

# Patterns in Greater Sage-grouse population dynamics correspond with public grazing records at broad scales

ADRIAN P. MONROE <sup>1,6</sup>, CAMERON L. ALDRIDGE <sup>1</sup>, TIMOTHY J. ASSAL <sup>2</sup>,  
KARI E. VEBLEN <sup>3</sup>, DAVID A. PYKE <sup>4</sup>, AND MICHAEL L. CASAZZA <sup>5</sup>

<sup>1</sup>Natural Resource Ecology Laboratory and Department of Ecosystem Science and Sustainability, Colorado State University in cooperation with the US Geological Survey, Fort Collins Science Center, Fort Collins, Colorado 80526 USA

<sup>2</sup>U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado 80526 USA

<sup>3</sup>Department of Wildland Resources and Ecology Center, Utah State University, Logan, Utah 84322 USA

<sup>4</sup>U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon 97331 USA

<sup>5</sup>U.S. Geological Survey, Western Ecological Research Center, Dixon, California 95620 USA

**Abstract.** Human land use, such as livestock grazing, can have profound yet varied effects on wildlife interacting within common ecosystems, yet our understanding of land-use effects is often generalized from short-term, local studies that may not correspond with trends at broader scales. Here we used public land records to characterize livestock grazing across Wyoming, USA, and we used Greater Sage-grouse (*Centrocercus urophasianus*) as a model organism to evaluate responses to livestock management. With annual counts of male Sage-grouse from 743 leks (breeding display sites) during 2004–2014, we modeled population trends in response to grazing level (represented by a relative grazing index) and timing across a gradient in vegetation productivity as measured by the Normalized Vegetation Difference Index (NDVI). We found grazing can have both positive and negative effects on Sage-grouse populations depending on the timing and level of grazing. Sage-grouse populations responded positively to higher grazing levels after peak vegetation productivity, but populations declined when similar grazing levels occurred earlier, likely reflecting the sensitivity of cool-season grasses to grazing during peak growth periods. We also found support for the hypothesis that effects of grazing management vary with local vegetation productivity. These results illustrate the importance of broad-scale analyses by revealing patterns in Sage-grouse population trends that may not be inferred from studies at finer scales, and could inform sustainable grazing management in these ecosystems.

**Key words:** *Centrocercus urophasianus*; Greater Sage-grouse; land use; livestock grazing; population dynamics; scale.

## INTRODUCTION

Globally, livestock production is one of the most common forms of land use (Asner et al. 2004), and effects of livestock grazing on vegetation structure and composition can influence suitability of areas for many wildlife species (Milchunas et al. 1998, Vickery et al. 2001, Fuhlendorf et al. 2012). However, our understanding of how grazing effects translate to population responses of interacting animals is often limited to local and short-term (i.e.,  $\leq 2$  yr) studies (Milchunas et al. 1998, Foster et al. 2014) and may not correspond with trends at broader spatial and temporal scales. For instance, population dynamics at a given site also may be influenced by the amount and distribution of suitable habitat in the surrounding landscape (Pickett and Cadenasso 1995) and connections with other populations (Hanski 1998). Importantly, local vegetation productivity and adaptations for grazing tolerance may influence how a site responds to grazing practices (Maschinski and Whitham

1989, Milchunas and Lauenroth 1993, Cagney et al. 2010), and because vegetation productivity can be determined by precipitation and soil characteristics that vary over broad scales (Sala et al. 1988, Milchunas and Lauenroth 1993, Paruelo and Lauenroth 1995), studies at fine scales may not adequately consider how grazing effects vary across moisture and productivity gradients (Milchunas and Lauenroth 1993). A lack of studies evaluating interactions between livestock grazing and wildlife populations at broad scales may therefore leave us with an incomplete picture of this important land use.

In the western United States, plants in sagebrush-dominated (*Artemisia* spp.) communities can be maladapted to certain management practices for livestock because these plants have a relatively short evolutionary history of grazing (Milchunas and Lauenroth 1993, Adler et al. 2004, Cagney et al. 2010, Boyd et al. 2014). Nevertheless, livestock grazing is ubiquitous within these ecosystems, often pitting conservation interests against the livelihood of ranchers (Brown and McDonald 1995). Populations of one sagebrush-obligate bird, the Greater Sage-grouse (*Centrocercus urophasianus*; hereafter Sage-grouse), declined substantially during the last half-century

Manuscript received 9 December 2016; accepted 9 January 2017. Corresponding Editor: David S. Schimel.

<sup>6</sup>E-mail: adrian.monroe@colostate.edu

(Schroeder et al. 2004, Garton et al. 2011), and livestock grazing is often implicated because it reduces herbaceous cover (Boyd et al. 2014) and could thereby negatively affect Sage-grouse nesting and brood-rearing habitat (Hagen et al. 2007). Reduced stocking rates, deferment, or rest from grazing are recommended to reduce or avoid impacts to vegetation for nesting Sage-grouse, but the consequences of these recommendations are uncertain because we currently lack studies that directly link population dynamics of Sage-grouse to the timing and level of grazing across these vast landscapes (Boyd et al. 2014).

Much of the land in the western United States is public, and records of livestock grazing offer an opportunity to characterize grazing at broad spatial scales. The U.S. Department of the Interior-Bureau of Land Management (BLM) administers livestock use on nearly 61 million ha (BLM 2013), but until recently (Veblen et al. 2011), records from these public lands (allotments) could not be readily used to evaluate effects of grazing because they were not linked to a geospatial database. Here, we use spatially referenced grazing data from allotments in Wyoming, USA (Fig. 1) to characterize grazing management at an unprecedented scale. We then use Sage-grouse as a model organism to evaluate effects of grazing timing and level in sagebrush-dominated rangelands. Given that vegetation communities in Wyoming range from higher-productivity northern mixed-grass prairie to lower-productivity desert shrublands (Fig. 1; Knight 1994), we also have the opportunity to examine how effects of grazing management may vary across a

gradient of vegetation productivity. For example, grazing early during the growing season (late spring) may damage cool-season ( $C_3$  photosynthetic pathway) grasses typical of lower-productivity sagebrush ecosystems and invite opportunities for exotic annual grasses to dominate (Laycock 1967, Bork et al. 1998), whereas early-season grazing on more productive, moister sites may be preferable to grazing later by allowing regrowth of vegetation (Boyd and Svejcar 2004, Vermeire et al. 2008, Stephenson et al. 2015).

We hypothesized that Sage-grouse responses to grazing level and timing are mediated by changes in herbaceous cover. We predicted that Sage-grouse populations would respond positively to grazing levels and timings that minimize negative impacts to herbaceous cover, specifically through reduction or deferment of grazing to avoid impacts to less grazing-tolerant herbaceous plants or to allow for regrowth during a growing season. We also predicted that the response of Sage-grouse populations to grazing level and timing would vary with local vegetation productivity.

## METHODS

### Study area

Our study encompassed areas around 743 breeding display sites of Sage-grouse (leks) in grazing allotments administered by the BLM across Wyoming (Fig. 1). Nearly 70% of the state contains sagebrush-dominated ecosystems

