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Research Article

Effects of Lek Count Protocols on Greater Sage-Grouse Population Trend Estimates

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ABSTRACT Annual counts of males displaying at lek sites are an important tool for monitoring greater sage-grouse populations (*Centrocercus urophasianus*), but seasonal and diurnal variation in lek attendance may increase variance and bias of trend analyses. Recommendations for protocols to reduce observation error have called for restricting lek counts to within 30 minutes of sunrise, but this may limit the number of lek counts available for analysis, particularly from years before monitoring was widely standardized. Reducing the temporal window for conducting lek counts also may constrain the ability of agencies to monitor leks efficiently. We used lek count data collected across Wyoming during 1995–2014 to investigate the effect of lek counts conducted between 30 minutes before and 30, 60, or 90 minutes after sunrise on population trend estimates. We also evaluated trends across scales relevant to management, including statewide, within Working Group Areas and Core Areas, and for individual leks. To further evaluate accuracy and precision of trend estimates from lek count protocols, we used simulations based on a lek attendance model and compared simulated and estimated values of annual rate of change in population size (λ) from scenarios of varying numbers of leks, lek count timing, and count frequency (counts/lek/year). We found that restricting analyses to counts conducted within 30 minutes of sunrise generally did not improve precision of population trend estimates, although differences among timings increased as the number of leks and count frequency decreased. Lek attendance declined >30 minutes after sunrise, but simulations indicated that including lek counts conducted up to 90 minutes after sunrise can increase the number of leks monitored compared to trend estimates based on counts conducted within 30 minutes of sunrise. This increase in leks monitored resulted in greater precision of estimates without reducing accuracy. Increasing count frequency also improved precision. These results suggest that the current distribution of count timings available in lek count databases such as that of Wyoming (conducted up to 90 minutes after sunrise) can be used to estimate sage-grouse population trends without reducing precision or accuracy relative to trends from counts conducted within 30 minutes of sunrise. However, only 10% of all Wyoming counts in our sample (1995–2014) were conducted 61–90 minutes after sunrise, and further increasing this percentage may still bias trend estimates because of declining lek attendance. Published 2016. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Centrocercus urophasianus*, greater sage-grouse, lek attendance, monitoring, observation error, population trends, sampling theory, Wyoming.

Long-term population monitoring is an important tool for natural resource management and research (Nichols et al. 1995, Hutto and Young 2002, Field et al. 2007). Monitoring has been used successfully to examine invasive species spread (Blossey 1999, Bled et al. 2011), response to land-use change and management (Chamberlain et al. 2000, Riffell et al. 2008), and other basic and applied questions (Nichols 1991). Monitoring also is valuable for identifying population declines (Stuart et al. 2004, Brennan and Kuvlesky 2005) and predicting extinction thresholds (Hefley et al. 2013).

One species that has garnered increasing attention due to population declines is the greater sage-grouse (*Centrocercus urophasianus*, hereafter, sage-grouse; Connelly and Braun 1997, Connelly et al. 2004, Garton et al. 2011). The range of sage-grouse has been reduced by nearly half from its historical extent (Schroeder et al. 2004) and this species was recently considered for listing under the United States Endangered Species Act (U.S. Fish and Wildlife Service 2015). During the breeding season male sage-grouse gather

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at display grounds known as leks, and counting of males at lek sites is the primary method for monitoring sage-grouse populations (Connelly et al. 2003). The importance of lek counts is illustrated in Wyoming, where burgeoning oil and gas development and concern for conflicts with sage-grouse populations prompted a 9-fold increase in number of leks monitored since the 1960s (Sage- and Columbian Sharp-tailed Grouse Technical Committee 2008).

Despite the common use of lek counts for monitoring sage-grouse, the relationship between indices such as lek counts and true population dynamics has long been questioned because of imperfect detection (Anderson 2001, Pollock et al. 2002). A major component of observation error for sage-grouse lek counts is male lek attendance, which may vary diurnally and seasonally (Emmons and Braun 1984, Walsh et al. 2004, Blomberg et al. 2013). Nevertheless, indices derived from lek counts may still be useful for estimating population trends (Applegate 2000, Engeman 2003, Johnson and Rowland 2007), particularly with greater temporal (Blomberg et al. 2013) and spatial (Fedy and Aldridge 2011) replication. One approach to reduce observation error from indices is by standardizing count protocol (Johnson and Rowland 2007, Etterson et al. 2009). Although there is a general consensus regarding the seasonal period for when peak male attendance can be adequately characterized, between early-April and mid-May (Connelly et al. 2003), there is less agreement regarding the diurnal timing of lek counts. Earlier guidelines discouraged conducting counts >30 minutes after sunrise (Patterson 1952, Rogers 1964) and these early guidelines are supported by subsequent studies of lek attendance and detectability (Walsh et al. 2004, Fremgen et al. 2016). However, current monitoring guidelines recommend conducting counts until 60 minutes after sunrise (Connelly et al. 2003, Christiansen 2012), whereas 1 study suggested that counts up to 90 minutes after sunrise may adequately characterize male abundance at leks (Jenni and Hartzler 1978). Although restricting counts to within 30 minutes of sunrise could increase precision and reduce bias of lek counts (Walsh et al. 2004, Fremgen et al. 2016), lek count datasets may contain a substantial number of counts conducted >30 minutes after sunrise, particularly from years before lek counts were uniformly standardized (Wyoming Game and Fish Department [WGFD] 2003). Restricting counts to within 30 minutes of sunrise could limit opportunities for retrospective analyses for this species and constrain the ability of observers to monitor multiple leks within a morning.

To evaluate the effect of lek count timing on population trend estimates, we compared estimates derived from counts conducted within 30 minutes of sunrise to those conducted between 30 minutes before and 60 or 90 minutes after sunrise. We used lek counts from Wyoming to calculate the finite rate of population change (λ) for each count timing during 5-year intervals (1995–2014) and at scales relevant to management decisions, including statewide, within Working Group Areas (WGFD 2003), Wyoming Core Population Areas (hereafter, Core Area; State of Wyoming 2015), and for individual leks (Fig. 1). Observation error may be influenced by the number of lek sites and the frequency of lek counts per year (Carlson and Schmiegelow 2002, Field et al. 2005, Fedy and Aldridge 2011), so we compared estimates and precision of λ among count timings and in relation to the number of leks and count frequency. We used simulations to further evaluate the effect of lek count timing on λ, comparing simulated and estimated trends from scenarios with varying numbers of leks, and from single counts or peak-samples from 3 counts/lek. Although a previous study assessed population trends from single counts and peak-samples (Fedy and Aldridge 2011), in this study we consider interactive effects of count timing and count frequency on trend estimates. We predicted a decrease in precision and an increase in bias when including timings >30 minutes after sunrise compared to analyses restricted to counts within 30 minutes of sunrise, whereas analyses from a greater

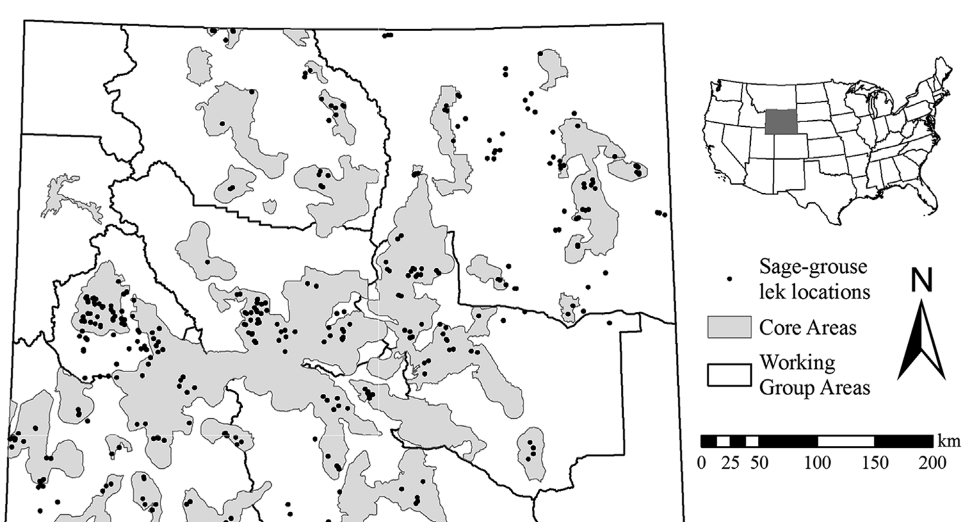

Figure 1. Distribution of greater sage-grouse lek sites (1995–2014, $n = 348$) used in analyses, Core Areas ($n = 33$), and Working Group Areas ($n = 10$) across Wyoming, USA, 1995–2014.

number of leks, and repeated counts at leks within a season, should increase precision and decrease bias of trend estimates.

