (range = 60–1645 leks surveyed per year) regardless of the number of repeated counts within the year, provided they fell within the period of typical male attendance at leks (1 Mar–31 May). If a lek was counted $\geq$2 times annually, we selected the peak (maximum) number of males for that year.

Using the overall state-wide model we calculated the population change for a series of pair-wise comparisons. We used the approach described in Fewster et al. (2000:1976), which uses the bootstrap replicates to "find approximate confidence intervals for the percentage population change between any two years." We considered the change between 2 years significant if the 95% confidence interval of the change estimate did not contain zero. Because sage-grouse populations in Wyoming appear cyclic, we compared peak values to peak values and trough-to-trough values when addressing pair-wise comparisons.

RESULTS

The number of leks surveyed within a climate division varied considerably (Fig. 1, Table 1). For all divisions with sufficient data (excluding divisions 1 and 2) we used GAMs to estimate historical population trends based on the peak-sample data and the 50 re-sampled datasets (Table 1, Fig. 2). Most trend lines we calculated using the re-sampled data showed a similar pattern to lines we calculated on the peak-sample data (Fig. 2). Across all years and divisions the re-sampled trend data resulted in 9,750 trend points. Of these points, 12 $\pm$ 8% (SD) fell outside of the 95% confidence interval. Most points that fell outside the 95% confidence interval of the peak model were below the confidence interval (10%), and only 2% of points occurred higher than the confidence interval (Figs. 2 and 3).

We identified significant change points for 6 of the 8 divisions (Fig. 2). These points represented either a significant increase or decrease in the rate of change in the abundance index. The re-sampled data identified similar change points as the peak-sample models. Across all 9,750 re-

Table 1. Re-sampled Wyoming greater sage-grouse lek trend model accuracies by climate division. We dropped divisions 1 and 2 due to lack of lek counts (see text). We present the number of years included in each set of models, the percentage of points from re-sampled models that were lower than the 95% confidence intervals, the percentage of points from re-sampled models that were higher than the 95% confidence intervals, and the total percentage of points outside the 95% confidence intervals. Years included varied by climate division and ranged from 1977 to 2007. We also present a summary of the accuracy of re-sampled models in correctly identifying significant change points (downturns and upturns, explained in text) and the percentage of Type I and Type II errors committed by re-sampled models in correctly identifying significant change points.

Climate zone	No. of years	Points low of CI (%)	Points high of CI (%)	Total points outside CI (%)	Type I errors		Type II errors	
					Downturns (%)	Upturns (%)	Downturns (%)	Upturns (%)
3	29	7	2	9	0	5	3	4
4	29	12	0	12	4	2	6	1
5	8	2	4	6	0	9	0	0
6	9	4	3	8	0	0	0	12
7	10	0	6	6	0	4	0	0
8	10	2	0	2	3	0	2	3
9	15	11	2	13	0	1	0	0
10	31	29	0	30	2	1	0	1
All zones	31	19	0	19	0	0	1	2
Average	19.2	9.6	2.0	11.6	0.9	2.5	1.2	2.6
Standard error		3.2	0.7	2.8	0.4	1.0	0.6	1.3

