



## Research Article

# Improved Analysis of Lek Count Data Using $N$ -Mixture Models

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**ABSTRACT** The greater sage-grouse (*Centrocercus urophasianus*) is a species of conservation concern in western North America that is experiencing ongoing population declines due to habitat loss, energy development, disease, and other factors. It is therefore imperative to have robust estimates of population size and trends in this species across its range as part of monitoring, management, and conservation efforts. Greater sage-grouse are typically monitored by conducting counts of males at breeding leks, but the relationship between this index and true population size is unknown. In an attempt to improve the analyses of this population index, we examined the potential of  $N$ -mixture models to evaluate population size, detection probability, and trend in greater sage-grouse using lek count data collected over space and time. We used simulations to test how well the models recovered abundance and growth rate parameters with increasingly sparse count data. We found that the models correctly recovered parameters for scenarios with both constant and variable detection probability, even with up to 90% of the data missing, where 95% of simulations contained the true population growth rate parameter value within the 95% credible interval. We then applied the model to 13 years of lek count data from Montana, USA, collected at 2 spatial scales. Statewide, we determined that the population was decreasing by 7% per year on average over this time period, and that mean annual detection probability ranged from 0.20 to 0.76. In contrast, regressions of naïve counts over time showed a 9% annual decrease in population size with a confidence interval spanning 0. High interannual variability in detection probability demonstrates that naïve counts do not accurately measure interannual variability in population size, and may lead to misleading trends in population size over time. Although  $N$ -mixture models still have limitations, they are a promising approach for conducting robust analyses of population trends for species that aggregate at discrete breeding sites, even when datasets are sparse or uneven. © 2016 The Wildlife Society.

**KEY WORDS** abundance, Bayesian model, *Centrocercus urophasianus*, greater sage-grouse, hierarchical model, Montana, population trend, simulation.

One of the most fundamental, yet challenging, tasks in the conservation of imperiled species is the accurate estimation of population size and trend over time. A rich field of research and methodological development in this area has provided numerous tools for such estimation. These tools generally account for imperfect detection of individuals on the landscape through a variety of methods (e.g., distance sampling, double count methods, mark-recapture techniques; Williams et al. 2002). However, applying these methods can be difficult for a number of reasons. First, many species cannot be monitored using these methods because individuals are simply too cryptic or because they

cannot be individually marked or identified. Second, even if certain populations can be accurately monitored at a small scale, sampling methods that correct for imperfect detection are hard to implement across a large geographic range or for many populations. Finally, many species have been monitored historically using indices of population size such as counts, whereby there is an incentive to continue index-based population monitoring for continuity. Therefore, many species continue to be monitored using methods that do not correct for imperfect detection. For species of conservation concern, robust estimates of total population size and trend are necessary to determine range-wide dynamics in relation to management and conservation needs.

One tool for estimating population size using only count data is the binomial, or  $N$ -, mixture model (Royle 2004, Royle and Dorazio 2008). This model uses temporal and spatial replication of count data to simultaneously estimate

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abundance and detection probability without relying on identification of individuals in the populations. Furthermore, extensions of this model across seasons allow for explicit estimation of population trend (Kéry et al. 2009, Dail and Madsen 2011). To date,  $N$ -mixture models have been applied to a variety of species, including birds (Kéry et al. 2005, Kéry and Royle 2010, Deluca and King 2014, Jakob et al. 2014), reptiles (Kéry et al. 2009), fish (Kanno et al. 2014), mammals (Priol et al. 2014), and amphibians (Dodd and Dorazio 2004) to answer a variety of questions in basic and applied population ecology.

Species that use a lek mating system may be particularly good candidates for improved analysis of population trends using  $N$ -mixture models. In this mating system, males aggregate at consistent breeding sites called leks during the breeding season, where they attempt to woo females to mate with them (Emlen and Oring 1977). Examples of lekking species include mammals (Apollonio et al. 1992), birds (Wiley 1978, McDonald and Potts 1994), insects (Campanella and Wolf 1974), and amphibians (Emlen 1976). These breeding site aggregations are generally the only time individuals of these species are consistently seen, so they may provide the only opportunity to acquire estimates of population size and trend. Typically, males are the focus of lek-based population studies because they maintain territories or display for long periods of time on the lek. Although in some cases, mark-recapture methods have been used successfully to estimate male population size and survival rates in distinct populations (Pilliod et al. 2010), these data-intensive methods are hard to apply across large spatial scales. Therefore, researchers have often relied on counts of males and females at the breeding lek to gain insight into population dynamics. However, lek count data merely represent an index of population size, and the relationship between this index and true population size is not known and could change over space and time. Correcting count data from breeding leks for varying detection probabilities is key to developing more robust inference into the dynamics of lekking species, such as the greater sage-grouse (*Centrocercus urophasianus*).

The greater sage-grouse is an upland bird widely distributed across western North America in association with sagebrush (*Artemisia* spp.) communities (Schroeder et al. 1999). Yet it has experienced significant declines in population and range size over the past 40 years coincident with the loss and degradation of the sagebrush habitats on which it depends (Connelly et al. 2004, Garton et al. 2011). Current range size is estimated to be half of its historical range (Schroeder et al. 2004), with threats from energy development (Naugle et al. 2011), habitat conversion (Walker et al. 2007), and disease (Walker and Naugle 2011) continuing to affect the species (Taylor et al. 2013). Concerns over declines have prompted state and federal agencies, local groups, industry, and private landowners to monitor sage-grouse on their lands, and to work on assessing and addressing risks to populations (Connelly et al. 2004). Therefore, reliable estimates of population size and trend are necessary for the ongoing management and conservation of this species.