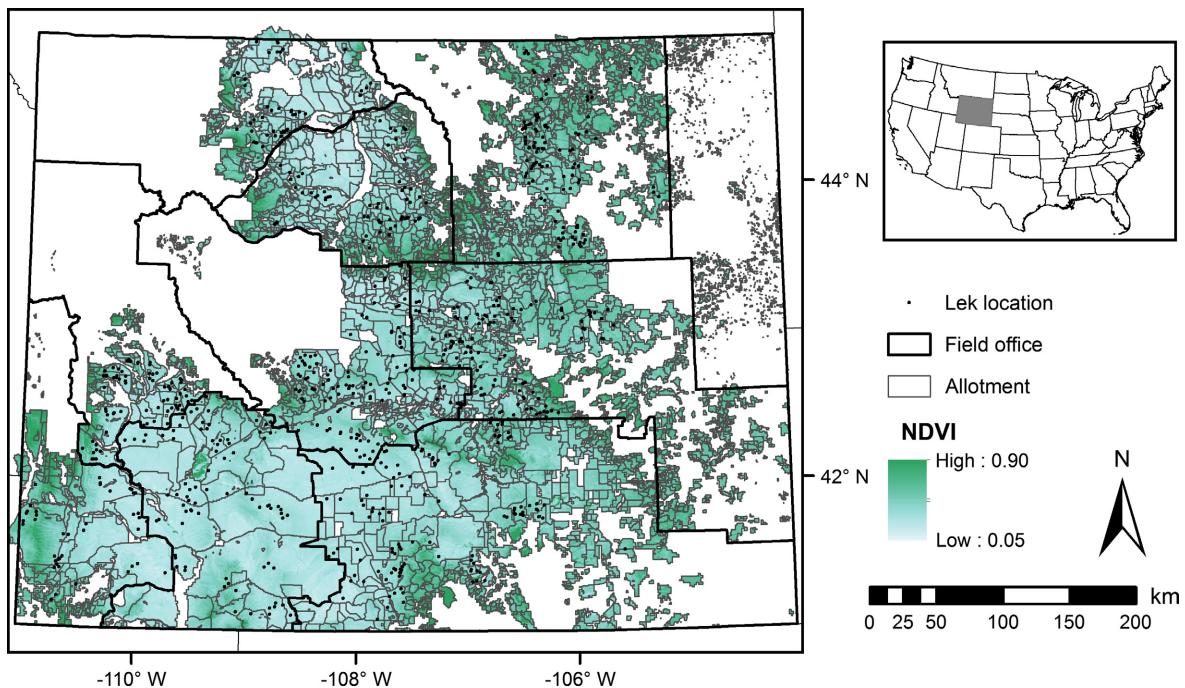


FIG. 1. Distribution of Greater Sage-grouse (*Centrocercus urophasianus*) leks ( $n = 743$ ) among grazing allotments ( $n = 3335$ ) and Bureau of Land Management field offices ( $n = 10$ ) in Wyoming, USA. Mean annual maximum vegetation productivity (NDVI; 2002–2013) is also shown. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

where Sage-grouse are known to occur (Fedy et al. 2014). Across the state, climate is characterized as semiarid, and summers are relatively brief but hot (range in mean July maximum: 29° to 35°C, depending on elevation and topography) whereas winters are long and cold (range in mean January minimum, -15° to -12°C; National Oceanic and Atmospheric Administration [NOAA] 1985). Precipitation falls mostly during late spring and early summer, and can range from 178 to 406 mm annually (NOAA 1985). Lek sites analyzed in this study were located between 1111 and 2535 m in elevation.

#### *Sage-grouse population data*

We modeled Sage-grouse population trends using annual counts of males at leks conducted each spring between 2004 and 2014 by the Wyoming Game and Fish Department and partnering agencies. During the breeding season, male Sage-grouse gather at lek sites to display and court females, and counts of males at leks are important indices for monitoring Sage-grouse populations (Connelly et al. 2003). Counts at each lek were conducted three or more times a year, and we used the maximum number of males observed as an index of annual population size for each lek and year. Lek counts were conducted by trained participants following a statewide protocol that included conducting counts during periods of peak male attendance and on days without precipitation or winds  $\geq 16$  km/h (Christiansen 2012). We restricted analyses to counts conducted from 30 min before through 60 min after sunrise and between mid-March and mid-May each year (sensu Monroe et al. 2016). We further restricted analyses to leks with >1 yr of data during 2004–2014.

#### *Vegetation productivity data*

We quantified the Normalized Difference Vegetation Index (NDVI) around lek sites, which is indicative of photosynthetic capacity of a plant canopy and has been used as a proxy for vegetation productivity (Rouse et al. 1974, Tucker et al. 1985, Paruelo and Lauenroth 1995). We acquired Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI 16-d composite (MOD13Q1) data during growing seasons (1 April–31 October; Huete et al. 2002). MODIS data represent the maximum NDVI value obtained from daily atmosphere-corrected, bidirectional surface reflectance over a 16-d period at 250-m spatial resolution. The 16-d composite indices provide consistent spatial and temporal comparisons of vegetation canopy greenness, a composite property of leaf area, chlorophyll, and canopy structure. Because we were modeling Sage-grouse rates of population change during 2004–2014 with covariates lagged up to 2 yr (see *Statistical analyses*), we collected MODIS data from 2002 to 2012. During each growing season we averaged NDVI values from each composite period within 6.44 km around leks, a scale relevant to space use and population dynamics of

Sage-grouse (Walker et al. 2007, Fedy et al. 2014). For each lek and year, we then determined the maximum NDVI value recorded within a growing season (hereafter, NDVI). For each grazing allotment and year, we also determined the date of the 16-d composite period when the mean maximum NDVI value was collected (date of peak NDVI). We acquired and processed all MODIS data using R (R Development Core Team 2016).

#### *Grazing data*

To characterize grazing management, we acquired bill data (grazing fee-years 2002–2012) for allotments managed by the BLM in Wyoming from their Rangeland Administration System (RAS). Characterizing grazing management at broad spatial and temporal scales using standard finer-scale measures such as Animal Unit Month (AUM) is challenging because the impacts of livestock to vegetation can vary among vegetation communities through their adaptations to withstand herbivory (Boyd et al. 2014). Therefore, to characterize grazing levels consistently among allotments across Wyoming, we calculated a relative index of grazing level for each allotment in each year as the ratio of the reported livestock use (Billed Use AUMs) to the maximum number of AUMs authorized by the BLM (Permitted Active AUMs). Permitted Active AUMs is based on forage available to livestock on BLM administered lands and may be adjusted periodically based on soil and vegetation trends recorded from monitoring sites and evaluation of Land Health Standards to ensure rangelands are at, or trending toward, properly functioning ecosystems (BLM 2005). Grazing use at the maximum of the permit (relative grazing index level = 1.0) does not indicate an over-utilization of available forage, but rather a level of grazing that has been deemed sustainable for the allotment. The minimum grazing level was 0.0, indicating no livestock use. We provide additional details on grazing bill data in Appendix S1.

To characterize annual grazing timing, we determined start and end dates of livestock grazing from the RAS dataset for each allotment and year and then used the duration of grazing prior to peak NDVI (see *Vegetation productivity data*) to calculate the percentage of the relative grazing index level occurring before peak NDVI:

$$\text{Timing} = \frac{\text{Level of Grazing Index before peak NDVI}}{\text{Total Level of Grazing Index}} \times 100\%$$

Thus, high values of timing denoted relatively earlier grazing (before peak NDVI) whereas low values represented grazing later (after peak NDVI). We further elaborate our calculation of grazing timing in Appendix S1.

We joined the derived grazing data to spatial data of allotments from a published data series (Assal et al. 2012), converted polygons to rasters, and then averaged grazing level and timing each year from one or more

allotments occurring within 6.44-km buffers around leks using the spatialEco package in R (Evans 2016). Buffers around leks often partially overlapped areas for which we lacked grazing data, so we retained data only for a lek and year if >75% of the buffer overlapped areas within allotments with grazing data. We also restricted our analyses to leks with at least 2 yr of allotment data during 2002–2012 to allow modeling of grazing effects lagged up to 2 yr (see *Statistical analyses*). This resulted in 743 leks suitable for analysis and with buffers that overlapped at least parts of 1096 allotments. We tested the sensitivity of results to our choice of scale and threshold for buffer overlap of allotments, but we did not find that our inferences were substantially affected by either (Appendix S2).

Our analysis of annual grazing management could be confounded if grazing management is adjusted in response to allotments already in degraded condition or to prevent degradation during periods of drought. For example, population trends may suggest a negative population response to low annual grazing levels (prescribed to fulfill rangeland health standards) when Sage-grouse were actually responding to more long-term declines in rangeland condition. To investigate variation in grazing timing and level with rangeland condition, we used land health standards (LHS) evaluated for allotments in Wyoming during 2001–2008 (Veblen et al. 2011, 2014). We restricted analyses to allotments for which we had data for both grazing level (relative grazing index) and timing during the year after LHS were evaluated ( $n = 549$ ). Land health standards were categorized as either Upland, Riparian, or Biodiversity, and we combined failures attributable to current livestock grazing management and to other reasons. We then determined whether  $\geq 1$  LHS were not met and the grazing timing and level of each allotment the year following LHS evaluation. However, we could not account for allotment condition in our population models because LHS were evaluated on only 19% of our target allotments.