STUDY AREA

Sage-grouse occur across nearly 70% of Wyoming in habitat dominated by sagebrush (*Artemisia* spp.; Fedy et al. 2014). Climate in Wyoming is typically semiarid, with mean maximum temperatures in July between 29°C and 35°C and mean minimum temperatures in January between −15°C and −12°C (National Oceanic and Atmospheric Administration [NOAA] 1985). The majority of precipitation generally occurs during late-spring or early-summer, although temperature and precipitation vary with topography and elevation (NOAA 1985). We used data from 348 leks (Fig. 1) with counts during all 5 years of ≥1 time interval and count timing. All leks were located within 1 of 7 Working Group Areas where local working groups are tasked with implementing Wyoming's Greater Sage-grouse Conservation Plan (WGFD 2003; Fig. 1). Of these leks, 268 also occurred in 27 Core Areas established by the state to limit disturbance to sage-grouse (State of Wyoming 2015). Elevation at lek sites ranged from 1,111 m to 2,424 m. Site-level descriptions of vegetation, climate, and local land use at or near leks used in this study are reported in previous publications (Holloran et al. 2005, Doherty et al. 2008, Dzialak et al. 2011, Hess and Beck 2012, Kirol et al. 2012).

METHODS

As part of a statewide monitoring effort of sage-grouse populations, the WGFD and partnering agencies collected lek count data from across Wyoming using procedures approved by WGFD (Christiansen 2012). New leks were identified from systematic searches by aircraft or ground searches during spring (Christiansen 2012), and the number of leks monitored has steadily increased since the middle of the 20th century (WGFD 2003). We used lek count data to characterize an index of peak male abundance for each lek and year. We do not account for observation error in this analysis, and therefore we modeled change in the observed count of displaying males. We assumed that detectability of males during lek counts was high, although detectability may vary by factors such as sagebrush height and snow cover (Fremgen et al. 2016). To reduce observation error, trained participants conducted lek counts by following a statewide protocol (Christiansen 2012), which included restricting counts to times of peak male attendance (typically early to late Apr in Wyoming), from 30 minutes before through 60 minutes after sunrise, and to days without precipitation or winds ≥16 km/hour. Observers also conduct lek counts at least 3 times within a breeding season. We included counts conducted from mid-March to mid-May to increase the probability of capturing peak counts of each lek because peak male lek attendance may vary because of weather and elevation (Connelly et al. 2003). We characterized counts by diurnal timing, including counts conducted within 30 minutes of sunrise (hereafter, 30-minute timing), between 30 minutes before and 60 minutes after sunrise (60-minute timing), and between 30 minutes before and 90 minutes after sunrise (90-minute timing). Thus, 60-minute timings may contain counts from 30-minute timings, and 90-minute timings may contain counts from 30- and 60-minute timings. For each count timing, we averaged peak male counts across leks each year yielding 1 average lek count per year (Garton et al. 2011). We averaged lek counts across Wyoming for an annual statewide estimate, and within Working Group Areas and Core Areas. For individual leks, we characterized population size with the peak count recorded each year.

Statistical Analyses

We estimated λ by regressing the natural logarithm (log) of change in observed population count between years $\left(\log\left(\frac{y_{t+1}}{y_t}\right)\right)$ against time and derived the sample variance of the log-rate of population change (σ^2) from the regression mean square error (Dennis et al. 1991, Morris and Doak 2002). This type of model has received broad support (Morris et al. 1999, Morris and Doak 2002) and has been widely used to perform population viability analyses (PVA) for a variety of species (Nicholls et al. 1996, Gerber et al. 1999, Schultz and Hammond 2003). We included counts of 0 and we added 0.5 to all lek count averages (or peak counts when analyzing individual leks) to accommodate counts of 0 (Geissler and Noon 1981, Collins 1990). We transformed the change in population size and time elapsed to meet the assumption of equal variances in linear regression (Dennis et al. 1991, Morris and Doak 2002). We calculated the finite rate of population change from the exponent of the model's slope ($\lambda = e^{\mu}$). We performed analyses in R (Version 3.2.1, www.r-project.org, accessed 31 Aug 2015) using the popbio package (Version 2.4, https://cran.r-project.org/web/packages/popbio/index.html, accessed 31 Aug 2015). For the purpose of our comparisons of count timings, we did not consider density-dependent models. We calculated λ and σ^2 for each count timing and compared precision within 5-year intervals for statewide estimates, within Working Group Areas and Core Areas, and for individual leks in Wyoming. We also compared the number of leks and count frequency (counts/lek/yr) used in each analysis. Given the number of Working Group Areas, Core Areas, and individual leks, to facilitate comparisons we calculated correlations (Pearson's *r*) in λ or σ^2 between 60- or 90-minute timings and 30-minute timings. We restricted these comparisons to groups (or individual leks) with counts from 30-minute timings and 60- or 90-minute timings. We also calculated the difference between estimates from 60- or 90-minute timings and estimates from 30-minute timings, and evaluated these against the number of leks or count frequency from 60- or 90-minute timings, respectively. A positive difference would indicate a greater estimated population trend (or variance) from 60- or 90-minute timings than 30-minute timings, whereas a difference near 0 suggests no difference between timings.

To further investigate relationships between count timings and population trend estimates, we simulated datasets for a hypothetical 5-year sampling period and compared true (simulated) and estimated λ. For each simulated lek we randomly assigned an initial population size based on the observed distribution of peak lek counts across Wyoming in 2010 where $\geq$1 male was detected ($\bar{x} = 26.9$ M, SD = 25.5). We generated this initial population size at each lek i at year $t = 1$ from a negative binomial distribution:

$$N_{i,1} \sim \text{NB}(k, p)$$

with parameters for size ($k = 1.33$) and probability ($p = 0.05$). We restricted initial population sizes to between 1 and 75 to ensure all leks were initially active while avoiding subsequent population growth to sizes substantially larger than that observed among leks in our attendance model (see below). We then simulated population size in subsequent years based on simulated values of population growth λ_{sim}. For $t = 2-5$,

$$N_{i,t+1} = N_{i,t}e^{r}$$

with $r = \log(\lambda_{\text{sim}}) + \varepsilon_{i,t}$ and process error $\varepsilon_{i,t} \sim$ Normal $(0, 0.07)$. To parameterize the process error term, we used the residual standard error from regressing the log-change in statewide population sizes (2010–2014) with 90-minute timings.