Lek counts are the dominant method by which biologists and natural resource managers currently monitor greater sage-grouse populations and trends across their range. In greater sage-grouse, leks provide an opportunity for surveying and counting birds that are otherwise elusive and cryptic. Lek counts started in the 1940s across the range of the species, providing a long historical dataset on male use of breeding sites (Johnson and Rowland 2007). Many leks are surveyed multiple times each year, whereas others are much less frequently surveyed. Researchers and managers typically rely on the maximum number of males observed at a given lek in a given year for population inference. Much time and effort has been spent standardizing lek count methodology so that data collection is consistent (Connelly et al. 2003), though these standards are not always implemented and problems remain. Lek counts are therefore likely to continue to be the dominant method for monitoring birds into the future over a large scale, because of the extensive historical dataset and the established protocol for lek count monitoring. The problems with the current use of lek count data in sage-grouse have been identified and studied (Beck and Braun 1980, Walsh et al. 2004, Johnson and Rowland 2007, Walsh et al. 2010, Blomberg et al. 2013), and researchers have suggested solutions to account for these issues. However, these solutions often involve time- and data-intensive approaches, where individual birds are tracked over time (Walsh et al. 2004, Clifton and Krementz 2006, Walsh et al. 2010). Thus, a method that can easily build on the existing lek count data while providing robust estimates of population size and trend that account for varying detection probability is needed to advance statistically robust monitoring and management of this species. Even a method that can lead to better inference from past data while improved monitoring techniques are implemented would be useful.

$N$ -mixture models provide an exciting and appealing framework for the analysis of unmarked populations (Dénes et al. 2015, Kéry and Royle 2016), but they have key assumptions that can be difficult to address in greater sage-grouse. First, all counts within a site (in our case, lek) and year are assumed to be closed to movement. For greater sage-grouse, some movement among leks within a year certainly occurs, and lek attendance by individual birds is not consistent over the entire closed survey period. Efforts to minimize violations of closure are thus important to consider. Second, the model assumes that individuals are counted only once per survey: there are no false positives. For large leks in particular, it may be difficult to avoid all double-counting, though this is not a problem unique to  $N$ -mixture models. Third, the model assumes that all individuals are being detected independently. Ways to address correlated detection if this assumption is violated have recently been developed (Martin et al. 2011, Dorazio et al. 2013), and may merit attention for sage-grouse. Fourth, all individuals at a given site and survey are assumed to have the same detection probability. For greater sage-grouse, yearling and adult males may have different detection probabilities (in addition to different lek attendance rates), which could also vary over

time. Violations of this assumption cannot be addressed with current methods but could be a topic of future research. Although aspects of sage-grouse ecology thus present a challenge for using  $N$ -mixture models, we examine these assumptions and consider how this modeling approach could provide improved inference on population dynamics, and how it could further be refined with ongoing advances in both  $N$ -mixture modeling methods (Dénes et al. 2015) and our understanding of sage-grouse ecology.

We tested the performance of  $N$ -mixture models for evaluating population size and trend in greater sage-grouse using lek count data. Because lek count data have been unevenly sampled over time and space, we first conducted a simulation study to examine how  $N$ -mixture models perform with increasingly sparse datasets, which could include missing lek count data both within and across years. Second, we conducted a case study where we used  $N$ -mixture models to analyze lek count data at 2 spatial scales in Montana.

## STUDY AREA

Our case study used lek count data collected across the entire state of Montana, as well as for a single county (Phillips County). Across Montana, greater sage-grouse use sagebrush (*Artemisia* spp.) dominated habitats, which are widespread in southwestern, central, and eastern Montana. The primary sagebrush ecosystems in Montana include big sagebrush steppe, which is found in the central and eastern portions of the state, and montane sagebrush steppe, which is most prominent in southwest Montana. Big sagebrush steppe is dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*), and a variety of xeromorphic shrubs and bunchgrasses. It occurs at elevations between 1,500 m and 2,500 m. Montane sagebrush steppe occurs at higher elevations (1,844–3200 m) in southwestern Montana, receives a higher amount of annual precipitation than big sagebrush steppe, and is dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). Phillips County (13,500 km<sup>2</sup>) is located in north-central Montana, bounded by Canada to the north and the Missouri river to the south. The county is rural and contains a mixture of big sagebrush steppe, grasslands, and agricultural land. Portions of the Charles M. Russell National Wildlife Refuge occupy the southern border of the county, and the remainder of the county largely comprises Bureau of Land Management and private lands.

## METHODS

### Review of Open $N$ -Mixture Models for Count Data

We used an open  $N$ -mixture modeling approach as described by Kéry et al. (2009), which extends the original  $N$ -mixture model presented by Royle (2004) across multiple primary sampling periods for explicit inference about population trends over time. For this model, we first assume that replicated counts  $y_{ijk}$  have been collected across a certain number of sites ( $i$ ), surveys at each site within a year ( $j$ ), and years ( $k$ ). Surveys conducted within each year are assumed to

be from a demographically closed population, but individuals can enter or leave the population between years. The models are then defined by 2 processes. The first process, typically called the state process, refers to the true underlying state of the population, which is unknown and estimated as part of the analysis. The second process is the observation process, and refers to the observed count data. In the state process, spatial variation in the true, unknown population size at a given site in a given year ( $N_{ik}$ ) is described by a Poisson distribution with rate parameter  $\lambda_{ik}$ :

$$N_{ik} \sim \text{Poisson}(\lambda_{ik}) \quad (1)$$

In our case, we explicitly estimated trend in unobserved abundances by extending the state process as described in Kéry et al. (2009):

$$\log(\lambda_{ik}) = \alpha_i + r_i(k - 1) + \varepsilon_i \quad (2)$$

Here, for each site  $i$ , the log-transformed Poisson rate parameter in year  $k$  is the sum of the intercept  $\alpha_i$ , which represents the log population growth rate in year 1, the effect of the annual population growth rate ( $r_i$ ), and a site-specific random effect ( $\varepsilon_i$ ) to account for unobserved sources of variation in abundance. This equation could also be modified to include effects of other explanatory variables on abundance by adding covariate terms to the right side of the equation, such as day of the year or time of day.