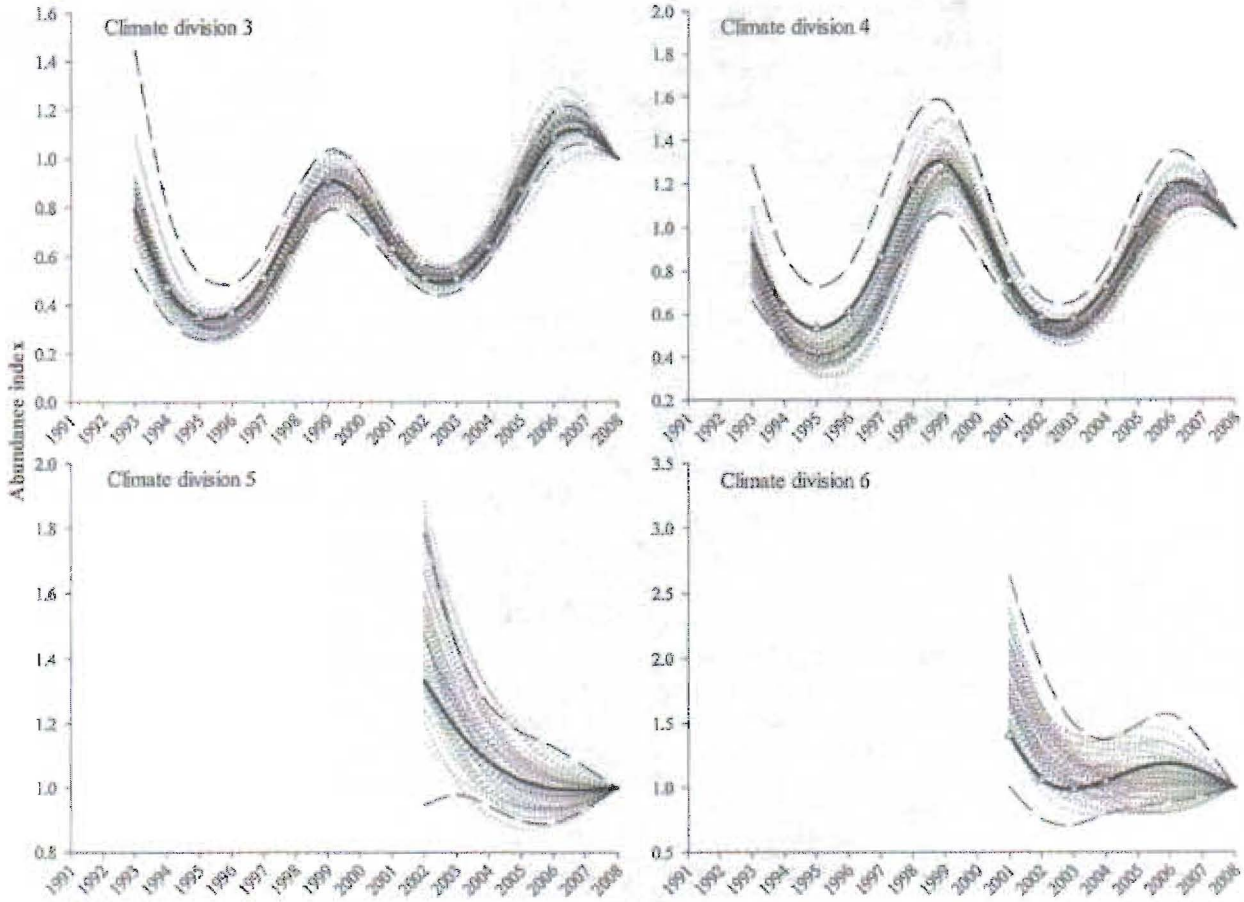

Figure 2. We generated trend estimates for greater sage-grouse in Wyoming within 8 National Oceanic and Atmospheric Administration's climate divisions using generalized additive models. We developed trend models using only those leks that had ≥3 repeated counts within a year. We calculated the abundance index as the ratio of the number of birds in a given year relative to year 2008 (base). Therefore, an abundance index of 1 represents no change between a given year and the base year of 2008. The thicker black line represents the model built using the peak male count from each collection of ≥3 counts for each year. Dashed lines represent the 95% confidence intervals about the peak model determined from 399 bootstrapped replicates. Triangles are statistically significant change points, which represent significant differences in the rate of increase or decline. Downward gray triangles are significant downturns and upward triangles indicate significant upturns. Thin dotted lines are the 50 unique trend models built using the re-sampled data. We re-sampled data to simulate visiting a lek only once per year by randomly selecting 1 of the 3 or more observations per lek per year. Years included for each division are presented along the *x*-axis.

sampled trend points, change points were correctly identified 92% of the time (Table 1). The re-sampled models showed similar rates of Type I (false positive; 4%) and Type II (false negative; 4%) errors.

We estimated trends using GAMs for each year within each division. The number of leks surveyed in each year by division ranged from 1 to 238. When we regressed the number of leks surveyed in a given year against the confidence interval associated with that year, a power trend line provided the best fit with ($R^2 = 0.67$, Fig. 4A). That regression suggested the decrease in confidence interval (i.e., increase in accuracy) began to level out at approximately 50 leks. We used the trend line model from the regression to describe the relationship between percent annual detectable change and the number of leks surveyed (Fig. 4B).