#### *Additional covariates*

We collected two additional metrics known to influence Sage-grouse populations: sagebrush cover (Fedy et al. 2014) and burned area (Beck et al. 2009, Coates et al. 2016). We characterized percent sagebrush cover within 6.44 km of leks from a spatial sagebrush mapping product developed based on field data collected in 2006–2007 (Homer et al. 2012). We estimated the area burned around each lek by compiling spatial and temporal data on fires in Wyoming (1994–2013) from multiple sources (Appendix S3). Fire may reduce grass and litter cover necessary for nesting, but this may recover within 4–10 yr post-fire (Beck et al. 2009), so for each year, we calculated the cumulative burned area (ha) within the last 10 yr around leks. Recovery of sagebrush after fire may require >10 yr (Beck et al. 2009), but any longer-term impacts of fire on sagebrush communities should be captured by the sagebrush covariate.

#### *Statistical analyses*

We used a state-space modeling approach within a Bayesian framework to model Sage-grouse population trends while accounting for process and observation error. This class of models can perform better than population models that do not distinguish between either source of error (de Valpine and Hastings 2002) and has been used successfully to model trends of other avian populations (Hefley et al. 2013, Ross et al. 2015). Process and observation error can be challenging to separate when modeling observed counts with a normal distribution (Dennis et al. 2006), so we assumed the maximum count of males at lek  $i$  in year  $t$  ( $y_{it}$ ) resulted from a Poisson process with mean  $N_{it}$  for the latent (unobserved) population size:

$$y_{it} \sim \text{Poisson}(N_{it}).$$

For the first year (2004), latent population size for each lek was drawn from a log-normal distribution with mean  $\mu_N$  and variance  $\sigma_N^2$ :

$$\log(N_{it}) \sim N(\mu_N, \sigma_N^2).$$

The population-level mean was drawn from a normal distribution with the log of the mean peak count from 2004 ( $\log[25.8] = 3.25$ ) for the mean and a variance of 10:  $\mu_N \sim N(3.25, 10)$ . Population size in subsequent years ( $N_{it+1}$ ) was then a function of the current population size ( $N_{it}$ ) and population growth rate ( $\lambda_{it}$ ):  $N_{it+1} = N_{it}\lambda_{it}$ , where  $\lambda_{it} = \exp(r_{it})$ . We accounted for variation in  $r_{it}$  with an intercept ( $\beta_0$ ), coefficients ( $\beta$ ), and covariates ( $\mathbf{x}_{it}$ ). In all models, we also included a process error term ( $\epsilon_{it}$ ) and error terms for allotment  $f$  ( $\delta_f$ ) and BLM field office  $g$  (management unit,  $\eta_g$ ; Fig. 1), each drawn from a normal distribution with mean 0 and variance  $\sigma^2$  (e.g.,  $\delta_f \sim N[0, \sigma_\delta^2]$ ). Process error should capture any additional variation in population trends due to factors not included in this model (Hobbs and Hooten 2015). Error terms for field office and allotment account for variation in trends within management units and among leks within the same allotment, respectively. We thus specified the process model as:

$$r_{it} = \beta_0 + \beta\mathbf{x}_{it} + \delta_f + \eta_g + \epsilon_{it}.$$

We imputed missing grazing data (7.4% and 7.1% missing for data lagged by 1 and 2 yr, respectively) from normal distributions with their respective priors for population-level mean ( $\mu$ ) and variance ( $\sigma^2$ ; Royle 2009). Before analyses, we standardized each continuous covariate to a mean of 0 and standard deviation of 1. In all models, we specified vague priors, including  $\exp(\beta_0) \sim \text{Uniform}(0, 3)$ ,  $\beta \sim \text{Uniform}(-1, 1)$ ,  $\mu \sim N(0, 100)$ , and  $\tau = \sigma^{-2} \sim \text{Gamma}(0.001, 0.001)$ . We analyzed models using JAGS (version 4.2.0; Plummer 2003) and the R packages rjags (Plummer et al. 2016) and dclone (Solymos

2016). We discarded 50000 iterations for burn-in, then sampled 100000 iterations from the posterior distribution along three parallel chains. We report additional details on model code and assessment of fit and convergence in Appendix S4.

*Model selection*

Because Sage-grouse chicks that hatch and survive to yearlings in the next year are not adequately represented in annual lek counts (Walsh et al. 2004), we considered grazing and NDVI covariates lagged by 1 and 2 yr (lag-1 and lag-2, Fig. 2). To avoid problems related to multicollinearity, we did not include in the same model covariates that were highly correlated ( $|\text{Spearman's } \rho| > 0.70$ ). This included correlations in level (relative grazing index) and NDVI between their respective lags, so we modeled effects from each lag separately. We fit models with each individual covariate for grazing level (linear and quadratic effects), timing, and NDVI, a model with sagebrush cover and burned area (fire) covariates, and a model with no covariates (null). We also constructed models with progressively more complex additive and interactive effects among grazing and NDVI covariates. In all models, we accounted for potential density dependence by specifying a covariate for the Gompertz form ( $\log[N_{it} + 1]$ ), which was used for other species (Dennis et al. 2006, Ross et al. 2015) and Sage-grouse specifically

(Garton et al. 2011). This resulted in 34 candidate models for comparison. We compared models using a score derived from  $K$ -fold cross-validation, which characterizes the predictive ability of a model based on data withheld from fitting (Hooten and Hobbs 2015). We focused our cross-validation on counts from the last year in our study (2014), which evaluates the ability of models to predict counts into the future (Link and Sauer 2016). With this approach, we randomly assigned each peak male count  $j$  to one of  $K$  groups (in this case,  $K = 10$ ), and fit the model using all counts except one left-out group. From each analysis, we calculated the log predictive density of counts in the left-out group ( $y_{jk}$ ), given data from the remaining groups ( $y_{-jk}$ ) and model  $\theta$ , and saved the mean posterior log predictive density. This was repeated for each of  $K$  folds, and we computed a score from the log predictive density multiplied by  $-2$  and summed across  $J$  counts and  $K$  groups (Hooten and Hobbs 2015)

$$\text{C-V score} = -2 \sum_{k=1}^K \sum_{j=1}^J \log \left[ y_{jk} \mid y_{-jk}, \theta \right]$$

The interpretation is that models with a lower score are relatively better at prediction than models with higher scores, and the model with the lowest score has the best predictive ability out of the models under consideration (Hooten and Hobbs 2015).