Given a particular realization of the state process at site  $i$  in year  $k$ , repeated observations  $y_{ijk}$  follow a binomial distribution with parameter  $N_{ik}$  describing the number of trials and success parameter  $p_{ijk}$  (the probability of detecting an individual male on a given lek during a given count, which is assumed to be constant for all males at that site and time):

$$(y_{ijk} | N_{ik}) \sim \text{Bin}(N_{ik}, p_{ijk}) \quad (3)$$

We can then describe the logit-transformed detection probability at site  $i$  in during survey  $j$  in year  $k$  as an intercept  $\alpha_{ijk}$  plus the effects of a covariate of interest  $\beta_w$  of the  $w$ th covariate with value  $x_{ijkw}$  and a site-survey-year-specific random effect ( $\delta_{ijk}$ ) to account for unobserved variation in detection probability, as explained in Kéry et al. (2009):

$$\text{logit}(p_{ijk}) = \alpha_{ijk} + \beta_w \times x_{ijkw} + \delta_{ijk} \quad (4)$$

We used this basic model structure for the simulation study and case study, and specify the equations used for each component of our study below.

### Simulation Study

We examined how  $N$ -mixture models perform with different quantities of data using simulations. We simulated data for a population of 100 leks (i.e., sites;  $i$ ), where each lek was surveyed 3 times per year ( $j$ ), and leks were surveyed for 10 years ( $k$ ). We set initial number of males/lek ( $\lambda_0$ ; hereafter starting population size) to 33 males for all leks, with population growth rate  $r = -0.05$ . We chose these values because they approximated values estimated in our Phillips

County, Montana case study. We did not include any covariates or random effects in our simulation study, either in the state or observation process. We examined 12 different scenarios. In the first 6 scenarios, we set detection probability at a constant value for all sites and years ( $P=0.5$ ). In the second 6 scenarios detection probability varied by year, ranged from 0.2 to 0.8, and was drawn from a uniform distribution. Hence, we modeled true abundance with the following equations:

$$N_{ik} \sim \text{Poisson}(\lambda_k)$$

$$\log(\lambda_k) = \lambda_0 + r(k-1) \quad (5)$$

Our observation model was the same as Equation (3), where detection probability was either constant ( $p$ ) or varied by year ( $p_k$ ).

We examined 6 different data scenarios for both the constant and time-varying detection probability models: complete data (0% missing data), and then 10%, 30%, 50%, 70%, and 90% of the data missing. For each model run, we simulated a full, balanced dataset with the parameters described above, and then randomly removed a percent of the lek counts in accordance with the scenario before estimating parameters using the  $N$ -mixture model. We simulated 100 replicate datasets for each of the 12 scenarios, and estimated detection probability ( $p$ ), population growth rate ( $r$ ), and initial lek abundance ( $\lambda_0$ ) from each model. We estimated detection probability as a single value for the constant  $p$  models, and annually for the variable  $p$  models. We examined the mean and distribution of recovered population parameters. For each of the 12 scenarios, we also determined, for each parameter of interest, what proportion of simulations contained the true parameter value within the 95% credible interval (CRI) of the estimated parameter. Finally, we examined the precision of our recovered population growth rate parameter by measuring the distribution of the standard deviation of the population growth rate estimate across simulations for each scenario. To examine how our simulation results related to specific sampling effort, we summarized what percent of leks were surveyed 0, 1, 2, or 3 times under each missing data scenario, which we averaged across years.

### Case Study

We examined population size and trends using male lek counts from Montana, USA conducted between 2002 and 2014. The lek count database for the state of Montana is maintained by Montana Fish, Wildlife, and Parks and contains all counts conducted at known leks across the state. We chose this time frame because records of multiple annual counts per year were not consistently included in the Montana lek survey database prior to 2002. We examined lek counts for a single county (Phillips County) and for the entire state. Personnel conducting lek counts followed an established statewide protocol for monitoring leks (Montana Sage Grouse Work Group 2005), which includes minimizing disturbance to birds during the counts by maintaining appropriate distances from leks and counting birds from a

vehicle or blind using a spotting scope. We examined the statewide database from 2002–2014 to compare naïve population trend estimates from raw counts to the  $N$ -mixture population trends estimated at a large scale, with inconsistent and variable counts. The leks in Phillips County were consistently sampled from 2002 to 2014, with many leks counted  $>2$  times per year. We chose this smaller-scale area for the case study because there were a large number of leks with consistent counts of birds over many years, and multiple counts within years. In this sense, this county might be considered a best-case scenario for  $N$ -mixture models. We consider each lek to represent 1 site in our model.

Prior to analysis, we removed counts from the statewide database that were conducted in the evening or in the middle of the night, so that timing of counts covered the typical period of approximately 30 minutes before sunrise to 2 hours after sunrise, following conventions for standardizing lek counts over space and time (Connelly et al. 2003). We also removed rare counts that were conducted during fall and winter. Finally, we removed leks that were surveyed only once during our survey period from the dataset (i.e., 1 survey in 1 year).

For the statewide database, we fit 2 models. First, we estimated annual population size by including a year-specific intercept ( $\alpha_k$ ) and random effect of site ( $\varepsilon_i$ ) in the model of abundance. We fit this model to demonstrate interannual variation in mean number of males/lek and detection probability. Secondly, we fit a model that explicitly estimated population trend ( $r$ ) by using the following equation for the model of abundance, as described above:  $\log(\lambda_{ik}) = \alpha + r(k-1) + \varepsilon_i$ . We fit this model to demonstrate how population trend could be estimated within the model structure, while accounting for variable detection probabilities over time. For both models, our observation model used Equation (3) and included a random effect of site, survey, and year on detection probability ( $\delta_{ijk}$ ) to allow for unexplained variation in individual surveys, and separate intercepts for each year:  $\text{logit}(p_{ijk}) = \alpha_k + \delta_{ijk}$ . We did not include covariates in either the state or observation process because we had no consistently collected covariates present in the database to test.