Our results comparing peak-sample and re-sampled models informed our ability to use all data for analysis of the overall patterns of sage-grouse abundance in Wyoming. Data used to assess trends based on the 400 re-sampled models (50 per climate region) were similar to the respective peak-sample models; thus, we included all leks surveyed across Wyoming for overall assessment of trends, which allowed us to include leks with only 1 or 2 counts per year and expand the length of the time series as older surveys had fewer annual counts per lek.

The Wyoming overall model showed a decreasing trend in the abundance of sage-grouse in Wyoming based on male lek counts (Fig. 5). This modeling approach also allowed clear description and presentation of the cyclic nature of these counts. Since 1965, based on male lek counts, these populations seem to cycle with a periodicity of 6–9 years. Regular fluctuations in populations resulted in identification of many change points in the model (Fig. 5). Confidence intervals, which were large prior to the 1980s, decreased dramatically toward 2008. Pair-wise comparisons of percentage annual change based on the overall model were generally significant at the 95% level and showed a trend of negative percentage change until the 1990s when the pair-wise percentage change between years switched to a positive direction (Tables 2 and 3).

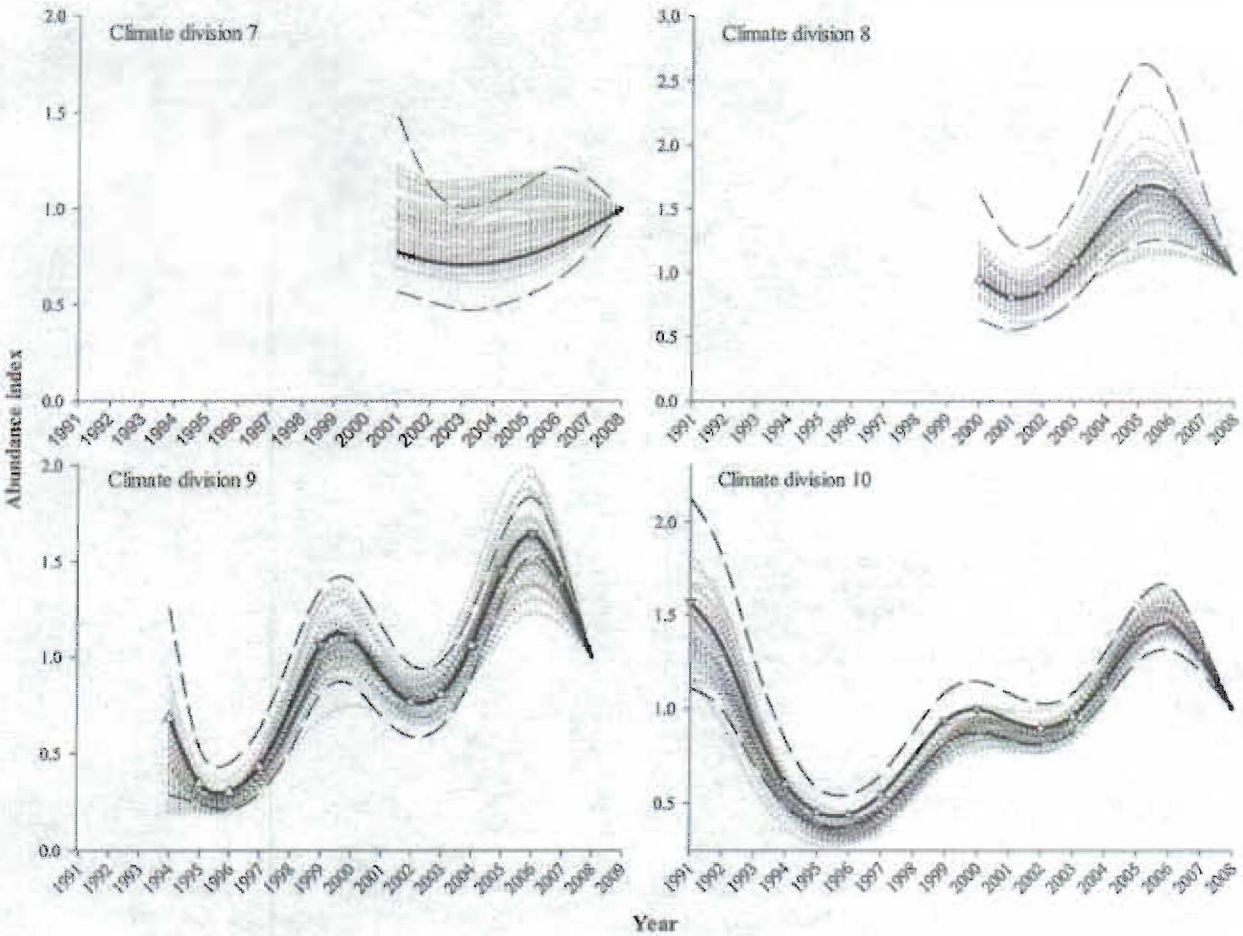

Figure 2. (Continued)