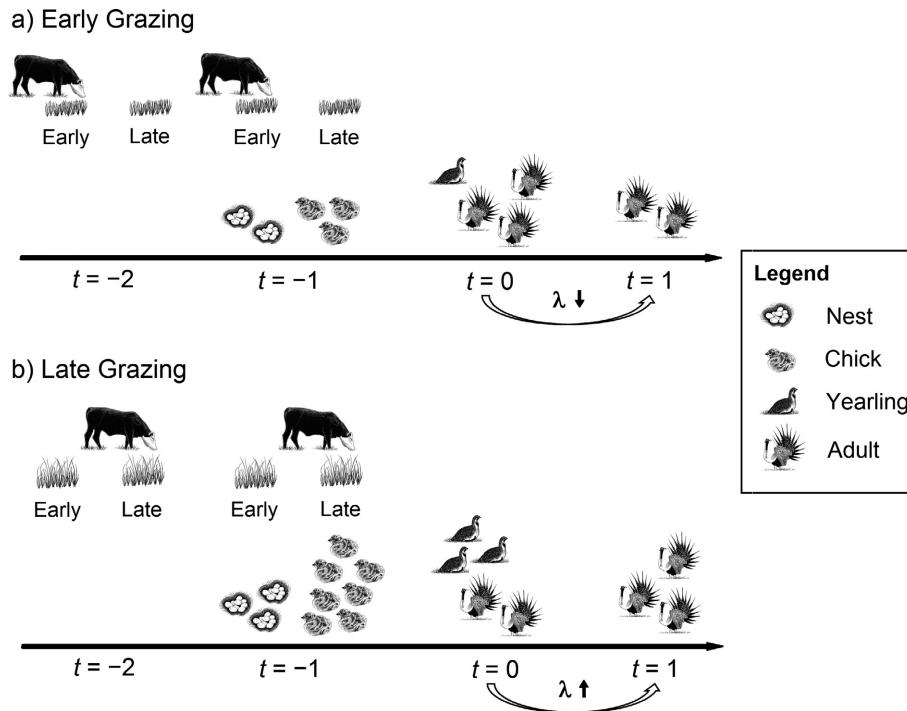


FIG. 2. Differential effects of early and late grazing (relative to date of peak vegetation productivity) at high relative grazing index level on population trends of adult male Greater Sage-grouse detected during lek counts from  $t = 0$  to  $t = 1$ . Increasing or decreasing population trends are denoted by  $\lambda \uparrow$  and  $\lambda \downarrow$ , respectively. At  $t = -1$  (lagged by 1 yr), grazing that occurred (a) early relative to the peak growing period may leave less herbaceous cover for nesting and brood-rearing Sage-grouse compared with (b) grazing later at an equivalent level.

To interpret models, we plotted predictions of  $\lambda$  based on combinations of grazing level and timing (and NDVI if an interaction with NDVI was supported). We made predictions within the range of 95% of relative grazing index and timing data, and for low (2.5th percentile) and high (97.5th percentile) NDVI data. We did not include effects from sagebrush cover or burned area (fire), and instead assumed predictions had the population mean for both covariates. We also excluded the effect of density dependence in our predictions. Additionally, we computed the proportion of iterations where the predicted population trend was greater than the intercept ( $\lambda > \exp[\beta_0]$ ), where  $P > 0.95$  indicated a high certainty that the population was increasing, whereas  $P < 0.05$  suggested high certainty that the population was declining, relative to the overall population trend. We also extended our interpretations by predicting population trends when the overall population trend was increasing  $\sim 10\%$  per year ( $\beta_0 = 0.1$ ), stable ( $\beta_0 = 0.0$ ), or declining  $\sim 10\%$  per year ( $\beta_0 = -0.1$ ). We then computed the proportion of iterations where the predicted population trend was greater than stable ( $\lambda > \exp[0.0]$ ).

*Land health standard analysis*

To understand potential confounding effects of manager responses to an allotment failing to meet LHS, we modeled failure of  $\geq 1$  LHS by allotment  $i$  ( $y_i = 1$ ) as the outcome of a Bernoulli process with probability ( $p_i$ ):  $y_i \sim \text{Bernoulli}(p_i)$ . We specified covariates for  $p_i$  on the logit scale for grazing management the year after LHS were evaluated, thus evaluating whether allotments with different grazing timings and levels (relative grazing index) were more likely to have failed  $\geq 1$  LHS the previous year. We also included a random error term for BLM field office. We again computed  $K$ -fold cross-validation scores based on log predictive densities of the left-out responses ( $y_{jk}$ ), given the remaining data ( $y_{-jk}$ ) and model  $\theta$ , to compare models of increasing complexity, including grazing level, timing, level + timing, and level  $\times$  timing. We specified vague priors similar to those in our state-space model, and models were run using JAGS from R. We sampled from the posterior distribution along three parallel chains for 30000 iterations after discarding 5000 iterations for burn-in. We report mean parameter estimates and their 95% credible intervals, and we interpreted parameter estimates using odds ratios.

RESULTS AND DISCUSSION

When modeling Sage-grouse population trends in response to grazing management and vegetation productivity, we found lag-1 effects were generally supported over lag-2 effects (Table 1). The best-predicting model included a two-way interaction between level of relative grazing index (quadratic) and grazing timing (each lag-1), although this model was ranked only slightly above a

TABLE 1. Model selection results from 10-fold cross-validation (C-V) scores (Hooten and Hobbs 2015) of state-space models for lek counts of male Greater Sage-grouse in Wyoming (2004–2014) and covariates measured within 6.44 km of lek sites.

Model	C-V score
Level <sub>lag-1</sub> <sup>2</sup> $\times$ Timing <sub>lag-1</sub> + NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7024.74
Level <sub>lag-1</sub> <sup>2</sup> $\times$ Timing <sub>lag-1</sub> $\times$ NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7026.45
Level <sub>lag-1</sub> $\times$ Timing <sub>lag-1</sub> $\times$ NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7032.82
Level <sub>lag-1</sub> $\times$ NDVI <sub>lag-1</sub> + Timing <sub>lag-1</sub> + Sagebrush + Burned area	7038.00
Level <sub>lag-1</sub> $\times$ Timing <sub>lag-1</sub> + NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7041.63
Sagebrush + Burned area	7041.81
Level <sub>lag-1</sub> <sup>2</sup> $\times$ NDVI <sub>lag-1</sub> + Timing <sub>lag-1</sub> + Sagebrush + Burned area	7042.80
(Level <sub>lag-1</sub> + Timing <sub>lag-1</sub> ) $\times$ NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7045.26
Level <sub>lag-1</sub> + Timing <sub>lag-1</sub> + NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7048.07
(Level <sub>lag-1</sub> <sup>2</sup> + Timing <sub>lag-1</sub> ) $\times$ NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7049.39
Level <sub>lag-1</sub> <sup>2</sup> + Timing <sub>lag-1</sub> + NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7050.97
Level <sub>lag-1</sub> + Timing <sub>lag-1</sub> $\times$ NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7053.01
Level <sub>lag-1</sub> <sup>2</sup> + Timing <sub>lag-1</sub> $\times$ NDVI <sub>lag-1</sub> + Sagebrush + Burned area	7054.18
Level <sub>lag-1</sub>	7054.96
Level <sub>lag-1</sub> <sup>2</sup>	7059.12
Level <sub>lag-2</sub>	7059.13
Timing <sub>lag-1</sub>	7059.69
Level <sub>lag-2</sub> <sup>2</sup>	7065.90
Null	7069.91

Notes: Grazing level (linear and quadratic), timing, and vegetation productivity (NDVI) covariates were lagged by 1 or 2 yr. Lower scores indicate models with relatively better predictive ability than models with higher scores. We present only models ranked above the null model (18 out of 33), and the null for comparison (with only an intercept, density dependence, and random terms for allotment and field office).

three-way interaction model among grazing level, timing, and NDVI (Table 1). Given that one of our objectives was to evaluate interactions between grazing management and vegetation productivity, we interpreted both the best- and second-best-ranked models while acknowledging model selection uncertainty. In both models, we estimated a positive population response to sagebrush cover, whereas effect of burned area was not supported (Tables 2 and 3). We also estimated a negative effect from density dependence, and the overall population trend ( $\beta_0$ ) indicated a 6% annual decline, although credible intervals overlapped 0. Plotting interactions between grazing timing and level from the best-predicting

TABLE 2. Mean, standard deviation, and 95% credible intervals for posterior samples of parameters from the best-predicting state-space model for lek counts of male Greater Sage-grouse in Wyoming (2004–2014) and covariates† measured within 6.44 km of lek sites.