From the generated population sizes, we simulated an encounter history of lek counts based on seasonal and diurnal variation in male lek attendance. We parameterized this observation process by modeling repeated lek counts from the Wyoming dataset, using only leks that were counted $\geq$30 times within years, and between 1 hour before and 3 hours after sunrise. These included lek counts conducted in Fremont County, Wyoming, as part of studies on the effects of anthropogenic noise on lek attendance (Blickley et al. 2012) and other behavioral research (Krakauer et al. 2009, Patricelli and Krakauer 2009). We retained counts from leks in certain years that were treated with anthropogenic noise during the entire breeding period because these were representative of conditions for other leks in the state (Blickley et al. 2012), but we excluded 2 leks from 2009 that received intermittent noise treatments. Other leks received occasional playback of sage-grouse sounds or the presentation of a robotic female sage-grouse, but we retained these leks because such manipulations occurred later in the morning after peak lek counts were recorded (A. H. Krakauer, University of California, Davis, personal communication). Our sample therefore included 1,177 counts from 12 leks (2006–2014, excepting 2009 and 2010), with a maximum of 82 counts/lek/year. Several leks had counts from multiple years, and 4 leks had repeated counts within a day. Mean count date occurred 4 April (range = 2 Mar–9 May), and mean count time was 19 minutes after sunrise (range = 58 min before to 164 min after sunrise). Peak counts ranged from 10 to 184 males (median = 62 M).

Assuming the maximum observed number of males was the potential peak count for each lek i and year t ($N_{i,t}$), we fit the observed number of males from count k ($y_{i,t,k}$) using a generalized linear mixed model with a binomial link function. We specified covariates including linear, quadratic, and cubic effects of ordinal date and time (minutes after sunrise), and a covariate for maximum observed count to account for differences in attendance due to lek size. We standardized each continuous covariate by subtracting the mean and dividing by the standard deviation. We also included a covariate for anthropogenic noise treatment, as well as random error terms for lek (ε_i) and year (ω_t):

$$\begin{aligned}\text{logit}\left(p_{i,t,k}\right) = \beta_1 + \beta_2\text{date}_{i,t,k} + \beta_3\text{date}^2_{i,t,k} + \beta_4\text{date}^3_{i,t,k} + \beta_5\text{time}_{i,t,k} \\ + \beta_6\text{time}^2_{i,t,k} + \beta_7\text{time}^3_{i,t,k} + \beta_8\text{size}_{i,t} + \beta_9\text{noise}_{i,t} + \varepsilon_i + \omega_t\end{aligned}$$

$$y_{i,t,k} \sim \text{Binomial}\left(N_{i,t}, p_{i,t,k}\right).$$

We fit this model with the lme4 package (Version 1.1–9, https://cran.r-project.org/web/packages/lme4/index.html, 17 Nov 2015) in R, and we examined plots of the residuals against fitted values from the model for evidence of lack of fit. A likelihood ratio test indicated that the model was supported over a null (without covariates) mixed model ($\chi^2_8 = 5{,}622.8$, $P < 0.001$). We used parameter estimates from this model (excepting effect from noise treatment) to simulate the number of individuals from the true population size of lek i in year t present during count k ($y_{i,t,k}$) given date d and time since sunrise m:

$$\text{logit}\left(p_{i,t,k}\right) \sim \text{Normal}\left(\mu_{d,m}, \sigma_{d,m}\right)$$

$$y_{i,t,k} \sim \text{Binomial}\left(N_{i,t}, p_{i,t,k}\right)$$

where $\mu_{d,m}$ and $\sigma_{d,m}$ are the mean and standard deviation of male lek attendance probability (on the logit scale) predicted from the lek attendance model, accounting for uncertainty from fixed effects only.

We determined that count times from recent (2010–2014) Wyoming lek counts were characterized well by a negative binomial distribution (adjusting the minimum time, 60 min before sunrise, to 0), so we randomly assigned count times from this distribution ($k = 5.97$ and $p = 0.07$). Although lek count protocol for Wyoming recommends $\geq$3 repeated counts at leks each year (Christiansen 2012), a previous study suggested estimates from 1 count/year may be sufficient for estimating trends with >50 leks (Fedy and Aldridge 2011), so we ran simulations for scenarios with 1 or 3 lek counts annually. Lek count protocol requires counts to be conducted every 7–10 days, so we randomly assigned 1 count date from a normal distribution with a mean at the date of peak male attendance predicted from the lek attendance model. Because the true date of peak attendance is not likely to be known by observers and may fluctuate among sites and years, we allowed this initial count date to vary from a normal distribution (SD = 3.5 days) so that nearly 95% of count dates fell within 1 week of the true date of peak attendance. For peak-sample scenarios, we simulated 2 additional count dates 7–10 days before and after the initial count date.

For each lek and year, we drew 1 or 3 simulated counts of males ($y_{i,t,k}$), and for scenarios with >1 lek we averaged either the single count or the maximum of 3 counts (peak-sample) across all leks each year to characterize the overall population size. We then used these population indices to estimate λ and σ^2. For all analyses, we only included leks with counts for all 5 years. We simulated 1,000 iterations for all count timings (up to 90 min after sunrise) and for each timing separately with varying simulated λ (0.80 through 1.20, in increments of 0.05), lek number (1, 10, 25, 50, and 100 leks), and single counts or peak-samples. We also calculated the root mean square error (RMSE) for each scenario as a measure of accuracy (difference between simulated and estimated λ) and precision. Finally, we determined the proportion of iterations where confidence intervals of λ from each scenario did not contain 1.00, or the frequency when a change in population size was detected ($\lambda \neq 1.00$). This is analogous to a 2-tailed power analysis where β is the probability of not rejecting a false null hypothesis, and power is $1 - \beta$. We decided a priori that $\beta = 0.05$ was acceptable, indicating a 95% probability of detecting a change in population size, given a true change (Gerrodette 1987). R code and data for running these simulations can be obtained from the corresponding author.

RESULTS

Trend Estimates

Across all leks (1995–2014), the statewide dataset contained 29,635 lek counts suitable for analysis (i.e., between 30 min before and 90 min after sunrise, counts without strong winds or precipitation). These included 65.4% of counts conducted within 30 minutes of sunrise, 24.4% of counts conducted 31–60 minutes after sunrise, and 10.2% of counts conducted 61–90 minutes after sunrise. Mean estimates of λ were similar among timings within each 5-year interval (Fig. 2A), whereas precision tended to increase from 1995–1999 to 2010–2014. This trend in precision likely reflected the increase in number of leks over time, whereas precision and mean trend estimates differed little among timings during 2000–2014, when number of leks was >50 (Fig. 2B). Number of leks included in population trend analysis increased 28–43% when using 60-minute over 30-minute timings; use of 90-minute timings increased the number of leks slightly more (0–9% more leks compared to 60-minute timings). Count frequency during each interval also increased from 30-minute to 90-minute timings but changed little over time (Fig. 2C). Count frequency increased 12–22% from 30-minute to 60-minute timings, and increased 6–13% from 60-minute to 90-minute timings.

Number of Working Group Areas with sufficient counts to estimate trends (i.e., suitable counts during all 5 years of a given interval) was the same among count timings, increasing over time and totaling 21 samples of Working Group Areas across all 5-year intervals (Table 1). Twenty and 21 samples had additional counts for 60-minute and 90-minute timings, respectively. Among Working Group Areas with 60- and 90-minute timings, estimates of λ tended to be highly correlated with estimates from 30-minute timings ($r = 0.93$ and 0.98 for λ_{60} and λ_{90}, respectively; Fig. 3). Estimates of σ^2 also were similar to those from 30-minute timings ($r = 0.92$ and 0.91 for σ^2_{60} and σ^2_{90}, respectively; Fig. 3), with a mean σ^2