We compared the estimates from the latter open  $N$ -mixture model to an analysis of naïve high male counts, obtained by determining the high count of males for each lek in each year. For each year, we calculated the naïve total population size (adding up all high male counts across all surveyed leks) and the naïve mean number of males/lek ( $n$ ; total naïve population size/no. leks surveyed in that year). We calculated the mean ( $\hat{r}$ ) and variance ( $\hat{\sigma}^2$ ) of the naïve log population growth rate for  $q$  time intervals following Dennis et al. (1991) and Morris and Doak (2002):

$$\hat{r} = \log\left(\frac{n_t}{n_0}\right)/t$$

$$\hat{\sigma}^2 = \left(\frac{1}{q-1}\right) \sum_{i=1}^q \left(\log\left(\frac{n_q}{n_{q-1}}\right) - \hat{r}\right)^2 \quad (6)$$

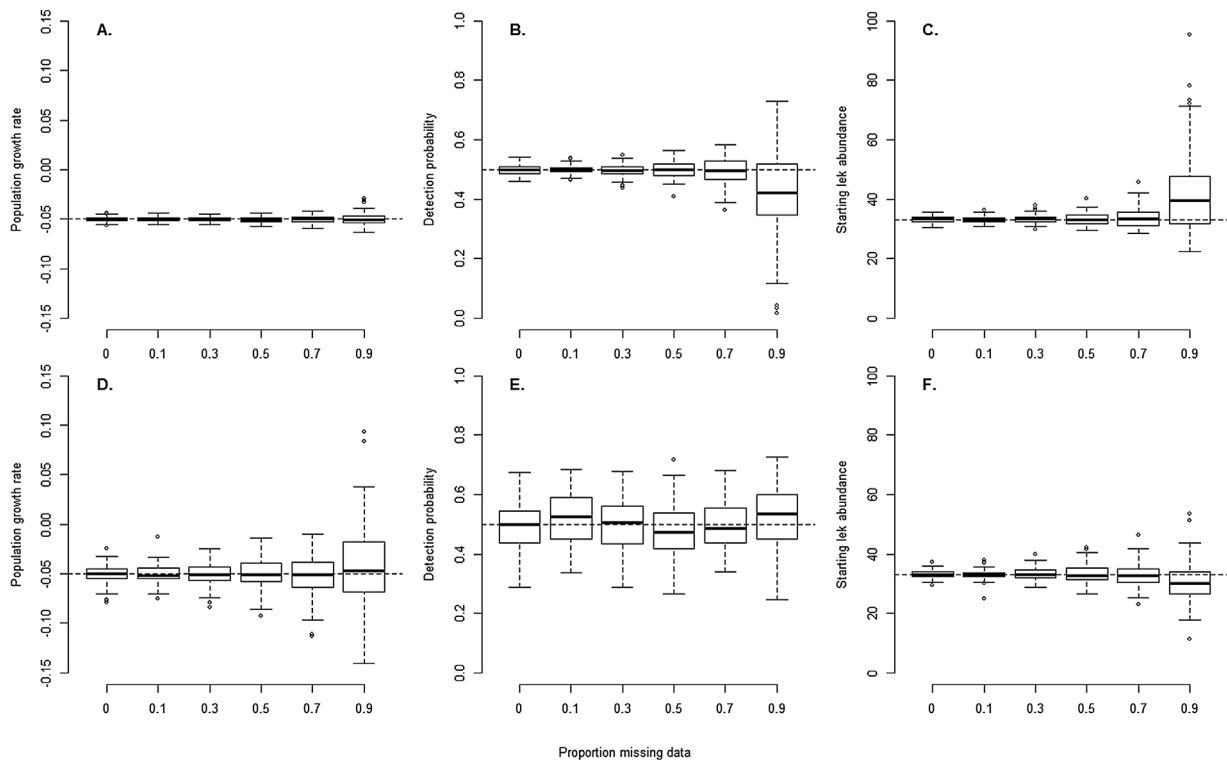
For the Phillips County models, we used the equations described for the statewide model that explicitly included the

population trend, and for the observation process we also considered covariates that might explain variation in detection probability, as described in Equation (4). Preliminary exploration of the data suggested that both time of day and day of the year could be correlated with detection probability, so we considered a range of models with linear and quadratic effects of time and date on detection probability, and compared models using the Deviance Information Criterion (Spiegelhalter et al. 2002). We removed counts conducted during bouts of particularly poor visibility (e.g., fog or snowstorms) and the few aerial counts conducted in this county prior to analysis.

### Model Implementation

We used a Bayesian approach to estimate  $N$ -mixture model parameters. We combined our described models with prior distributions for each parameter. We assumed vague priors for all analyses to express the absence of prior information about model parameters. For the case study, we chose a normal (0, 0.1) distribution for the intercept of log annual abundance, uniform (-5, 5) distributions for time and date coefficients where applicable, a uniform (-1, 1) distribution for the population growth rate  $r$ , and uniform (0, 1) distributions for the year-specific intercepts of detection probability. Finally, we used uniform (0, 5) distributions for the standard deviation of 2 normal distributions used to

describe the unexplained spatial and temporal variation in the log of site-level abundance and the logit of detection probability. We used Markov chain Monte Carlo (MCMC) methods to sample from the joint posterior distribution. We scaled and centered date and time covariates used in the Phillips County models to a mean of 0 and a standard deviation of 1 to ease convergence of the MCMC sampler. We ran all models in R version 3.0 (R Foundation for Statistical Computing, Vienna, Austria) and JAGS (Plummer 2003). For the simulation models, we ran 3 parallel chains for 700,000 iterations, discarded the first 300,000 iterations as a burn-in period, and thinned the remaining iterations by 1 in 10, resulting in 120,000 draws of the posterior distribution for inference. For each of the case study models, we ran 3 parallel chains for 100,000 iterations, discarded the first 40,000 iterations as a burn-in period, and thinned the remaining iterations by 1 in 20, resulting in 9,000 draws of the posterior distribution for inference. For all models, this led to convergence of all parameters ( $\hat{R} < 1.01$ ; Gelman and Hill 2007). We assessed the adequacy of our case study models by computing a Bayesian  $P$ -value, which is a summary of a posterior predictive check (Gelman et al. 1996). Here, the posterior distribution of a defined fit statistic (i.e., discrepancy measure) is constructed from summed Pearson residuals and compared to the posterior distribution of that fit statistic for a hypothetical perfect data



**Figure 1.** Simulation results showing the true parameter values (dashed lines) and a summary of the estimated median values from 100 simulated datasets of greater sage-grouse lek counts assuming populations with constant (A–C) or variable (D–F) detection probabilities, where 0%, 10%, 30%, 50%, 70%, and 90% of the count data are randomly missing, for population growth rate (A and D), detection probability (B and E), and starting abundance (C and F). The black line in the middle of each box represents the median value (of the 100 median points estimated from the dataset), the outer lines of the box show the interquartile range, and the whiskers show the highest and lowest values within  $\pm 1.5$  times the interquartile range. Outliers are points beyond that range. For (E), detection probabilities were drawn from a uniform distribution (0.2–0.8) in all scenarios, so this panel shows the distribution of values drawn across 100 iterations of each scenario.

set where the model is known to be correct. A Bayesian *P*-value close to 0.5 is considered a good model (Kéry and Royle 2016).