DISCUSSION

Population time-series models we developed using data that represented only one count per year were similar to models based on repeated measures (≥ 3) within a year at certain spatial scales. Sample size (number of leks) had more influence on the precision of GAM estimated trends than repeated measures at a lek within a year. We developed a non-linear trend model for sage-grouse in Wyoming. The GAM techniques we applied allowed us to accurately assess non-linear trends in sage-grouse abundance across large spatial extents and indentify years where significant changes in abundance occurred. Pair-wise comparisons provided percentage change between years with associated 95% confidence intervals and demonstrated most declines in sage-grouse lek counts occurred between 1965 and the 1990s.

Our study represents one of the first applications of non-linear methods to the assessment of sage-grouse trends (Fedy and Doherty 2011). Population trends in many species, including sage-grouse, are often examined using linear trend estimations (Thomas 1996). Many grouse (*Tetrioninae*) populations are cyclic (Moss and Watson 2001). Indeed the application of the non-linear approaches in our study revealed the cyclic nature of male attendance at leks in Wyoming. Berryman (2002:5) defined a cyclic population as "one that exhibits an oscillation in population numbers or density that has an obviously regular period of three or more years." If lek counts are a useful index of population size, then our data show that sage-grouse populations in Wyoming demonstrate regular periodicity of 6–9 years. Fedy and Doherty (2011) showed rhat sage-grouse in Wyoming cycled on a period of 8 years from 1982 to 2008 and that lek counts are tracking biologically meaningful fluctuations in the system. Furthermore, it is unlikely the cyclicity observed in long-term sage-grouse trends is the result of sampling protocols (Fedy and Doherty 2011). Fewster et al. (2000) applied GAM techniques with $0.3T$ df to 12 farmland bird species using the Common Bird Census of the British Trust for Ornithology over a 30-year period using the same model parameters. For those 12 species, the maximum number of change points identified was 15, half the years surveyed. Our application of these techniques to sage-grouse identified many more change points (37 of 42 years possible for the overall model), suggesting the rate of change within sage-

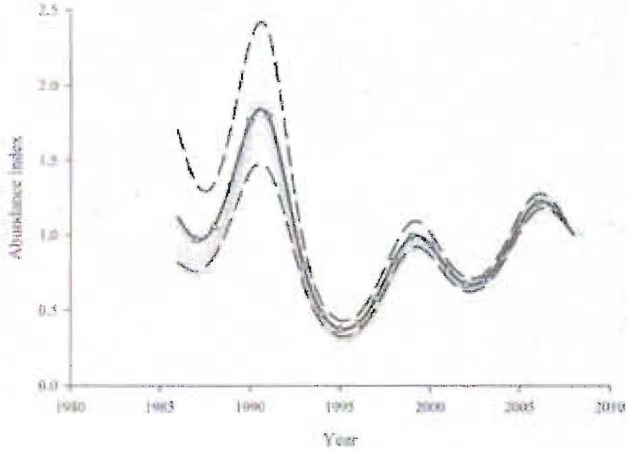

Figure 3. We developed Wyoming-wide re-sampled greater sage-grouse trend models using only those leks that had ≥3 repeated counts within a year using generalized additive models. We calculated the abundance index as the ratio of the number of birds in a particular year to year 2008. The thicker black line represents the model built using the peak male from each collection of ≥3 for each year. Dashed lines represent the 95% confidence intervals about the peak model determined from 199 bootstrapped replicates. Triangles are statistically significant change points, which represent significant differences in the rate of increase or decline. Downward gray triangles are significant downturns and upward triangles indicate significant upturns. Thin dotted lines are the 50 unique trend models built using the re-sampled data. We re-sampled data to simulate visiting a lek only once per year by randomly selecting 1 of the 3 or more observations per lek per year. Trend estimates are presented from 1986 to 2008.