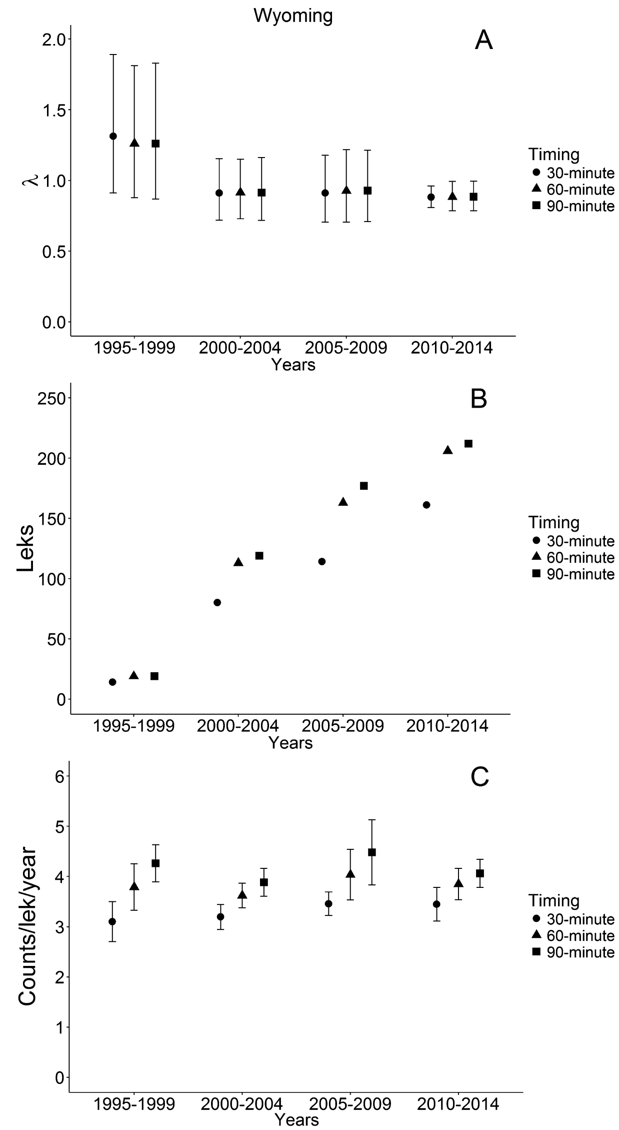

Figure 2. Mean estimates (and 95% CI) of finite rate of population change (λ; A), number of leks monitored each year (B), and mean count frequency ($\pm$1 SD; C) by timing of lek count (within 30 min of sunrise, and between 30 min before and 60 min after sunrise or 90 min after sunrise) for 5-year periods of greater sage-grouse lek counts across Wyoming, USA, 1995–2014.

of 0.04 (SD = 0.03) for 60- and 90-minute timings and a maximum σ^2 of 0.15 for 60-minute timing. Differences in λ between 60- or 90-minute timings and 30-minute timings were similar ($\bar{x} = 0.01$, SD = 0.03 for each) and narrowly distributed around 0 (Fig. S1, available online in Supporting Information). Differences in σ^2 also were similar for 60- and 90-minute timings ($\bar{x} = 0$, SD = 0.01; Fig. S2). Differences in λ and σ^2 between 60- or 90-minute timings and 30-minute timings remained relatively constant despite changes in number of leks or count frequency (Figs. S1 and 2). Mean number of leks/Working Group Area was 24.1 (SD = 11.15) for 60-minute timings and 25.1 (SD = 11.45) for 90-minute timings (range = 5–59 leks). Mean count frequency increased 8% from 30-minute timings to 3.66 counts/lek/year (SD = 0.92) for 60-minute timings and 20% to 4.07 counts/lek/year (SD = 1.12) for 90-minute timings.

Table 1. Number of Working Group Areas, Core Areas, and individual leks with sufficient counts to estimate population trends by 5-year interval and lek count timing in Wyoming, USA. Samples were restricted to leks with counts from all 5 years of a given interval, and count timings represented counts conducted within 30 minutes of sunrise (30-min), and between 30 minutes before and 60 minutes after sunrise (60-min) or 90 minutes after sunrise (90-min).

	Working Group Area			Core Area			Individual lek		
Years	30-min	60-min	90-min	30-min	60-min	90-min	30-min	60-min	90-min
1995–1999	1	1	1	1	1	1	14	19	19
2000–2004	6	6	6	12	14	14	80	113	119
2005–2009	7	7	7	18	20	20	114	163	177
2010–2014	7	7	7	17	20	20	161	206	212

Number of Core Areas with sufficient counts to estimate trends increased over time, totaling 48 samples of Core Areas for 30-minute timings and 55 samples for 60- and 90-minute timings (Table 1). There were additional counts from 60- and 90-minute timings for 44 and 38 Core Area samples, respectively. Estimates of λ were somewhat less correlated with estimates from 30-minute timings than for Working Group Areas ($r = 0.86$ and 0.87 for λ_{60} and λ_{90}, respectively; Fig. 3). Correlations also were lower among σ^2 estimates ($r = 0.88$ and 0.55 for σ^2_{60} and σ^2_{90}, respectively; Fig. 3), and