## RESULTS

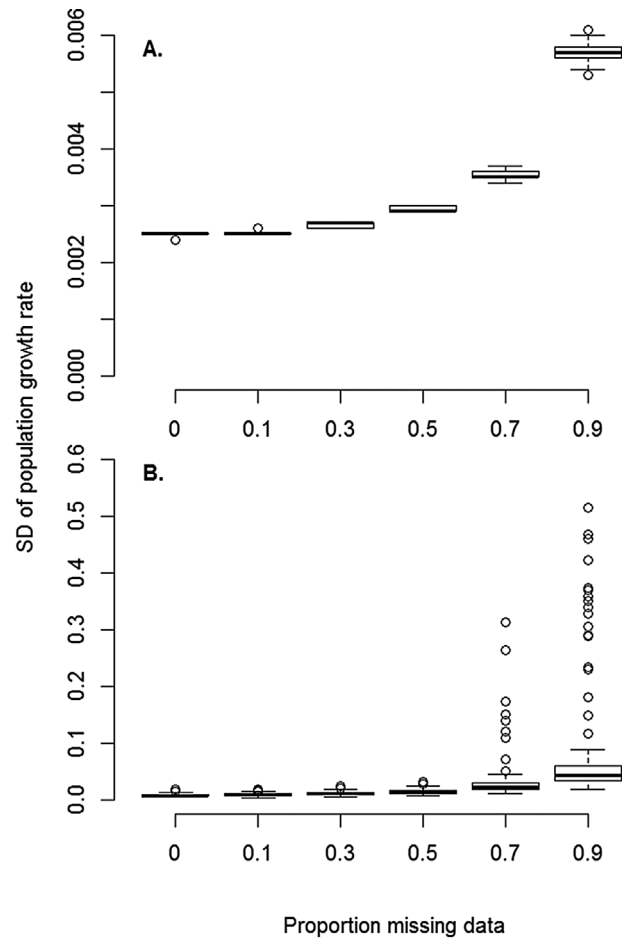
### Simulation Study

Our results show that the ability of our models to recover population growth rate parameters was generally robust to missing data, under both the constant and variable detection probability scenarios (Fig. 1). In the constant detection probability model, population growth rate was recovered even when 90% of the data were missing, detection probability was underestimated, and starting population size was concurrently overestimated (Fig. 1A–C). Under the constant detection probability models, 92–97% of estimates of population growth rate, starting population size, and detection probability included the true parameter value within the 95% credible interval across all missing data scenarios (Table 1). Further, precision of recovered population growth rate was high across all scenarios (Fig. 2A).

Under the variable detection probability models, estimates of recovered population growth rate and starting population size were more variable when 70% and 90% of the data were missing (Fig. 1D–F). However, under these models, 94–97% of estimates of population growth rate still included the true

**Table 1.** Percent of simulations of greater sage-grouse lek counts across a range of missing data where the 95% credible interval (CRI) of the parameter of interest contained the true parameter value.

Detection probability scenario	Parameter	Proportion missing data	Coverage (95% CRI)
Constant	Starting population size	0	0.93 (0.86–0.97)
		0.1	0.94 (0.88–0.97)
		0.3	0.94 (0.88–0.97)
		0.5	0.98 (0.93–0.99)
		0.7	0.96 (0.90–0.98)
		0.9	0.94 (0.88–0.97)
	Detection probability	0	0.94 (0.88–0.97)
		0.1	0.96 (0.90–0.98)
		0.3	0.94 (0.88–0.97)
		0.5	0.98 (0.93–0.99)
		0.7	0.95 (0.89–0.98)
		0.9	0.96 (0.90–0.98)
Variable	Starting population size	0	0.94 (0.88–0.97)
		0.1	0.92 (0.85–0.96)
		0.3	0.96 (0.90–0.98)
		0.5	0.97 (0.92–0.99)
		0.7	0.95 (0.89–0.98)
		0.9	0.92 (0.85–0.96)
	Population growth rate	0	0.96 (0.90–0.98)
		0.1	0.95 (0.84–0.98)
		0.3	0.95 (0.89–0.98)
		0.5	0.89 (0.81–0.94)
		0.7	0.94 (0.88–0.97)
		0.9	0.96 (0.90–0.98)
Variable	Population growth rate	0	0.95 (0.89–0.98)
		0.1	0.97 (0.92–0.99)
		0.3	0.97 (0.88–0.98)
		0.5	0.94 (0.89–0.98)
		0.7	0.95 (0.90–0.98)
		0.9	0.95 (0.88–0.97)



**Figure 2.** Precision of recovered population growth rate estimates of greater sage-grouse from the simulation study incorporating (A) constant detection probability scenarios and (B) variable detection probability scenarios across a range of proportions of missing lek count data.

population growth rate within the 95% credible interval across all missing data scenarios (Table 1). We found equally good coverage for estimates of starting population size (Table 1). Precision of recovered population growth rate was much lower for the variable detection probability models, especially when 70–90% of data were missing (Fig. 2B).

As we subsequently removed more data, the percent of leks that were counted at least 1 time per year decreased, as did the percent of leks counted >1 time a year (Table 2). The proportion of leks counted at least once a year began to decline dramatically when 70% and 90% of the data were removed, which corresponded with recovered population growth rate and starting population size parameter estimates that were less precise, especially in variable detection probability models (Figs. 1D, F and 2B).