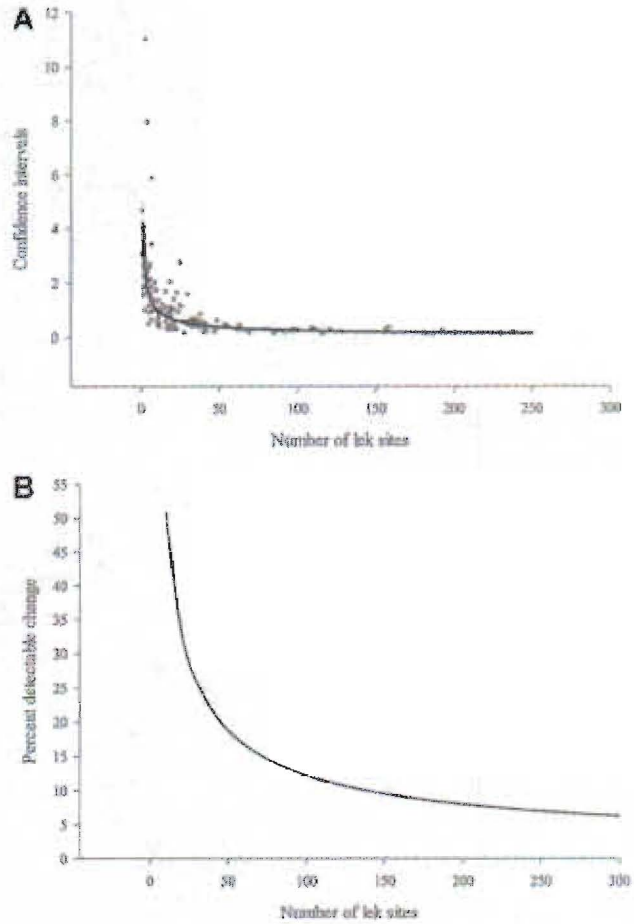

Figure 4. (A) Relationship between the number of greater sage-grouse leks surveyed within a year across Wyoming and the associated confidence interval width determined by 399 bootstrap replicates. These data are from the peak lek count models we developed for each climate division. Years included varied by climate division and ranged from 1977 to 2007. A power trend line ($y = 4.22x^{-0.62}$) explained a large portion of the variation in the relationship ($R^2 = 0.67$). (B) Sample size and percent detectable annual trend for sage-grouse in Wyoming as calculated by the power equation $y = 4.22x^{-0.62}$.

grouse populations fluctuates more than other avian species. For populations suspected to be cyclic in nature, linear models may force a degree of smoothing or linearity that could mask important fluctuations.

Climate change is thought to influence the disappearance of cycles of several cycling species in Europe (voles, grouse, insects; Ims et al. 2008). Cycles still appear to occur with the same periodicity for sage-grouse in Wyoming, but given the long-term decline in sage-grouse we demonstrated here and previously described by others (e.g., Braun 1998, Connelly et al. 2004), it is not surprising the amplitude of those cycles appears to have decreased (Fig. 5).

The application of pair-wise comparisons between years allowed us to estimate the percentage annual change. Connelly and Braun (1997) used male lek count data to estimate a 17% decline in sage-grouse populations in Wyoming. Based on our trend models using lek count data, the 1968 historical peak cycle compared to the 1999 peak, suggest a more drastic decline of 69% (95% CI = 60–77%) for Wyoming sage-grouse over a similar time frame. Including more recent data and comparing the latest peak cycle in 2006 suggested a slightly damped decline of 54% (95% CI = 41–64%), which is mainly due to the apparent increase in numbers we have documented from a historical low in 1995 to 2008 (Fig. 5) and is closer to the estimated decline of approximately 49% from 1965 to 2003 reported by Connelly et al. (2004). Our results are generally consistent with those published in a report prepared for WAFWA by the Sage- and Columbian Sharp-tailed Grouse Technical Committee in 2008. Using linear mixed-model approaches