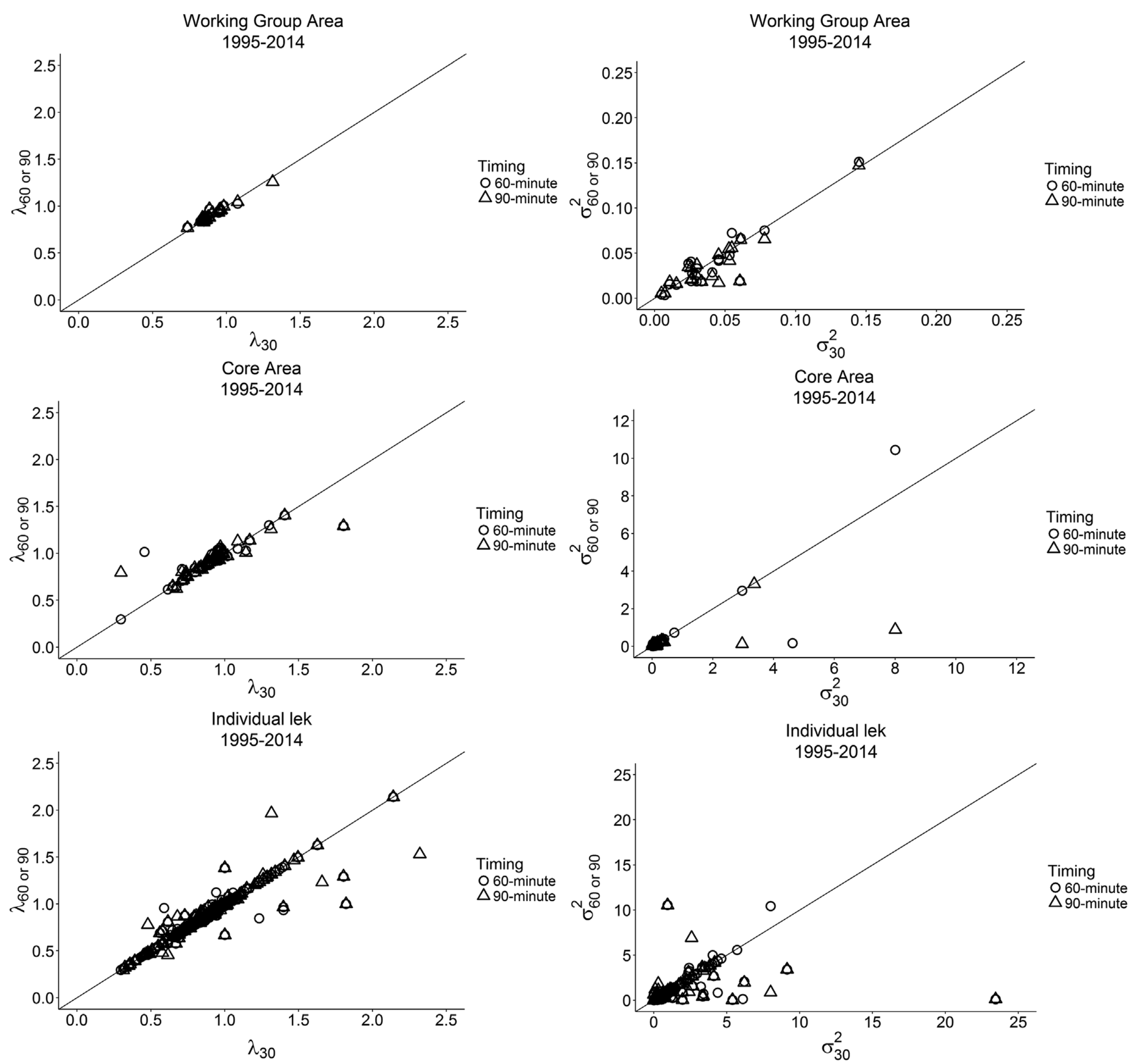

Figure 3. Mean estimates of rate of population change (λ) and variance in the log-rate of change (σ^2) for greater sage-grouse lek counts from 3 scales in Wyoming, USA, during 5-year intervals (1995–2014). We plotted estimates from 30-minute timings (within 30 min of sunrise) against estimates from 60- or 90-minute timings (between 30 min before and 60 min or 90 min after sunrise, respectively), and we restricted inferences to lek groupings (or individual leks) where 60- or 90-minute timings increased the number of counts used for analysis over 30-minute timings. Diagonal solid lines represent 1:1 relationships.

estimates tended to be less precise than for Working Group Areas ($\bar{x} = 0.31$, SD = 1.23 for σ^2_{60} and σ^2_{90}). Differences in estimates were again around 0 for λ ($\bar{x} = 0.01$, SD = 0.12; Fig. S1) and σ^2 ($\bar{x} = -0.15$, SD = 1.01; Fig. S2). However, in contrast to Working Group Areas, the range of differences in λ and σ^2 among Core Areas varied with the number of leks and count frequency (Figs. S1 and 2). The range of differences in λ was greater among Core Areas with $\leq$5 leks (range = −0.51 to 0.56; $n = 53$) compared with >5 leks (range = −0.14 to 0.07; $n = 29$), and among Core Areas with <4 lek counts/year (range = −0.51 to 0.56; $n = 57$) than with $\geq$4 lek counts/year (range = −0.14 to 0.10; $n = 25$). The range of differences in σ^2 was greater among Core Areas with $\leq$5 leks (range = −7.12 to 2.44; $n = 53$) compared with >5 leks (range = −0.11 to 0.02; $n = 29$), and among Core Areas with <4 lek counts/year (range = −7.12 to 2.44; $n = 57$) than with $\geq$4 lek counts/year (range = −0.11 to 0.12; $n = 25$). Number of leks/Core Area were relatively fewer than among Working Group Areas for 60-minute timings ($\bar{x} = 8.41$, SD = 12.21) and 90-minute timings ($\bar{x} = 10.26$, SD = 13.17), and ranged from 1 to 57 leks. Count frequencies were similar to Working Group Areas, averaging 3.61 (SD = 0.88) for 60-minute timings and 4.26 (SD = 2.67) for 90-minute timings.

Number of individual leks with sufficient counts to estimate trends increased over time, with 369, 501, and 527 samples of leks from 30-minute, 60-minute, and 90-minute timings, respectively, over all 5-year intervals (Table 1). There were additional counts for 281 and 181 lek samples from 60- and 90-minute timings, respectively. Estimates of λ tended to be correlated with estimates from 30-minute timings ($r = 0.94$ and 0.90 for λ_{60} and λ_{90}, respectively; Fig. 3). Correlations were lower for estimates of σ^2 ($r = 0.48$ and 0.30 for σ^2_{60} and σ^2_{90}, respectively; Fig. 3), and estimates tended to be less precise than estimates from Working Group or Core Areas ($\bar{x} = 0.60$, SD = 1.23 for σ^2_{60} and σ^2_{90}). Differences in λ ($\bar{x} = -0.01$, SD = 0.11; Fig. S1) and σ^2 ($\bar{x} = -0.19$, SD = 1.87; Fig. S2) were both on average around 0. However, similar to Core Areas, the range of differences in λ and σ^2 among leks varied with count frequency. The range of differences in λ was greater among leks with <7 lek counts/year (range = −0.82 to 0.65; $n = 420$) than with $\geq$7 lek counts/year (range = −0.05 to 0.07; $n = 42$). The range of differences in σ^2 was greater among leks with <7 lek counts/year (range = −23.32 to 9.61; $n = 420$) than with $\geq$7 lek counts/year (range = −0.31 to 0.08; $n = 42$). Count frequency averaged 4.34 counts/year (SD = 3.61) for 60-minute timings and 5.28 counts/year (SD = 4.72) for 90-minute timings.

Simulation Study

From our lek attendance model, we estimated a positive effect of lek size on attendance probability ($\beta = 0.28$, SE = 0.09). For small ($n = 15$ M) and large ($n = 150$ M) leks, lek attendance probability suggested a stronger response to seasonal than diurnal variation in lek count timing, and predicted a peak male count around 15 April (Fig. 4). Counts within mornings increased slightly to a peak near sunrise, then declined thereafter. Attendance probability tended to be somewhat higher, and persist longer during mornings, for large leks than small leks (Fig. 4).

Results from simulations indicated that overall (using all lek counts conducted up to 90 min after sunrise) estimates of λ were sensitive to the number of leks used for trend estimates. Point estimates of λ and σ^2 were most variable for analyses from 1 lek and RMSE decreased as the number of leks increased (Fig. S3). Restricting to single counts resulted in greater RMSE and greater estimates of σ^2 for smaller sample sizes than with peak-samples with 3 counts/lek/year, whereas trends were more similar between single counts and peak-samples as the number of leks increased. Mean estimates were similar within scenarios irrespective of sample size or count frequency, suggesting that more frequent counts across a greater number of leks increases precision but not accuracy of population change estimates. In addition, there was adequate power ($1-\beta = 0.95$) with peak-samples to detect population change ($\lambda \neq 1.00$) with $\geq$25 leks when $\lambda \leq 0.90$ or $\lambda \geq 1.10$ (or a 10% annual decline or increase, respectively; Fig. 5). In comparison, single count estimates required $\geq$50 leks and an equivalent rate of change to detect population change.

For timing-specific comparisons from single counts, point estimates of λ and σ^2 were most variable (Figs. S4 and 5) and RMSE was greatest (Fig. S6) for counts collected within 30 minutes of sunrise. This pattern may be attributed to lower observed number of leks used in analyses (Fig. S7). Number of leks was greatest, and RMSE smallest, for 90-minute counts, although RMSE for 60-minute timings was only slightly greater. There was a slight tendency to overestimate population growth when $\lambda > 1.00$ for single counts (Fig. S4), but mean estimates of λ were similar among timings. A lack of counts from leks across all 5 years prevented estimating trends for simulated scenarios from 30- and 60-minute timings and up to 50 potential leks. Estimates from peak-samples tended to be less variable (Figs. S8 and 9), and RMSE smaller (Fig. S10), than estimates from single counts. Overall, trends in precision and accuracy of λ from peak-samples were similar to estimates from single counts, and RMSE also generally decreased as the simulated and observed number of leks increased (Fig. S11).

Additionally, adequate power to detect a change in population size with single counts was only possible with $\geq$50 leks, 90-minute timings, and $\geq$10% annual decline ($\lambda \leq 0.90$) or increase ($\lambda \geq 1.10$, Fig. S12). With peak-samples, detecting population change from similar population trends was likely for 60-minute timings and $\geq$25 leks (Fig. S13). Counts restricted to within 30 minutes of sunrise yielded lower power to detect population change, with only adequate power from $\geq$50 leks, peak-samples, and $\geq$10% annual population changes.

DISCUSSION

Seasonal and diurnal variabilities in lek attendance by male sage-grouse are well documented (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004, Fremgen et al.