### Case Study

Across the state of Montana, we used data from 1,322 lekking sites, which were monitored anywhere from 0 to 13 times a year between 2002 and 2014 for 18,138 observations. Average number of males counted on a lek was 11, and median number was 5. Lek counts varied from 0 to 166 birds in a given visit (Table 3). In Phillips County, Montana, we

**Table 2.** Summary of lek sampling effort for a simulation study on greater sage-grouse under different data removal scenarios.

Percent data removed	Percent of leks surveyed				
	At least once	0 times	1 time	2 times	3 times
10	99.9	0.1	2.8	24.2	72.9
30	97.3	2.7	18.8	44.2	34.3
50	87.6	12.4	37.6	37.6	12.4
70	65.7	34.3	44.2	18.8	2.7
90	27.1	68.9	24.3	2.7	0.1

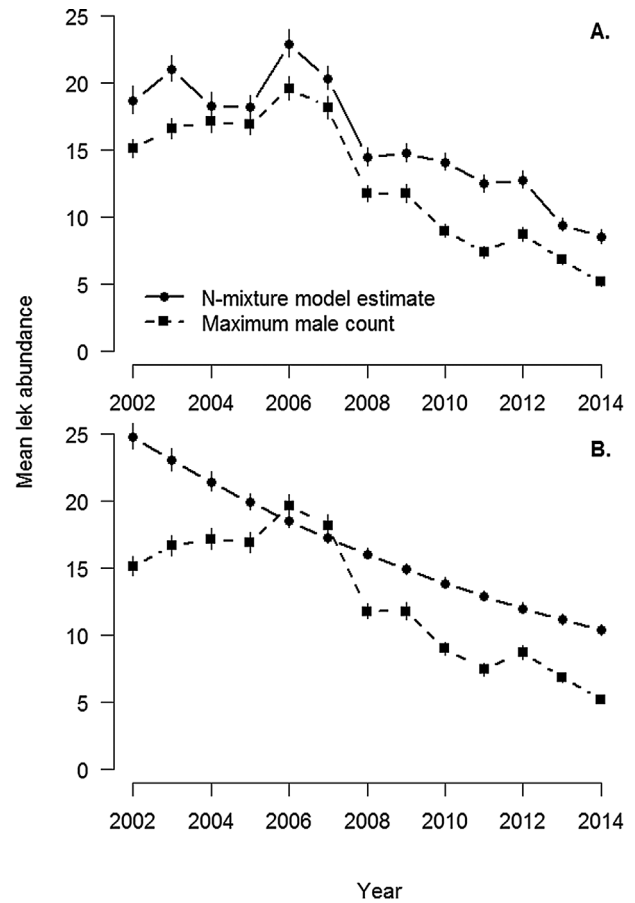
used data from 81 lekking sites, which were monitored 0–9 times a year between 2002 and 2014 for 1,327 observations. Lek counts varied from 0 to 111 males in a given visit, with an average of 25 birds, and a median of 20 birds counted on a lek across visits and years.

For the statewide analysis, we found that annual estimates of mean number of males/lek ranged from 23 birds to 9 birds over time, and that estimates from *N*-mixture models were consistently higher than naïve calculation of mean number of males/lek (Fig. 3A). The model estimating annual population size was a good fit for the data, with a Bayesian *P*-value of 0.45. For our second model, where we explicitly included population growth rate in the estimate of abundance, we found that the population was declining at about 7% per year ( $r = -0.073$  [−0.078 to −0.068 CRI]; Fig. 3B), and that detection probabilities varied from 0.20 to 0.76 across all years (Fig. 4). The Bayesian *P*-value of 0.44 suggested that this model was also a good fit. Mean population growth rate estimated as the mean number of males/lek over time using the naïve high male counts was  $\hat{r} = -0.089$  (−0.210–0.032 95% CI).

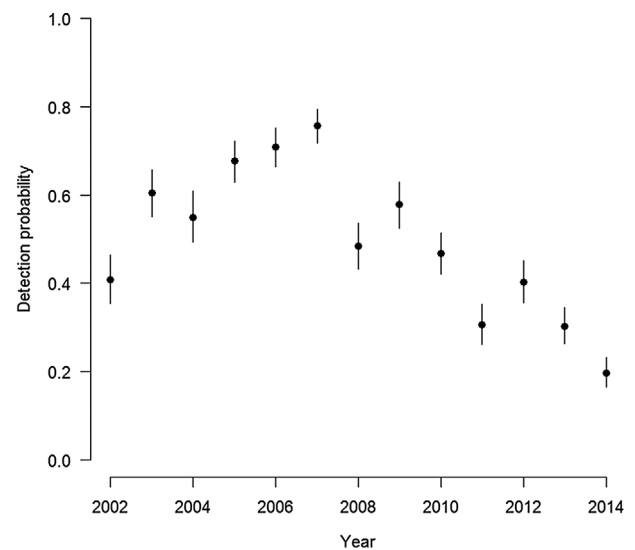
The best model for Phillips County included a linear effect of time of day ( $\beta_{\text{time}} = -0.214$  [−0.415 to −0.014 CRI]) and quadratic effect of survey date ( $\beta_{\text{date}} = 0.209$  [0.090–0.334 CRI];  $\beta_{\text{date}^2} = -0.095$  [−0.171 to −0.021 CRI]) on detection probability. Mean population growth rate across all sites was  $-0.051$  (−0.063 to −0.039 CRI). However, the model with no covariates (with all variation in detection probability captured by a random effect by site, survey, and

**Table 3.** Summary of lek survey effort and raw counts of greater sage-grouse over time in the state of Montana from 2002–2014. Bird numbers refer to males only.

Year	Counts	Sites visited	No. of birds seen	$\bar{x}$ birds/lek
2002	966	503	13,366	15
2003	1,077	579	17,956	17
2004	947	474	14,527	17
2005	1,194	557	18,789	17
2006	1,254	656	21,154	20
2007	1,319	578	20,995	18
2008	1,458	617	14,032	12
2009	1,366	641	15,281	12
2010	1,884	899	17,167	9
2011	1,589	773	10,680	7
2012	1,675	769	14,408	9
2013	1,835	817	12,171	7
2014	1,573	814	8,861	5



**Figure 3.** Estimated mean lek population size of male greater sage-grouse in the state of Montana from 2002–2014, where circles with solid lines represent the model estimates (with 95% credible intervals), and squares with dotted lines represent raw counts (with SE) from lek survey data using (A) a model of annual estimates of abundance, and (B) a model with population growth rate explicitly estimated in the model.