Parameter	Mean	SD	95% credible interval	
			Lower	Upper
$\beta_0$	-0.061	0.037	-0.131	0.011
Level <sub>lag-1</sub>	-0.003	0.015	-0.031	0.026
Level <sub>lag-1</sub> <sup>2</sup>	-0.014	0.008	-0.030	0.002
Timing <sub>lag-1</sub>	-0.010	0.013	-0.035	0.016
Level <sub>lag-1</sub> × Timing <sub>lag-1</sub>	-0.033	0.013	-0.059	-0.007
Level <sub>lag-1</sub> <sup>2</sup> × Timing <sub>lag-1</sub>	-0.020	0.008	-0.034	-0.005
NDVI <sub>lag-1</sub>	-0.008	0.014	-0.036	0.021
Sagebrush	0.014	0.012	-0.009	0.037
Burned area	-0.001	0.010	-0.020	0.018
Density dependence	-0.030	0.009	-0.047	-0.013
$\sigma_{\text{fieldoffice}}$	0.063	0.024	0.029	0.122
$\sigma_{\text{allotment}}$	0.059	0.017	0.026	0.093
$\sigma_{\text{process}}$	0.546	0.011	0.524	0.569
$\mu_N$	2.810	0.082	2.648	2.969
$\sigma_N$	1.776	0.082	1.622	1.942

Note: Parameters are  $\beta_0$ , intercept, or mean annual rate of population change; Level<sub>lag-1</sub>, relative grazing index representing the ratio of the reported livestock use (Billed Use animal unit months [AUMs]) to the maximum number of AUMs authorized by the BLM (Permitted Active AUMs), with 1-yr lag; Timing<sub>lag-1</sub>, percentage of relative grazing index occurring before date of peak NDVI, with 1-yr lag; NDVI<sub>lag-1</sub>, maximum annual vegetation productivity, with 1-yr lag; Sage, percent sagebrush cover; Burned area, area (within 6.44 km of lek) burned cumulatively during previous 10 yr; density dependence, Gompertz form ( $\log[N_{it} + 1]$  for lek  $i$  and year  $t$ );  $\sigma$ , standard deviation for random terms;  $\mu_N$ , mean initial population size (log-scale);  $\sigma_N$ , standard deviation for initial population size (log-scale).

†Covariates were standardized (subtracting the mean, dividing by the standard deviation of each covariate sample).

model indicated that at intermediate to low levels of the relative grazing index (<0.8), predicted Sage-grouse population trends did not vary with grazing timing and were similar to the overall population trend (Fig. 3). However, at higher levels (>0.8), where permittees were grazing near the maximum allowable number of AUMs, populations declined when grazing timing was early (>20% of relative grazing index level occurred before peak NDVI), whereas populations increased when grazing occurred later (timing <10%). The varying effects of grazing level with timing could reflect direct impacts to herbaceous cover and forage for nesting and brood-rearing Sage-grouse because mean date of peak NDVI among our study sites during 2002–2012 was 30 May (SD = 24 d) and so earlier grazing would coincide with Sage-grouse nesting (Holloran et al. 2005). This trend also may reflect more long-term effects to forage species, because excessive grazing of perennial cool-season (C<sub>3</sub>) grasses during their peak growing periods can reduce long-term production potential (Laycock 1967, Bork et al. 1998). Grazing early (before and during peak vegetation productivity) may

increase mortality of grasses and forbs, whereas grazing later may have less of an impact on these plants (Laycock 1967, Bork et al. 1998, Adler et al. 2005). Grazing later also may stimulate subsequent growth of grasses and forbs if cattle remove standing dead vegetation (Willms et al. 1979) or reduce shrub coverage (Vallentine 2001). Mechanistically, these results suggest grazing is directly impacting vegetation growth and availability of herbaceous cover and forage for nesting and brood-rearing Sage-grouse, thereby altering recruitment of birds for population counts in subsequent years (Fig. 2). To our knowledge this is the first analysis, at broad scales, to support previous reviews suggesting the reduction or delay of grazing may be compatible with Sage-grouse populations (Crawford et al. 2004, Cagney et al. 2010, Boyd et al. 2014).

Predicted effects of grazing management on Sage-grouse also should be considered relative to changes in the overall rate of population change ( $\beta_0$ ). For example, using the best-predicting model (two-way interaction between level of relative grazing index and timing), we predicted population trends from late-season, high grazing levels that were positive when the overall population trend was stable ( $\beta_0 = 0.0$ ; Appendix S5: Fig. S1b) or that did not differ from stable when the overall population trend was

TABLE 3. Mean, standard deviation, and 95% credible intervals for posterior samples of parameters from the second-best predicting state-space model for lek counts of male Greater Sage-grouse in Wyoming (2004–2014) and covariates† measured within 6.44 km of lek sites.

Parameter	Mean	SD	95% credible interval	
			Lower	Upper
$\beta_0$	-0.058	0.035	-0.127	0.012
Level <sub>lag-1</sub>	-0.015	0.017	-0.047	0.018
Level <sub>lag-1</sub> <sup>2</sup>	-0.012	0.009	-0.030	0.006
Timing <sub>lag-1</sub>	-0.007	0.014	-0.034	0.019
Level <sub>lag-1</sub> × Timing <sub>lag-1</sub>	-0.035	0.015	-0.064	-0.007
Level <sub>lag-1</sub> <sup>2</sup> × Timing <sub>lag-1</sub>	-0.025	0.011	-0.046	-0.004
Level <sub>lag-1</sub> × NDVI <sub>lag-1</sub>	-0.012	0.015	-0.041	0.016
Level <sub>lag-1</sub> <sup>2</sup> × NDVI <sub>lag-1</sub>	0.010	0.008	-0.006	0.026
Timing <sub>lag-1</sub> × NDVI <sub>lag-1</sub>	0.017	0.015	-0.013	0.048
Level <sub>lag-1</sub> × Timing <sub>lag-1</sub> × NDVI <sub>lag-1</sub>	0.007	0.015	-0.023	0.036
Level <sub>lag-1</sub> <sup>2</sup> × Timing <sub>lag-1</sub> × NDVI <sub>lag-1</sub>	-0.005	0.009	-0.022	0.012
NDVI <sub>lag-1</sub>	-0.015	0.016	-0.045	0.016
Sagebrush	0.012	0.012	-0.011	0.035
Burned area	-0.001	0.010	-0.020	0.018
Density dependence	-0.031	0.009	-0.048	-0.014
$\sigma_{\text{fieldoffice}}$	0.058	0.023	0.026	0.113
$\sigma_{\text{allotment}}$	0.059	0.017	0.027	0.093
$\sigma_{\text{process}}$	0.547	0.011	0.524	0.569
$\mu_N$	2.812	0.082	2.650	2.973
$\sigma_N$	1.778	0.084	1.620	1.950

Note: Parameter definitions are listed as a footnote in Table 2. †Covariates were standardized (subtracting the mean, dividing by the standard deviation of each covariate sample).

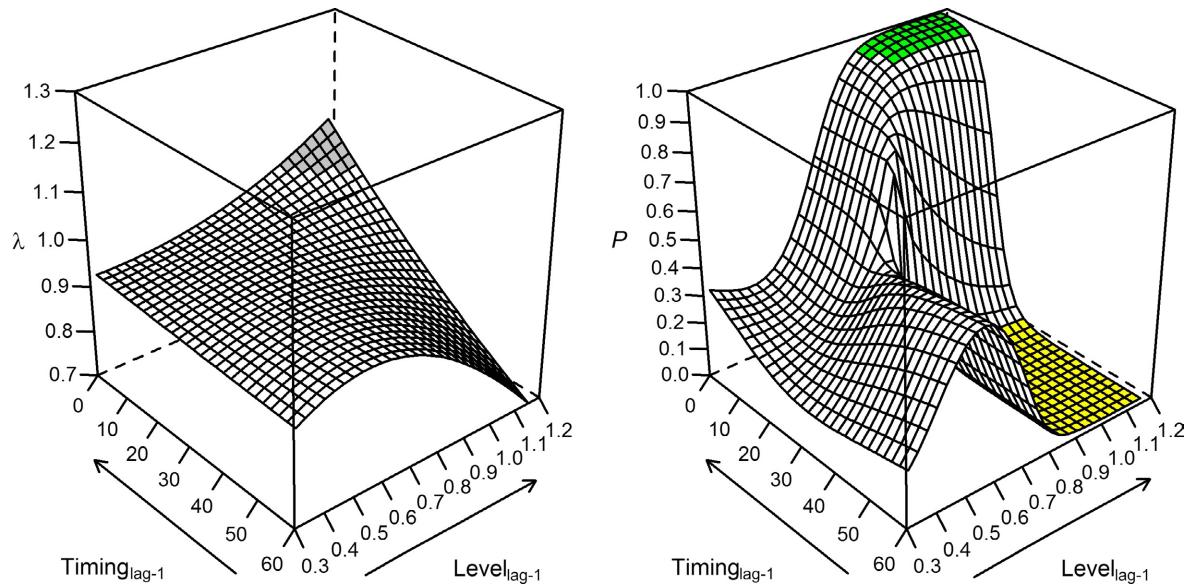


FIG. 3. Predicted interactive effects (each lagged by 1 yr) of grazing level (ratio of the reported livestock use [Billed Use AUMs] to the maximum number of AUMs authorized by the BLM [Permitted Active AUMs]) and timing (% of grazing index level occurring before date of peak NDVI) on population rate of change ( $\lambda$ ) of male Greater Sage-grouse attending leks in grazing allotments across Wyoming, 2004–2014. We highlight regions in gray where mean predicted rate of population change was increasing ( $\lambda > 1.0$ ). We also present the probability that  $\lambda$  is increasing ( $P[\lambda > \exp(\beta_0)] > 0.95$ ; green) and  $\lambda$  is decreasing ( $P[\lambda > \exp(\beta_0)] < 0.05$ ; yellow), relative to the overall population trend ( $\beta_0$ ). Covariates were measured within 6.44 km of lek sites, and responses were predicted from 95% of the range of grazing level (0.3–1.2) and timing (0–60%) during our study. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