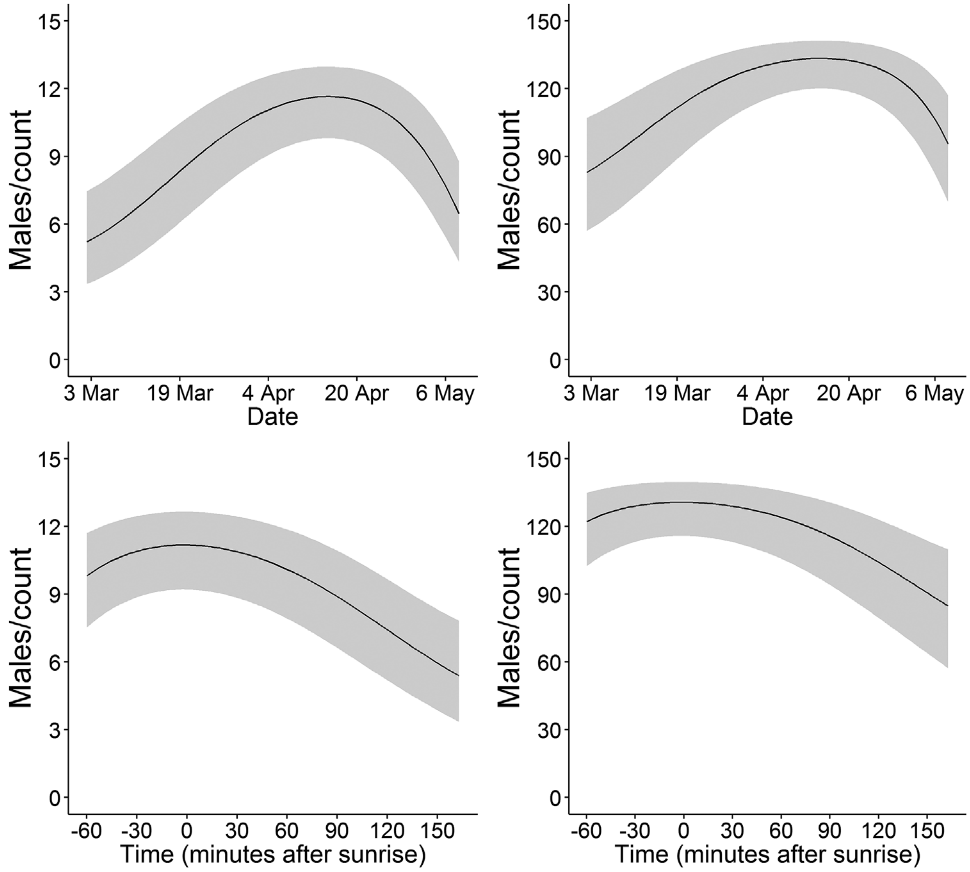

Figure 4. Predicted counts based on estimates from our model of greater sage-grouse lek attendance with linear, quadratic, and cubic effects of date and time, and an effect of lek size (peak number of males observed in a season). We plotted predictions for a small ($n = 15$ M; left) and a large ($n = 150$ M; right) lek. Prediction plots for date are based on a mean count time of 19 minutes after sunrise, whereas plots for time are based on mean count date of 4 April. Confidence intervals (95%, shaded in gray) were based on uncertainty from fixed effects only.

2016), casting doubt on the use of lek counts as a relevant population index. The narrowest threshold proposed for count timing is within 30 minutes of sunrise (Patterson 1952, Rogers 1964, Walsh et al. 2004, Fremgen et al. 2016), and we investigated the effect of using lek counts conducted up to 60 minutes and 90 minutes after sunrise on population trend estimates in Wyoming. Based on our results, we estimate that restricting analyses to counts collected within 30 minutes of sunrise is not likely to reduce bias or increase precision of trend estimates compared to other lek count timings considered here. When differences occurred between timings, there was no consistent tendency for over- or underestimating population trends or variance. Furthermore, this restrictive protocol reduced the number of leks used for analyses, and this may reduce precision of trend estimates and restrict inferences. Our lek attendance model confirmed that attendance was highest within 30 minutes of sunrise, as previously reported (Walsh et al. 2004, Fremgen et al. 2016), yet our simulations did not suggest that including counts conducted 31–90 minutes after sunrise resulted in biased estimates compared with 30-minute timings. On the contrary, use of 90-minute timings led to an increase in lek numbers in samples, which increased precision of trend estimates, despite potential bias from lower lek attendance later in the morning. Our results, therefore, indicate that increasing the number of leks sampled may be more effective for increasing precision of trend models than restricting counts to within 30 minutes of sunrise, even if some counts are conducted >30 minutes after sunrise.

Long-term monitoring is valuable for understanding how zspecies such as sage-grouse respond to a changing environment, and counts from previous decades may provide a comparison to recent or current conditions. Increasing the number of leks sampled within a year (and count frequency) should increase the precision of annual mean abundance estimates, which can then increase the power to detect population trends (Gerrodette 1987). The number of leks monitored each year in Wyoming increased steadily during the 20 years covered by this study, and at the largest scale (statewide) precision of trend estimates also increased over time. Use of 60-minute and 90-minute timings increased count frequency compared to 30-minute timings, but mean estimates and precision differed little among timings, suggesting that at the statewide scale, and with a large number of leks, the number of leks monitored had a greater effect on trend estimates than count frequency. This was supported by our simulation results, which indicated similar trend estimates and precision as the number of leks increased to 100, irrespective of count frequency or count timing.

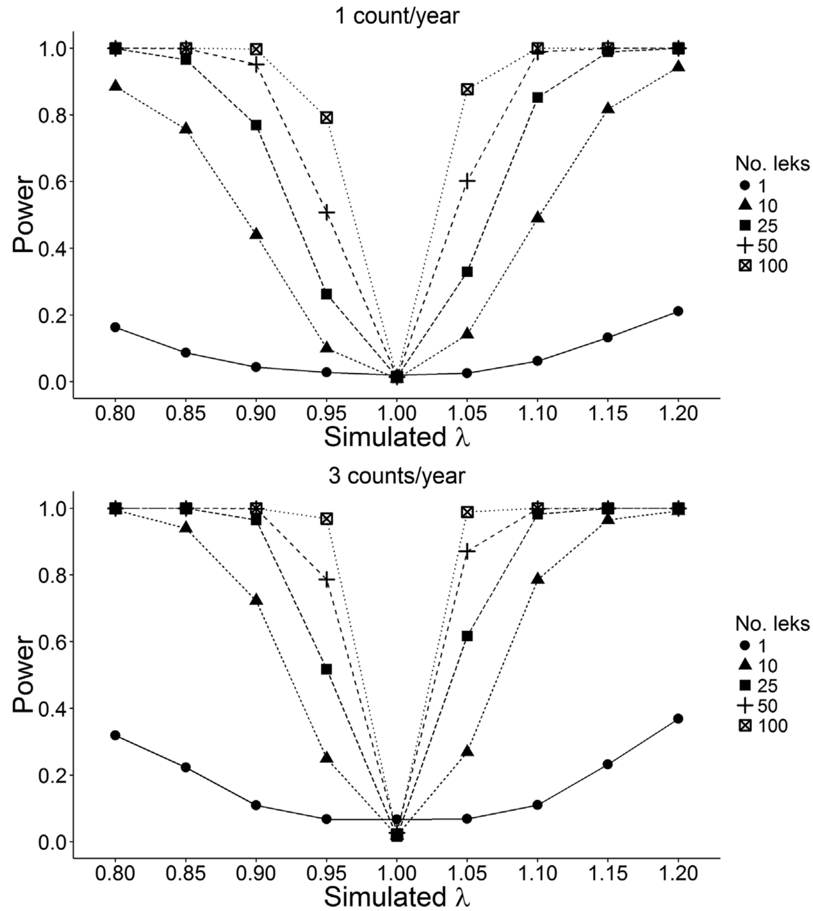

Figure 5. Power ($1-\beta$) to detect a true change in greater sage-grouse population size from 1,000 iterations of simulation scenarios for single counts at sage-grouse leks and peak-samples from 3 counts/year. Simulation parameters were informed by lek counts from Wyoming, USA, and included all counts between 30 minutes before and 90 minutes after sunrise, and varied with simulated rate of population change (λ) and number of leks in groupings.