**Figure 4.** Estimated detection probability over time for male greater sage-grouse in the state of Montana from 2002–2014 (with 95% credible intervals) for a model where population growth rate is explicitly estimated in the model.

year) was the second best model, and had a nearly identical estimate of population growth rate ( $r = -0.050$  [ $-0.062$  to  $-0.038$  CRI]). Both models appeared adequate for our dataset, given Bayesian  $P$ -values of 0.36 and 0.37, respectively.

## DISCUSSION

Using both simulations and a case study, we demonstrate that  $N$ -mixture models are a promising tool for estimating male lek population trends for the greater sage-grouse and other lekking species. Our simulation study shows that estimation of population trend using these models is robust to data that are patchy across time and space, and where detection probability varies over time. Our case study shows the extent to which detection probability varies over time, and how this can influence short- and long-term estimated trends in abundance. Analyses of naïve counts alone can be misleading if variation in perceived annual abundance is dominated by observation error. We also demonstrate how covariates can be included in  $N$ -mixture models to explain variation in true abundance or detection probability. Lek counts are the dominant way that greater sage-grouse are monitored across their range, so our results suggest that this modeling approach may allow more robust inference from data that is already being collected in conjunction with ongoing monitoring programs. Moreover,  $N$ -mixture models offer an opportunity to improve estimates of male abundance from data collected in the past.

### Simulation Study

Our simulation results demonstrate that  $N$ -mixture models can adequately recover population growth parameters of interest under scenarios with increasingly uneven and patchy count data. This suggests that these models would be a good fit for lek count data that are variable in space and time. Although sage-grouse biologists have recommended conducting a minimum of 3 counts per lek each year to address concerns over the validity of lek counts (Connelly et al. 2000, 2004), many leks can only be counted once or twice a year, and others are not even counted once every year (Fedy and Aldridge 2011). Our results indicate that uneven sampling of leks in space and time may not pose a significant problem to gaining statistically robust estimates of population trend using  $N$ -mixture models. Fedy and Aldridge (2011) recently concluded that single surveys of a large sample of leks were better for identifying long-term trends from high male counts than multiple counts of a smaller number of leks. We show here that even if a subset of leks are visited multiple times a year, we can better estimate population size and trends by correcting for uneven detection probabilities over time and among leks.

Simulation studies have been, and should continue to be, used to explore the data requirements and limitations of  $N$ -mixture models. Previous simulation work has shown that  $N$ -mixture models can do a good job of estimating population size under a variety of circumstances, including low detection probability, low counts, and low numbers of sites (Yamaura 2013). It is typically recommended that a

minimum of 20 sites be used for inference (Royle 2004, Kéry et al. 2009, Kéry and Royle 2016), and models perform better with more sites, higher detection probability, and replicate counts for each site (Yamaura 2013). Future simulation work could be used to determine the minimum and ideal count effort needed for robust population inference given variable detection probability among leks and years. For example, is it better to conduct multiple counts every other year for certain leks rather than single counts every year? What proportion of leks needs to be counted multiple times a year, and how many repeat visits are needed?

Our results suggest that not all leks need to be counted every year, and as long as a certain proportion of leks are consistently counted multiple times a year, then not all leks need to be counted  $>1$  time per year. Specifically, our simulation results suggest that we can reasonably estimate parameters of interest when  $>75\%$  of leks are surveyed at least once a year and approximately 60% of those leks are surveyed multiple times within the year (e.g., 2 or 3 times). This level of sampling is consistent with what is already happening across the range of the species. This is encouraging because it suggests that we can develop stronger models for male population size and trend without significantly altering current monitoring plans or requiring additional resources.

### Case Study

Our analyses of Montana lek count data from 2002 to 2014 allowed us to acquire improved estimates of male population size and trends, and to compare results with analyses of lek counts uncorrected for detection probability. Although mean lek size trends from the  $N$ -mixture models generally tracked trends derived from high male counts, there were notable years where estimates from the  $N$ -mixture model between years showed opposing trends from the peak male counts (Fig. 3A) because of interannual variation in detection probability (Fig. 4). This discrepancy highlights the importance of accounting for variable detection probability over time. Furthermore, the naïve trend showed a steeper, yet less precise, estimate of population decline than our model.

The observed decline over the time period we analyzed is partially due to the window of lek count data to which we had access. As we mentioned, multiple within-year counts at leks were not reliably entered prior to 2002, so we were unable to use earlier data in our models. The early 2000s were years of very high counts at leks across Montana (Western Association of Fish and Wildlife Agencies 2008) compared to what was seen in the mid- to late-1990s. Some of the decline we observed may be due to natural or cyclic fluctuations in the populations over time. Secondly, the large drop in male population size seen from 2007 to 2008 is associated with an outbreak of West Nile virus in Montana (Center for Disease Control 2015). Although analyses of Phillips County and the state as a whole both showed declining trends, the magnitude of estimated decline was lower in Phillips County. Phillips County contains a protected population at the Charles M. Russell National Wildlife Refuge and large tracts of high-quality sagebrush



habitat on Bureau of Land Management lands, which may explain some of the difference in trends seen at these 2 spatial scales.

In general, count effort and number of leks monitored have increased over time, whereas number of birds seen has decreased (Table 3), and our model results showed a decline in mean lek size and total population size. This change in survey effort, accompanied by potential changes in detectability, highlights the problems with using uncorrected counts for detectability, particularly if counts are not corrected for the number of leks surveyed. Furthermore, in the *N*-mixture models, leks that are not surveyed on certain years are treated as missing data, and the missing values are estimated as part of the modeling process. This feature allows for flexibility in sampling of leks as long as a certain proportion of leks are sampled every year. Future developments in the use of *N*-mixture models for sage-grouse could also include estimates of the proportion of leks being surveyed each year. Our current model structure estimates population size only on known leks that are counted over the time period of interest but does not account for known or unknown leks that are never counted over that same period. Use of a dual frame sampling approach (Haines and Pollock 1998) is one way that researchers could estimate the number of leks on the landscape while monitoring known leks, and could allow biologists to better correct for changing sampling effort over time. Currently, our models are more useful in identifying trends in the number of males/lek (out of the leks currently surveyed) than in trying to estimate total male population size.