decreasing 10% annually ( $\beta_0 = -0.1$ ; Appendix S5: Fig. S1c). Conversely, the same grazing level occurring earlier corresponded with decreasing trends under all scenarios (Appendix S5: Figs S1a–c). Intermediate to low grazing levels, irrespective of timing, did not differ from the overall population trend in any scenario.

Interestingly, based on the second-best predicting model (three-way interaction with NDVI), we found similar relationships as the best-predicting model for low vegetation productivity sites (Fig. 4a; Appendix S5: Fig. S2). However, for high productivity sites the model predicted that intermediate grazing levels with early timing was preferable to grazing later or at higher levels (Fig. 4b). Implications of this pattern are apparent as the overall population trend ( $\beta_0$ ) varied (Appendix S5: Fig. S3). In high productivity sites when the overall population trend was increasing (Appendix S5: Fig. S3a), intermediate grazing levels later in the growing season corresponded with a stable population whereas grazing at the same level but early was associated with population increases. When the overall population trend was decreasing (Appendix S5: Fig. S3c), grazing late at intermediate levels led to declining population trends, whereas earlier grazing corresponded with stable population trends. Variation in effects of grazing timing with vegetation productivity may relate to the ability of forages to withstand and recover following defoliation. Patterns in productivity across Wyoming (Fig. 1) correspond to regional distributions of moisture availability as well as more local variation in topography, such as upland and riparian areas (Knight

1994). In contrast to low-productivity sites, early-season grazing in moister sites at intermediate (but not high) levels of the relative grazing index may allow adequate time for plant regrowth and could result in greater production over subsequent years than if grazing occurs later (Boyd and Svejcar 2004, Mousel et al. 2011, Stephenson et al. 2015). Patterns revealed by our population models may therefore provide insight into grazing management across a larger gradient of vegetation productivity than can be inferred from more fine-scale studies or from simpler models without interactions between grazing management and vegetation productivity.

Greater herbaceous cover at fine scales may increase Sage-grouse reproductive success (Holloran et al. 2005, Gregg and Crawford 2009), and despite finding important links between grazing and population trends, our results did not indicate that reductions in grazing levels (below the maximum permitted amount) would necessarily benefit Sage-grouse. On the contrary, in the best-predicting model (and the second-best model when predicting for low NDVI sites), we found that higher grazing levels after the peak in vegetation production corresponded with a positive response from Sage-grouse populations. However, it is important to emphasize that in our study high levels of the relative grazing index do not necessarily equate with overutilization of livestock forages, but instead represent grazing near the maximum allowable AUM set by the BLM, which is intended to minimize negative long-term impacts to forage species (BLM 2005). Furthermore, grazing may increase heterogeneity in structure and composition of

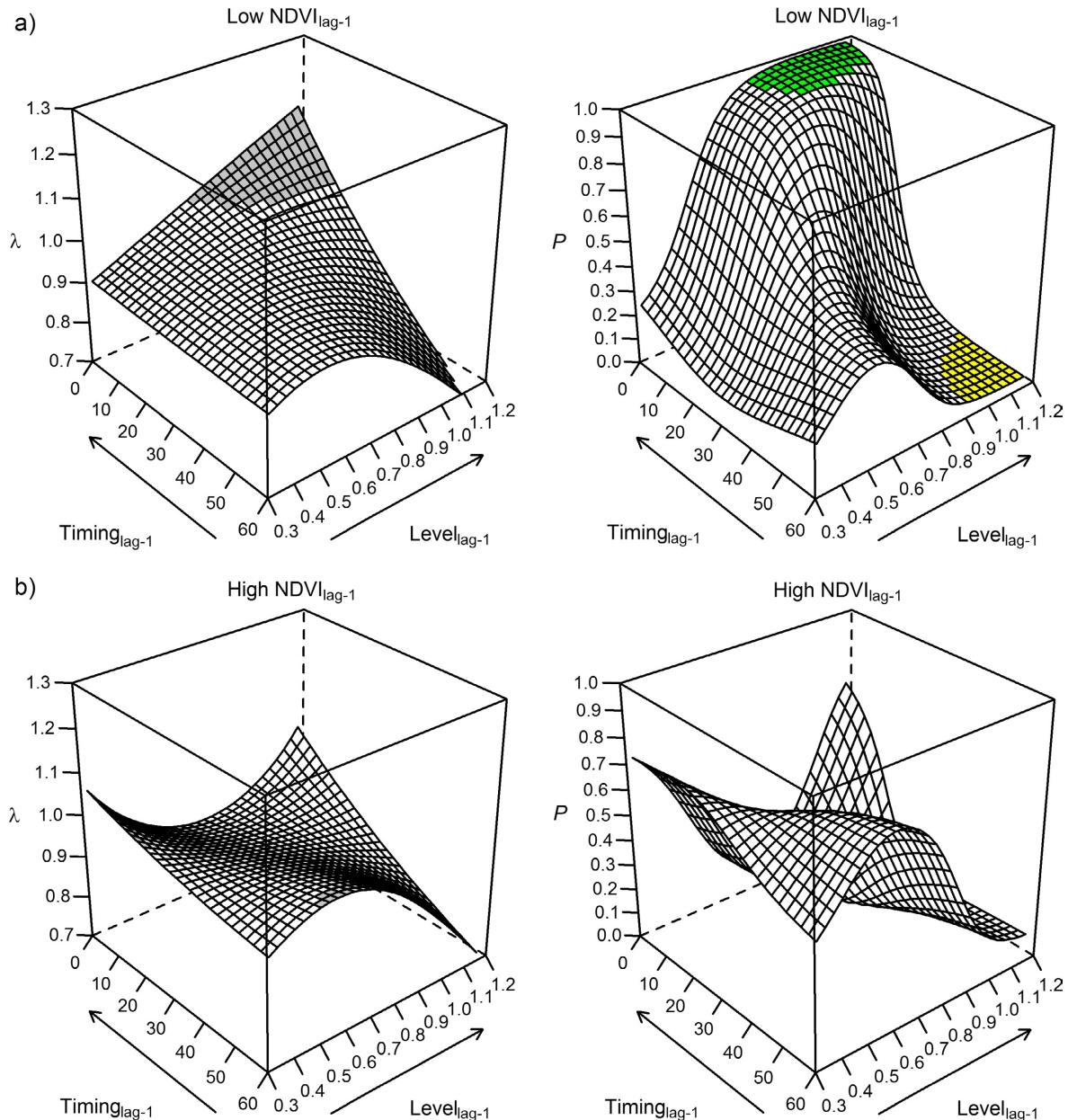


FIG. 4. Predicted interactive effects (each lagged by 1 yr) of grazing level and timing at (a) low and (b) high vegetation productivity (NDVI) sites on population rate of change ( $\lambda$ ) of male Greater Sage-grouse attending leks in grazing allotments across Wyoming, 2004–2014. We highlight regions in gray where mean predicted rate of population change was increasing ( $\lambda > 1.0$ ). We also present the probability that  $\lambda$  is increasing ( $P[\lambda > \exp(\beta_0)] > 0.95$ ; green) and  $\lambda$  is decreasing ( $P[\lambda > \exp(\beta_0)] < 0.05$ ; yellow), relative to the overall population trend ( $\beta_0$ ). Covariates were measured within 6.44 km of lek sites, and responses were predicted from 95% of the range of grazing level (0.3–1.2) and timing (0–60%), and low (NDVI = 0.2) and high (NDVI = 0.5) vegetation productivity during our study. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

vegetation, which could benefit Sage-grouse populations if females select sites to maximize fitness beyond the nesting stage (Streby et al. 2014). For instance, if grazing increases forb coverage (Smith et al. 1979, Evans 1986, Biondini and Manske 1996, Manley et al. 1997), enhanced foraging opportunities for Sage-grouse broods (Evans 1986, Aldridge and Boyce 2008) may increase chick survival (Gregg and Crawford 2009). Thus, caution is warranted when

generalizing results from previous fine-scale habitat studies when predicting effects of grazing management on Sage-grouse at broader scales (Wiens et al. 1986, Milchunas and Lauenroth 1993, Stohlgren et al. 1999).