As the number of leks in groupings decreased from Working Group Area to individual leks, correlation in variance estimates between count timings also decreased. Differences between estimates from 60- or 90-minute timings and 30-minute timings decreased as count frequency increased but only when lek groupings were small (e.g., for Core Areas or individual leks). However, differences between estimates were not consistently positive or negative, suggesting that use of counts >30 minutes after sunrise does not introduce a consistent bias. These results also were supported by our simulations, which indicated that, despite a decline in attendance >30 minutes after sunrise, greater sampling intensity from use of 60- and 90-minute timings (both in the number of leks monitored and repeated visits to those leks) can be effective at increasing precision of population trend estimates. Accuracy also remained similar within scenarios of simulated λ despite changes in timing, lek number, or count frequency.

Interestingly, our lek attendance model estimated a positive effect of lek size, predicting greater attendance diurnally and seasonally among large leks than small leks. A previous study did not find an effect of lek size on detectability (Fremgen et al. 2016), and although the extent of inferences from the 12 leks used in our attendance model is limited, the effect of lek size on availability for detection may deserve consideration when designing lek monitoring programs. For example, an underestimate of male population size among small leks could lead to an overestimate of population change as lek size increases. This may account for the slight bias in population trend estimates for scenarios when $\lambda > 1.00$ among single count simulations. Smaller leks may therefore necessitate a greater frequency of counts and within 30 minutes of sunrise to ensure counts are close to the true peak lek attendance. Fewer counts and counts up to 90 minutes after sunrise may be adequate to characterize population size of larger leks.

Our analyses of data from Wyoming indicated that use of 60- or 90-minute timings increased the number of leks and count frequency in samples, which also may increase precision of population trend estimates. In practice, observers in Wyoming may take advantage of 60-minute timings by visiting multiple leks within a morning, increasing efficiency and conserving resources (T. J. Christiansen, WGFD, personal communication). Restricting counts to within 30 minutes of sunrise could reduce the number of repeated visits to each lek, or the number of leks visited within a year, and thus reduce precision of population trend estimates. Greater monitoring efficiency also can ensure that counts are completed within a shorter seasonal period, when male lek attendance probability is greatest. However, it is important to note that only 10% of all Wyoming counts in our sample were conducted 61–90 minutes after sunrise, and their inclusion only modestly increased lek number and count frequency over 60-minute timings (Fig. 2). Our attendance model indicated a further decline in attendance probability >60 minutes after sunrise, so altering the current distribution of count timings by conducting a greater proportion of counts later in the morning may still bias population trend estimates.

Although a direct comparison between our study and that of Fedy and Aldridge (2011) is not possible because of differences in modeling approach and in number of years used to estimate trends, our simulations also indicated that single counts could yield similarly precise trend estimates as peak-samples when groupings of leks were sufficiently large (e.g., ≥50 leks). Fedy and Aldridge (2011) did not consider lek timing in their analyses, and in our simulations the similarity between single counts and peak-samples was most apparent when using 90-minute timings (Fig. S3). However, even when using 90-minute timings, power to detect trends with single counts was reduced compared to peak-samples. Precision was lower when we restricted analyses to 30-minute timings because fewer leks could be included in analyses than with 90-minute timings. Because of seasonal and diurnal variability in lek attendance, using 1 count/year instead of 3 to monitor a small number of leks (or individual leks) may reduce the probability that counts adequately represent the true peak in male abundance at each lek. We, therefore, do not recommend the use of single counts to monitor sage-grouse populations, unless this permits monitoring a greater number of leks (e.g., ≥50 leks) than would be possible using repeated visits (e.g., <25 leks; Fig. 5).

Our simulation approach was necessarily simplistic to facilitate comparisons among scenarios with varying lek count timings, lek number, and count frequency, and we did not consider other potential factors that may affect male lek attendance rates such as weather, observer error, phases of the moon, female attendance, or predator abundance. We also did not consider non-linear population trends or density dependence. Any of these factors could affect precision and accuracy of trend estimates and may require consideration when analyzing trends from indices. Furthermore, caution is warranted when extrapolating our simulation results to guide monitoring efforts because simulations to evaluate statistical power rely heavily on the assumptions and parameters from which they were generated (Seavy and Reynolds 2007). An important assumption of our simulation was that variability in lek count timing (seasonal and diurnal) originated randomly from probability distributions, and, therefore, any error associated with lek count timing also was random and often could be reduced with greater samples from their respective distributions. In field situations, errors in timing that are systematically skewed among leks could produce biased trend estimates. Small sample sizes from an otherwise random timing distribution also could result in a skewed sample. Additionally, we simulated annual change in abundance assuming a common mean and error term among leks, and therefore population change was similar within hypothetical lek groupings. However, in reality the delineation of lek groups may be more ambiguous. Spatial variation in lek trends may account for some of the increased variance in trend estimates for smaller groupings, and underscores the importance of carefully considering whether a priori groupings are appropriate before estimating population trends.

MANAGEMENT IMPLICATIONS

Despite greater precision from larger sample sizes as a result of extending the diurnal timing of lek counts, our results do not discount imperfect detection as an important limitation of using raw lek counts for trend analyses (Anderson 2001, Pollock et al. 2002). Nevertheless, recommendations for standardization and sample size requirements based on our results also may apply to analyses that attempt to account for imperfect detection (Field et al. 2007, Etterson et al. 2009, Hostetter et al. 2015). We maintain that variation in lek attendance, both seasonal and diurnal, is an important source of observation error, and protocols should aim to detect a consistent proportion of individuals each year (out of the true number of individuals attending a lek) for lek counts to be useful indices of population size for trend models. Careful adherence to count protocol, randomization of lek count timing (seasonal and diurnal) within periods that maximize the probability of detecting males attending leks, and increases in lek number and count frequency, should therefore be undertaken to decrease observation error in trend analyses. However, our results indicate that restricting counts to within 30 minutes of sunrise, in an attempt to reduce bias, may actually be counterproductive if this reduces the number of leks and count frequency in samples for analysis (for data already collected), or constrains the ability of observers to efficiently monitor leks. We also suggest that individuals and agencies that conduct monitoring should consider the scale at which they are interested in making inferences. At large scales, such as within Working Group Areas or statewide, more leks are available for monitoring and thus sampling a greater number of leks (e.g., ≥50) less frequently and up to 90 minutes after sunrise may be an appropriate strategy. At smaller scales such as Core Areas (e.g., 10–25 leks), repeated visits are likely necessary for obtaining useful estimates of population trends. Finally, those wishing to estimate absolute abundance or estimate trends for groupings of <10 leks may be better served using robust methods such as capture-mark-recapture (Walsh et al. 2004, Blomberg et al. 2013, Fremgen et al. 2016).

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LITERATURE CITED

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Applegate, R. D. 2000. Use and misuse of prairie chicken lek surveys. Wildlife Society Bulletin 28:457–459.

Blossey, B. 1999. Before, during and after: the need for long-term monitoring in invasive plans species management. Biological Invasions 1:301–311.

Bled, F., J. A. Royle, and E. Cam. 2011. Hierarchical modeling of an invasive spread: the Eurasian collared-dove *Streptopelia decaocto* in the United States. Ecological Applications 21:290–302.

Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology 26:461–471.

Blomberg, E. J., J. S. Sedinger, D. V. Nonne, and M. T. Atamian. 2013. Annual male lek attendance influences count-based population indices of greater sage-grouse. Journal of Wildlife Management 77:1583–1592.