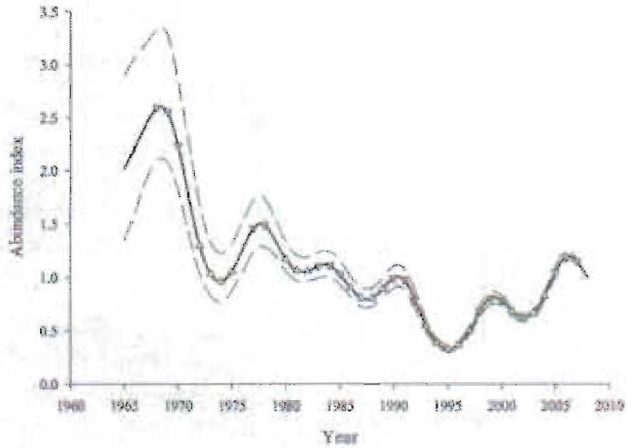

Figure 5. Overall Wyoming lek trend model estimating abundance index using generalized additive modeling approach. Model includes all surveyed greater sage-grouse leks in Wyoming from 1965 to 2008.

Table 2. Pair-wise comparisons of percent annual change between all peak years. We identified peak years as the highest predicted abundance index of Wyoming greater sage-grouse at the top of each cycle. We calculated percentage population change between years using bootstrap replicates. We considered the change between years significant if the 95% confidence intervals did not overlap zero. Values presented are the percent change between years. Values presented below percent change estimates represent the approximate upper and lower 95% confidence values estimated using the bootstrap replicates.

Peak years	1968	1978	1984	1990	1999
1978	−57%[a]				
95% CI	−66, −47				
1984	−42%[a]	−25%[a]			
95% CI	−57, −23	−39, −11			
1990	−62%[a]	−33%[a]	−10%[a]		
95% CI	−70, −53	−44, −21	−19, −1		
1999	−69%[a]	−46%[a]	−27%[a]	−19%[a]	
95% CI	−77, −60	−51, −42	−37, −18	−28, −10	
2006	−54%[a]	−20%[a]	7%	20%[a]	48%[a]
95% CI	−64, −41	−29, −12	−5, 19	7, 31	44, 53

[a] Significant values based on 95% confidence intervals.

the report also estimated trends in Wyoming from 1965 and presented much smaller confidence intervals around the model estimated values in recent years, similar to our approach. The report presented data in 5 year increments and also detected a decline in sage-grouse from 1965–1969 to 1990–1994, as we have presented here, and an increase from 1994–1999 to 2000–2004, also similar to our results (Tables 2 and 3). Of note, we also ran the overall model with 1965 as the base year (B. C. Fedy, unpublished data). As expected, confidence intervals about the abundance index were greater than when 2008 was the base year. However, compared to base year 2008, the relationship between sample size and confidence interval was similar (power trend line $R^2 = 0.45$), the years identified as significant change points were exactly the same, and the point estimates of percentage change were also identical with small deviations (<10) in the confidence intervals. The value added of the GAM approach to describing trends was in the capacity for the models to capture the cyclic nature of sage-grouse in Wyoming. However, it is important to note there still does not exist a comprehensive understanding of the link between male lek counts (the data we used) and population abundance (Walsh et al. 2004). Lek count data have several important advantages to other forms of assessing population trends in sage-grouse (Garton et al. 2007, Johnson and Rowland 2007, Sedinger 2007). Therefore, we encourage future research to continue examination of the relationships between male lek counts and population size.

The interpretation of historical population trends did not differ substantially between the peak-sample and re-sampled models. Most re-sampled points (88%) fell within the 95% confidence interval of the peak-sample model and identified similar change points. Furthermore, models built on re-sampled data were conservative estimates, from a biological standpoint, when they differed from the peak-sample models. However, re-sampled models occasionally predicted higher than average abundance than peak-sampled models. Re-sampled (single count) models could be higher than the peak-sample models because of our use of an abundance index referenced to a base year. We randomly selected the value we used for the base year in the re-sample models and therefore anytime we selected a low count for the base year, the subsequent abundance indices in earlier years would more often predict higher relative abundance than the peak-sample models. Re-sampled models were also consistent in their identification of change points and both up- and downturns were correctly identified in 92% of cases. Though re-sampled models occasionally showed slight deviations from the peak-sample models, the overall tendency was for close parallel tracking of the peak-sample estimations (Figs. 2 and 3). For example, division 10 re-sampled models accurately paralleled the peak-sample trend line, despite 30%

Table 3. Pair-wise comparisons of percent annual change between all trough years. We identified trough years as the lowest predicted abundance index of Wyoming greater sage-grouse at the bottom of a cycle. We calculated percentage population change between years using bootstrap replicates. We considered the change between years significant if the 95% confidence intervals did not overlap zero. Values presented are the percent change between years. Values presented below percent change estimates represent the approximate upper and lower 95% confidence values estimated using the bootstrap replicates.