An alternative to our vegetation heterogeneity-based interpretation above is that a lack of positive responses to low levels of the relative grazing index may reflect livestock management in allotments with degraded rangeland

TABLE 4. Model selection results from 10-fold cross-validation scores (Hooten and Hobbs 2015) for modeling the probability of allotments failing  $\geq 1$  Land Health Standards (LHS) given the relative grazing index level and timing the following year.

Model	C-V score
Level	1018.35
Level + Timing	1028.64
Level $\times$ Timing	1042.07
Null	1132.00
Timing	1139.74

*Note:* We specified a random term for field office in all models. We included a null model (with only an intercept and random term for field office) for comparison.

conditions. We found the model with a negative effect of grazing level ( $\beta = -0.48$ , 95% credible interval =  $-0.73$ ,  $-0.23$ ) was best supported for predicting the probability of failing  $\geq 1$  LHS (Table 4), indicating a tendency toward reduced grazing levels after an allotment was identified to have failed  $\geq 1$  LHS. Therefore, the lack of a positive response to lower levels of the relative grazing index may be attributed, at least in part, to correlations with management in response to degraded rangeland condition rather than causative effects from reduced annual grazing levels. Nevertheless, the estimated effect was modest, with a 2.86 times greater odds of failing  $\geq 1$  LHS (95% CrI = 1.62, 4.72) for a 0.5 reduction in the relative grazing index (e.g., from a mean grazing level of 0.9 to a grazing level of 0.4).

#### CONCLUSIONS

Given the extent and distribution of livestock grazing on public lands across the western United States (BLM 2013), records of livestock use could be an invaluable resource for examining broad-scale effects of grazing management for a variety of ecological and economic questions. Our study suggests livestock grazing may have both positive and negative effects to Sage-grouse population trends depending on the timing and level of grazing. Furthermore, modifications in grazing management could attenuate declines or even stabilize otherwise declining Sage-grouse populations, so livestock could be one tool among a number of management actions for maintaining or restoring habitat for this species. In addition, we found some support for the hypothesis that responses to grazing vary with local vegetation productivity, which suggests that a generalized understanding of managing livestock for species such as Sage-grouse may be applied incorrectly without considering vegetation productivity. These results also suggest the benefit of a broad-scale approach when evaluating effects of livestock management by revealing patterns that may not be readily inferred from more fine-scale studies, which could then inform sustainable grazing management across sagebrush-dominated rangelands. It is important to note that altering the timing or level of grazing may have economic implications for livestock producers, at least in the short term, including the need to purchase alternative

sources of forage or reduce herd sizes (Boyd et al. 2014). Still, grazing management that reduces or avoids impacts to less grazing-tolerant herbaceous plants as they approach their peak productivity could increase forage production potential in the long-term (Pyke 2011) and thereby benefit both ranching operations and species such as Sage-grouse.

#### ACKNOWLEDGMENTS

The U.S. Geological Survey (USGS) and the Wyoming Landscape Conservation Initiative provided support for this work. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We are grateful to T. J. Christiansen and M. S. O'Donnell for their help with accessing the Wyoming lek count data. M. S. O'Donnell, D. J. Manier, and D. A. Ignizio also helped compile our fire data. We thank K. C. Monroe, T.-V. Bui, N. T. Hobbs, L. L. Jackson, M. G. Karl, R. Mayberry, and two anonymous reviewers for providing comments that improved this manuscript. We also thank M. B. Hooten and K. M. Broms for advice on model selection. We obtained NDVI data from the Land Processes Distributed Active Archive Center (LP DAAC), located at the USGS Earth Resources Observation and Science (EROS) Center. This research used resources provided by the Core Science Analytics, Synthesis, and Libraries (CSASL) Advanced Research Computing (ARC) group at the U.S. Geological Survey.

#### LITERATURE CITED

- Adler, P. B., D. G. Milchunas, W. K. Lauenroth, O. E. Sala, and I. C. Burke. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41:653–663.
- Adler, P. B., D. G. Milchunas, O. E. Sala, I. C. Burke, and W. K. Lauenroth. 2005. Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonian steppe. *Ecological Applications* 15:774–792.
- Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: combining survival and selection when assessing wildlife–habitat relationships. *Israel Journal of Ecology and Evolution* 54:389–419.
- Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* 29:261–299.
- Assal, T. J., K. E. Veblen, M. A. Farinha, C. L. Aldridge, M. L. Casazza, and D. A. Pyke. 2012. Data resources for range-wide assessment of livestock grazing across the sagebrush biome. U.S. Geological Survey Data Series 690. U.S. Geological Survey, Reston, Virginia, USA.
- Beck, J. L., J. W. Connelly, and K. P. Reese. 2009. Recovery of Greater Sage-grouse habitat features in Wyoming Big Sagebrush following prescribed fire. *Restoration Ecology* 17:393–403.
- Biondini, M. E., and L. Manske. 1996. Grazing frequency and ecosystem processes in a northern mixed prairie, USA. *Ecological Applications* 6:239–256.
- Bork, E. W., N. E. West, and J. W. Walker. 1998. Cover components on long-term seasonal sheep grazing treatments in Three-tip sagebrush steppe. *Journal of Range Management* 51:293–300.
- Boyd, C. S., J. L. Beck, and J. A. Tanaka. 2014. Livestock grazing and Sage-grouse habitat: impacts and opportunities. *Journal of Rangeland Applications* 1:58–77.