Brennan, L. A. and W. P. Kuvlesky, Jr. 2005. North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Carlson, M., and F. Schmiegelow. 2002. Cost-effective sampling design applied to large-scale monitoring of Boreal birds. Conservation Ecology 6:11. http://www.consecol.org/vol6/iss2/art11. Accessed 22 Jul 2015.

Chamberlain, D. E., R. J. Fuller, R. G. H. Bunce, J. C. Duckworth, and M. Shrubb. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37:771–788.

Christiansen, T. 2012. Sage-grouse (*Centrocercus urophasianus*). Pages 12–1–12–55 *in* S. A. Tessman and J. R. Bohne, editors. Handbook of biological techniques, third edition. Wyoming Game and Fish Department, Cheyenne, USA.

Collins, B. T. 1990. Using rerandomizing tests in route-regression analysis of avian population trends. Pages 63–70 *in* J. R. Sauer and S. Droege, editors. Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish and Wildlife Service Biological Report 90(1), Laurel, Maryland, 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.

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, Wyoming, USA.

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

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61:115–143.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2008. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273. doi:10.1371/journal.pone.0026273

Emmons, S. R., and C. E. Braun. 1984. Lek attendance of male sage grouse. Journal of Wildlife Management 48:1023–1028.

Engeman, R. M. 2003. More on the need to get the basics right: population indices. Wildlife Society Bulletin 31:286–287.

Etterson, M. A., G. J. Niemi, and N. P. Danz. 2009. Estimating the effects of detection heterogeneity and oversdispersion on trends estimated from avian point counts. Ecological Applications 19:2049–2066.

Fedy, B. C., and C. L. Aldridge. 2011. The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. Journal of Wildlife Management 75:1022–1033.

Fedy, B. C., K. E. Doherty, C. L. Aldridge, M. O'Donnell, J. L. Beck, B. Bedrosian, D. Gummer, M. J. Holloran, G. D. Johnson, N. W. Kaczor, C. P. Kirol, C. A. Mandich, D. Marshall, G. McKee, C. Olson, A. C. Pratt, C. C. Swanson, and B. L. Walker. 2014. Habitat prioritization across large landscapes, multiple seasons, and novel areas: an example using greater sage-grouse in Wyoming. Wildlife Monographs 190:1–39.

Field, S. A., P. J. O'Connor, A. J. Tyre, and H. P. Possingham. 2007. Making monitoring meaningful. Austral Ecology 32:485–491.

Field, S. A., A. J. Tyre, and H. P. Possingham. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. Journal of Wildlife Management 69:473–482.

Fremgen, A. L., C. P. Hansen, M. A. Rumble, R. S. Gamo, and J. J. Millspaugh. 2016. Male greater sage-grouse detectability on leks. Journal of Wildlife Management 80:266–274.

Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and M. A. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293–381 *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 vol. 38, University of California Press, Berkeley, USA.

Geissler, P. H., and B. R. Noon. 1981. Estimates of avian population trends from the North American Breeding Bird Survey. Studies in Avian Biology 6:42–51.

Gerber, L. R., D. P. DeMaster, and P. M. Kareiva. 1999. Gray whales and the value of monitoring data in implementing the U.S. Endangered Species Act. Conservation Biology 13:1215–1219.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

Hefley, T. J., A. J. Tyre, and E. E. Blankenship. 2013. Statistical indicators and state-space population models predict extinction in a population of bobwhite quail. Theoretical Ecology 6:319–331.

Hess, J. E., and J. L. Beck. 2012. Disturbance factors influencing greater sage-grouse lek abandonment in north-central Wyoming. Journal of Wildlife Management 76:1625–1634.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Hostetter, N. J., B. Gardner, S. H. Schweitzer, R. Boettcher, A. L. Wilke, L. Addison, W. R. Swilling, K. H. Pollock, and T. R. Simons. 2015. Repeated count surveys help standardize multi-agency estimates of American oystercatcher (*Haematopus palliates*) abundance. Condor: Ornithological Applications 117:354–363.

Hutto, R. L., and J. S. Young. 2002. Regional landbird monitoring: perspectives from the Northern Rocky Mountains. Wildlife Society Bulletin 30:738–750.

Jenni, D. A., and J. E. Hartzler. 1978. Attendance at a sage grouse lek: implications for spring censuses. Journal of Wildlife Management 42:46–52.

Johnson, D. H., and M. M. Rowland. 2007. The utility of lek counts for monitoring greater sage-grouse. Pages 15–23 *in* K. P. Reese and R. T. Bowyer, editors. Monitoring populations of sage-grouse. Station Bulletin 88, College of Natural Resources Experiment Station, Moscow, Idaho, USA.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. Condor 114:75–89.

Krakauer, A. H., M. Tyrrell, K. Lehmann, N. Losin, F. Goller, and G. L. Patricelli. 2009. Vocal and anatomical evidence for two-voiced sound production in the greater sage-grouse *Centrocercus urophasianus*. Journal of Experimental Biology 212:3719–3727.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Morris, W., D. Doak, M. Groom, P. Kareiva, J. Fieberg, L. Gerber, P. Murphy, and D. Thomson. 1999. A practical handbook for population viability analysis. The Nature Conservancy, Arlington, Virginia, USA.

National Oceanic and Atmospheric Administration [NOAA]. 1985. Narrative summaries, tables and maps for each state with overview of state climatologist programs. Third edition. Gale Research Company. www.wrcc.dri.edu/climate-narratives/. Accessed 12 Feb 2016.

Nicholls, A. O., P. C. Viljoen, M. H. Knight, and A. S. van Jaarsveld. 1996. Evaluating population persistence of censused and unmanaged herbivore populations from the Kruger National Park, South Africa. Biological Conservation 76:57–67.

Nichols, J. D. 1991. Extensive monitoring programmes viewed as long-term population studies: the case of North American waterfowl. Ibis 133 Supplement 1:89–98.
Nichols, J. D., F. A. Johnson, and B. K. Williams. 1995. Managing North American waterfowl in the face of uncertainty. Annual Review of Ecology and Systematics 26:177–199.
Patricelli, G. L., and A. H. Krakauer. 2009. Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. Behavioral Ecology 21:97–106.
Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado, USA.
Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13:105–119.
Riffell, S., D. Scognamillo, and L. W. Burger. 2008. Effects of the Conservation Reserve Program on northern bobwhite and grassland birds. Environmental Monitoring and Assessment 146:309–323.
Rogers, G. E. 1964. Sage grouse investigations in Colorado. Technical Publication Number 16, Colorado Game, Fish and Parks Department, Denver, USA.
Sage- and Columbian Sharp-tailed Grouse Technical Committee. 2008. Greater sage-grouse population trends: an analysis of lek count databases 1965–2007. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Brauns, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, 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 106:363–376.
Schultz, C. B., and P. C. Hammond. 2003. Using population viability analysis to develop recovery criteria for endangered insects: case study of the Fender's blue butterfly. Conservation Biology 17:1372–1385.
Seavy, N. E., and M. H. Reynolds. 2007. Is statistical power to detect trends a good assessment of population monitoring? Biological Conservation 140:187–191.
State of Wyoming. 2015. Greater sage-grouse core area protection. Office of the Governor, Executive Order 2015-4, Cheyenne, Wyoming, USA.
Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.
U.S. Fish and Wildlife Service. 2015. Endangered and threatened wildlife and plants; 12-month finding on a petition to list Greater sage-grouse (*Centrocercus urophasianus*) as an endangered or threatened species. Federal Register 80:59858-59942.
Walsh, D. P., G. C. 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.
Wyoming Game and Fish Department [WGFD]. 2003. Wyoming Greater Sage-Grouse Conservation Plan. Wyoming Game and Fish Department, Cheyenne, USA.

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