Trough years	1974	1982	1988	1995
1982	10%			
95% CI	−8, 33			
1988	−16%	−24%[a]		
95% CI	−32, 2	−32, −16		
1995	−66%[a]	−69%[a]	−59%[a]	
95% CI	−72, −58	−73, −65	−63, −55	
2002	−35%[a]	−41%[a]	−23%[a]	88%[a]
95% CI	−50, −20	−48, −34	−30, −15	71, 103

[a] Significant values based on 95% confidence intervals.

of points falling outside the confidence interval (all other divisions range = 6–19%).

The precision of all models in terms of the confidence interval (peak-sample and re-sampled) was strongly influenced by the number of leks surveyed within a year. As sample size was lower in earlier years, all climate division models eventually had a confidence interval >1; recall that 2008 was the base year and confidence intervals increased backwards in time (Fig. 2). Understanding how sample size influences the precision of trend estimates is imperative to appropriate assessment of past and future changes in sage-grouse populations.

It is important to understand the role of both spatial scale and sample size. One observation per year is not sufficient for analyzing trends at smaller spatial units and sample sizes. When examining trends at large spatial scales, presence of within-year variation in counts at an individual lek is clearly insignificant in comparison to the variation among leks at larger spatial scales.

The precision of sage-grouse population trend models based on the number of males at a lek was not significantly affected by the inclusion of within-year repeated counts at large scales. Our results support the conclusion that for situations in which the number of leks surveyed is ≥50, then one visit per lek will result in similar accuracy for population trend estimation and change point identification, using the methods we outlined.

We can return explicitly to our questions posed in the introduction. Should researchers not use leks that have only been counted once in their analyses or is the effect on overall estimation minimal? Our research supports the validity of past work that has made use of lek counts at large scales. Our simple time-series models showed that conclusions from the models did not change substantially with the inclusion of data based on one annual visit to a lek. Our results validate the combination of leks counted under different monitoring protocols in previous and future modeling efforts aimed at understanding the trends and mechanisms of sage-grouse populations, provided sample sizes are large and inferences are made across large spatial extents.

MANAGEMENT IMPLICATIONS

Increased number of leks sampled decreased the confidence intervals on estimated population trends. For example, a population change of 25% could be detected with approximately 30 leks surveyed (Fig. 4B). Detection of an annual population change of 10% would require surveys of approximately 150 leks. Based on confidence interval widths using all active leks in Wyoming (approx. 1,600), we are confident that a state-wide annual population change of ±10% could be accurately measured with these models. However, interpretation of the width of bootstrapped confidence intervals must be made cautiously, as the confidence interval is constrained to zero at the base year. Therefore, the confidence interval reflects the variability in the base year and can be used to look at the influence of sample size, but other methods (e.g., pair-wise comparisons) should be used to determine the significance of changes between years. On a smaller scale, we recommend >1 count when individuals or organizations are interested in the trends at <50 leks. We suggest the GAM approach to describing trends does not require leks counted more than once, provided they are examining ≥50 leks.

Recognizing the cyclicity of populations can inform mechanistic studies of populations and better inform expectations and caution regarding the success of any particular population remediation or recovery efforts. For example, the interpretation of the effectiveness of a management decision or mitigation could be misleading if populations are on a down or upward component of their cycle. We see utility in using annual change points identified in our models as a future monitoring tool to help identify significant changes in the rate of either increase or decrease, which might invoke management actions from agencies responsible for managing sage-grouse populations and their habitats.

Our results indicate that single counts on a larger sample of leks are preferable to multiple counts on a smaller sample of leks. For agencies with limited person power, there is a direct trade-off between number of counts per lek and number of leks counted. We suggest it is better to count a larger sample of leks once than a smaller sample of leks 3 times, given inferences are needed for entire populations or geographic areas (e.g., sage-grouse management zones). Repeated sampling at leks is not necessary to calculate long-term trends, provided the leks are counted during the peak of lek activity and the scale of inference is ≥50 lek sites.

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