- Boyd, C. S., and T. J. Svejcar. 2004. Regrowth and production of herbaceous riparian vegetation following defoliation. *Rangeland Ecology and Management* 57:448–454.
- Brown, J. H., and W. McDonald. 1995. Livestock grazing and conservation on southwestern rangelands. *Conservation Biology* 9:1644–1647.
- Bureau of Land Management (BLM). 2005. Land use planning handbook. BLM manual H-1601-1, Rel. 1-1693. [https://www.blm.gov/style/medialib/blm/ak/aktest/planning/planning\\_general.Par.65225.File.dat/blm\\_lup\\_handbook.pdf](https://www.blm.gov/style/medialib/blm/ak/aktest/planning/planning_general.Par.65225.File.dat/blm_lup_handbook.pdf)
- Bureau of Land Management (BLM). 2013. Rangeland inventory, monitoring, and evaluation reports. BLM National Operations Center, Denver, Colorado, USA. [http://www.blm.gov/wo/st/en/prog/more/rangeland\\_management/rangeland\\_inventory.html](http://www.blm.gov/wo/st/en/prog/more/rangeland_management/rangeland_inventory.html)
- Cagney, J., E. Bainter, B. Budd, T. Christiansen, V. Herren, M. Holloran, B. Rashford, M. Smith, and J. Williams. 2010. Grazing influence, objective development, and management in Wyoming's Greater Sage-grouse habitat. Publication B-1203, University of Wyoming Cooperative Extension Service, Laramie, Wyoming, USA.
- Christiansen, T. 2012. Chapter 12: Sage grouse (*Centrocercus urophasianus*). Pages 1–53 in S. A. Tessman, and J. R. Bohné, editors. Handbook of biological techniques. Third edition. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.
- Coates, P. S., M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, T. Kroger, E. J. Blomberg, C. A. Hagen, and M. L. Casazza. 2016. Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. *Proceedings of the National Academy of Sciences USA* 113:12745–12750.
- 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.
- Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of Sage-grouse and Sage-grouse habitat. *Rangeland Ecology and Management* 57:2–19.
- de Valpine, P., and A. Hastings. 2002. Fitting population models incorporating process noise and observation error. *Ecological Monographs* 72:57–76.
- Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. 2006. Estimating density dependence, process noise, and observation error. *Ecological Monographs* 76:323–341.
- Evans, C. C. 1986. The relationship of cattle grazing to sage grouse use of meadow habitat on the Sheldon National Wildlife Refuge. Thesis. University of Nevada, Reno, Nevada, USA.
- Evans, J. 2016. spatialEco: Spatial analysis and modelling. R package version 0.1–5. <http://cran.r-project.org/package=spatialEco>
- Fedy, B. C., et al. 2014. Habitat prioritization across large landscapes, multiple seasons, and novel areas: an example using Greater Sage-grouse in Wyoming. *Wildlife Monographs* 190:1–39.
- Foster, C. N., P. S. Barton, and D. B. Lindenmayer. 2014. Effects of large native herbivores on other animals. *Journal of Applied Ecology* 51:929–938.
- Fuhlendorf, S. D., D. M. Engle, R. D. Elmore, R. F. Limb, and T. G. Bidwell. 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecology and Management* 65:579–589.
- 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. *Studies in Avian Biology* 38:293–381.
- Gregg, M. A., and J. A. Crawford. 2009. Survival of Greater Sage-grouse chicks and broods in the Northern Great Basin. *Journal of Wildlife Management* 73:904–913.
- Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis of Greater Sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. *Wildlife Biology* 13(sp1):42–50.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.
- 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.
- Hobbs, N. T., and M. B. Hooten. 2015. Bayesian models: a statistical primer for ecologists. Princeton University Press, Princeton, New Jersey, USA.
- 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.
- Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. J. Schnell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA: laying a foundation for monitoring. *International Journal of Applied Earth Observation and Geoinformation* 14:233–244.
- Hooten, M. B., and N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. *Ecological Monographs* 85: 3–28.
- Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83:195–213.
- Knight, D. H. 1994. Mountains and plains: the ecology of Wyoming landscapes. Yale University, New Haven, Connecticut, USA.
- Laycock, W. A. 1967. How heavy grazing and protection affect sagebrush-grass ranges. *Journal of Range Management* 20:206–213.
- Link, W. A., and J. R. Sauer. 2016. Bayesian cross-validation for model evaluation and selection, with application to the North American Breeding Bird Survey. *Ecology* 97: 1746–1758.
- Manley, W. A., R. H. Hart, M. J. Samuel, M. A. Smith, J. W. Waggoner Jr., and J. T. Manley. 1997. Vegetation, cattle, and economic responses to grazing strategies and pressures. *Journal of Range Management* 50:638–646.
- Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* 134:1–19.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327–366.
- Milchunas, D. G., W. K. Lauenroth, and I. C. Burke. 1998. Livestock grazing: animal and plant biodiversity of short-grass steppe and the relationship to ecosystem function. *Oikos* 83:65–74.
- Monroe, A. P., D. R. Edmunds, and C. L. Aldridge. 2016. Effects of lek count protocols on Greater Sage-grouse population trend estimates. *Journal of Wildlife Management* 80:667–678.
- Mousel, E. M., W. H. Schacht, P. E. Reece, A. E. Herron, and A. Koehler. 2011. Vegetation production responses to October grazing in the Nebraska Sandhills. *Rangeland Ecology and Management* 64:208–214.
- 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, Detroit, Michigan, USA. <http://www.wrcc.dri.edu/climate-narratives/>
- Paruelo, J. M., and W. K. Lauenroth. 1995. Regional patterns of normalized difference vegetation index in North American shrublands and grasslands. *Ecology* 76:1888–1898.
- Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269:331–334.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1–10 in K. Hornik, F. Leisch, and A. Zeileis, editors. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, March 20–22 2003, Vienna, Austria. <http://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf>
- Plummer, M., A. Stukalov, and M. Denwood. 2016. rjags: Bayesian graphical models using MCMC. R package version 4-5. <http://cran.r-project.org/web/packages/rjags/index.html>
- Pyke, D. A. 2011. Restoring and rehabilitating sagebrush habitats. *Studies in Avian Biology* 38:531–548.
- R Development Core Team. 2016. R: a language and environment for statistical computing, version 3.3.1. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Ross, B. E., M. B. Hooten, J.-M. DeVink, and D. N. Koons. 2015. Combined effects of climate, predation, and density dependence on greater and lesser scaup population dynamics. *Ecological Applications* 25:1606–1617.
- Rouse, J. W., R. H. Hass, J. A. Schell, D. W. Deering, and J. C. Harlan. 1974. Monitoring the vernal advancement of retrogradation (green wave effect) of natural vegetation. Type III, Final report. NASA/GSFC, Greenbelt, Maryland, USA.
- Royle, J. A. 2009. Analysis of capture–recapture models with individual covariates using data augmentation. *Biometrics* 65:267–274.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.
- Schroeder, M. A., et al. 2004. Distribution of Sage-grouse in North America. *Condor* 106:363–376.
- Smith, M. A., J. C. Malechek, and K. O. Fulgham. 1979. Forage selection by mule deer on winter range grazed by sheep in spring. *Journal of Range Management* 32:40–45.
- Solymos, P. 2016. dclone: data cloning and MCMC tools for maximum likelihood methods. R package version 2.1–1. <http://cran.r-project.org/web/packages/dclone/index.html>
- Stephenson, M. B., W. H. Schacht, J. D. Volesky, K. M. Eskridge, and D. Bauer. 2015. Time of grazing effect on subsequent-year standing crop in the Eastern Nebraska Sandhills. *Rangeland Ecology and Management* 68:150–157.
- Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* 9:45–64.
- Streby, H. M., J. M. Refsnider, and D. E. Andersen. 2014. Redefining reproductive success in songbirds: moving beyond the nest success paradigm. *Auk* 131:718–726.
- Tucker, C. J., C. L. Vanpraet, M. J. Sharman, and G. Van Ittersum. 1985. Satellite remote sensing of total herbaceous biomass production in the Senegalese Sahel: 1980–1984. *Remote Sensing of Environment* 17:233–249.
- Vallentine, J. F. 2001. *Grazing management*. Second edition. Academic Press, San Diego, California, USA.
- Veblen, K. E., D. A. Pyke, C. L. Aldridge, M. L. Casazza, T. J. Assal, and M. A. Farinha. 2011. Range-wide assessment of livestock grazing across the sagebrush biome. U.S. Geological Survey open-file report 2011–1263. U.S. Geological Survey, Reston, Virginia, USA.
- Veblen, K. E., D. A. Pyke, C. L. Aldridge, M. L. Casazza, T. J. Assal, and M. A. Farinha. 2014. Monitoring of livestock grazing effects on Bureau of Land Management land. *Rangeland Ecology and Management* 67:68–77.
- Vermeire, L. T., R. K. Heitschmidt, and M. R. Haferkamp. 2008. Vegetation response to seven grazing treatments in the Northern Great Plains. *Agriculture, Ecosystems and Environment* 125:111–119.
- Vickery, J. A., J. R. Tallwin, R. E. Feber, E. J. Asteraki, P. W. Atkinson, R. J. Fuller, and V. K. Brown. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* 38:647–664.
- Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater Sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management* 71:2644–2654.
- 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.
- Wiens, J. A., J. T. Rottenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. *Ecology* 67:365–376.
- Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1979. Interactions between mule deer and cattle on big sagebrush range in British Columbia. *Journal of Range Management* 32:299–304.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1512/full>

## DATA AVAILABILITY

Data associated with this work are available in ScienceBase at <https://doi.org/10.5066/F70K26RK>