Violations of *N*-mixture model assumptions could potentially affect their usefulness in the analysis of lek count data. One of the assumptions is that counts conducted within a year occur within a closed population. Without tracking individual birds, we were unable to assess how many birds may have moved among leks within a year. Recent work has showed that within-year movement among leks during the breeding season is low (Gibson et al. 2014), but other work has demonstrated variable rates of movement among leks (Walsh et al. 2004). Counts could be biased high if the same males are being counted on multiple leks within a given year. Aggregating leks that are adjacent to one another, or where individuals are known to use multiple leks, could be one way of addressing known or potential within-year movements among leks. In some cases, a group of leks may be a more appropriate site than a single lek (Taylor et al. 2013). However, aggregating nearby leks may not address cases of extensive yearling movement among multiple leks in their first year (Emmons and Braun 1984), or other larger scale movements by adult birds, which could bias estimates if immigration and emigration are not balanced. Even if males are not moving among leks, they will not all be on the leks consistently over the breeding period (Walsh et al. 2010). Recently, Chandler et al. (2011) demonstrated that if temporary emigration from count sites is random within a season (assumed to be closed), then estimates of population size will not be biased. If temporary emigration is not random, it could be accounted for within the *N*-mixture model framework in the future (Chandler et al. 2011).

We also assume that repeat counts within years are capturing the same group of birds on each lek, and that all males attend a lek each year. Because lek attendance at a given lek varies over time each year (Blomberg et al. 2013, Coates et al. 2013), entirely different groups of birds could be counted in subsequent surveys if lek counts become too spread out over the breeding period. In this case, *N*-mixture models would underestimate population size. Furthermore, *N*-mixture models do not address the fact that some males never attend a lek in a given year (Blomberg et al. 2013), which could also lead to underestimates of population size or biases in trends if the proportion of males not attending leks changes systematically over time. Finally, lek counts would ideally be centered on peak lek attendance in each year, but it is unclear that this is occurring uniformly in space and time. If counts are conducted well outside the window of peak attendance, then population size may be underestimated. Efforts to minimize violation of the closure assumption in survey methodology and site aggregation for analysis should reduce errors in these models.

Finally, model results may also be affected by assumptions that all individuals at a given site and survey have the same detection probability. This assumption is likely violated in greater sage-grouse monitoring because yearling and adult males show different rates of lek attendance and behavior (Jenni and Hartzler 1978). This assumption is a concern in most applications of *N*-mixture models, but it is hard to discern how much of a problem it is, and thus it deserves additional study (Kéry and Royle 2016). For sage-grouse, counts are sometimes tallied separately for yearling and adult males, so a partial solution might be to model yearling and adult abundance separately at smaller scales to determine whether there are large differences in detection probability between the 2 age classes. Although this would not fully address individual heterogeneity, it could address one source of within-survey variation in detection. Simulation studies and additional research are needed to address potential impacts of individual variation on detection probability.

One useful aspect of analyzing lek counts using *N*-mixture models is the ability to test how different covariates may affect true abundance and detection probability. In our models for Phillips County, we were able to add covariates to explain some of the variation in detection probability. In general, the ability to test the importance of covariates when modeling population size or detection probability is straightforward and can easily be added to these models. However, covariate data must be collected consistently across leks of interest and over time. For example, at the state-level, there were too many missing data to use information on survey date and time in our models. Most of the covariates in current databases could help address variation in detection probability (e.g., aerial vs. ground counts, weather conditions, time, date). Future models could test the importance of covariates of conservation concern that could affect lek population size, such as sagebrush habitat around the lek (Connelly et al. 2000, Walker et al. 2007), and proximity of energy development (Walker et al. 2007). It would also be

straightforward to model or test for differences in population growth rate among populations or regions of interest.

The use of *N*-mixture models for analyses of lek count data has promise for future areas of research of greater sage-grouse population ecology and for other lekking species. For example, if we had a better understanding of male-to-female sex ratio, we could use models of male population size on leks to inform female population size. The estimation of female population size is a key missing element of sage-grouse population ecology that is critical to understanding long-term population dynamics for the species. Secondly, results from *N*-mixture models could be used in integrated population models as a more robust estimate of population size over time than count models uncorrected for variation in detection probability (R. McCaffery and P. M. Lukacs, University of Montana, unpublished data).

## MANAGEMENT IMPLICATIONS

Our analyses demonstrate that *N*-mixture models can produce improved estimates of population size and trend using current, established protocols for monitoring leks. This modeling approach will be useful to managers seeking to gain a better understanding of long-term population trends and influences for this and other lekking species of interest. Because lek counts will continue to be the dominant method by which sage-grouse biologists and land managers survey populations (Naugle and Walker 2007), we recommend that these models, which incorporate existing field techniques and can be used on data collected in the past, be used to assess long-term trends in the absence of more robust monitoring approaches (e.g., mark-recapture, telemetry studies). Our case study and simulation study both show that estimates of population size and trend are robust to uneven sampling data, so that each lek does not need to be monitored multiple times in each year for robust estimates of population size and trends. Our case study shows that past lek count data collected across the species' range can be analyzed using *N*-mixture models, and we emphasize that multiple annual counts need to be recorded in lek count databases. Based on our simulation results, we conservatively recommend future annual surveys on  $\geq 75\%$  of known leks, with repeat surveys (2 or 3) on approximately 60% of the leks being surveyed that year. Surveyed leks should be a probability-based sample of all leks to ensure unbiased estimates. Known but unsurveyed leks will still be included in the model as missing data. Future simulation work and site-specific analyses could aid in refining this sampling design to reflect local or regional variation. Managers and biologists can thus select a sampling strategy that ensures that enough leks are sampled every year to achieve robust population size and trend estimates over time.

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