



ORIGINAL RESEARCH

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# Large-scale wildfire reduces population growth in a peripheral population of sage-grouse

Ian F. Dudley<sup>1,2,3</sup>, Peter S. Coates<sup>1\*</sup> Brian G. Prochazka<sup>1</sup>, Shawn T. O'Neil<sup>1</sup>, Scott Gardner<sup>3</sup> and David J. Delehanty<sup>2</sup>

## Abstract

**Background:** Drastic increases in wildfire size and frequency threaten western North American sagebrush (*Artemesia* L. spp.) ecosystems. At relatively large spatial scales, wildfire facilitates type conversion of sagebrush-dominated plant communities to monocultures of invasive annual grasses (e.g., *Bromus tectorum* L.). Annual grasses provide fine fuels that promote fire spread, contributing to a positive grass–fire feedback cycle that affects most sagebrush ecosystems, with expected habitat loss for resident wildlife populations. Greater sage-grouse (*Centrocercus urophasianus* Bonaparte, 1827) are sagebrush obligate species that are indicators of sagebrush ecosystem function because they rely on different components of sagebrush ecosystems to meet seasonal life history needs. Because wildfire cannot be predicted, chronic impacts of wildfire on sage-grouse populations have been largely limited to correlative studies. Thus, evidence from well-designed experiments is needed to understand the specific mechanisms by which wildfire is detrimental to sage-grouse population dynamics.

**Results:** Following a significant wildfire event in the southwest periphery of sage-grouse range, we implemented a before-after-control-impact study with long-term paired (BACIP) datasets of male sage-grouse surveyed from traditional breeding grounds (leks) within and outside the wildfire boundary. We estimated sage-grouse population rate of change in apparent abundance ( $\hat{\lambda}$ ) at burned and unburned areas before and after wildfire and derived BACIP ratios, which provide controlled evidence of wildfire impact. We found that  $\hat{\lambda}$  at leks within the wildfire boundary decreased approximately 16% relative to leks at control sites. Furthermore, we estimated a 98.5% probability that the observed change in  $\hat{\lambda}$  could be attributed to the wildfire.

**Conclusions:** We demonstrated adverse wildfire impacts on sage-grouse population growth using an experimental BACIP design, which disentangled the effect of wildfire disturbance from natural population fluctuations. Our results underscore the importance of active and comprehensive management actions immediately following wildfire (i.e., seeding coupled with planting sagebrush), that might offset short-term impacts of wildfire by timing rapid recovery of sagebrush to meet short-term species' habitat requirements. Burned leks likely have substantial immediate impacts that may extend beyond wildfire boundaries, especially if critical source habitats are removed. Such impacts could fragment habitat and disrupt connectivity, thereby affecting larger populations and possibly contributing to more widespread declines in sage-grouse populations.

**Keywords:** BACI design, *Centrocercus urophasianus*, cheatgrass, sagebrush obligate, sage-grouse, umbrella species, wildfire

\* Correspondence: [pcoates@usgs.gov](mailto:pcoates@usgs.gov)

<sup>1</sup>US Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, California 95620, USA  
Full list of author information is available at the end of the article

## Resumen

**Antecedentes:** Incrementos drásticos en el tamaño y frecuencia de incendios amenazan los ecosistemas de artemisia (*Artemisia L. spp.*) en Norte América. A escalas espaciales relativamente grandes, los incendios facilitan la conversión de comunidades dominadas por artemisia en monoculturas de especies de pastos anuales invasores (i.e., *Bromus tectorum L.*). Estos pastos anuales proveen los combustibles finos que promueven la propagación del fuego, contribuyendo a un ciclo de retroalimentación positiva que afecta la mayoría de los ecosistemas de artemisia, con la expectativa de pérdida de hábitat para las poblaciones residentes de fauna silvestre. El urogallo de las artemisas o gallo de salvia (*Centrocercus urophasianus* Bonaparte, 1827), es una especie obligada de los ecosistemas de artemisia, indicadora del funcionamiento de estos ecosistemas, dado que dependen de diferentes componentes de esos ecosistemas para cumplir con sus necesidades en su ciclo de vida. Dado que los incendios no pueden predecirse, los impactos crónicos de los incendios sobre las poblaciones del gallo de salvia han sido generalmente limitados a estudios correlativos. La evidencia de experimentos bien diseñados, es entonces necesaria para entender los mecanismos específicos por los cuales los incendios son perjudiciales para la dinámica poblacional del gallo de salvia.

**Resultados:** Luego de un evento de fuego significativo en la periferia sudoeste del hábitat del gallo de salvia, implementamos un estudio de impacto (previo-posterior y control de largo plazo), mediante un conjunto de datos apareados (BACIP) de machos del gallo de salvia relevados en lugares de apareo (*leks*) dentro y fuera del perímetro de los incendios. Estimamos la tasa de cambio de la población en abundancia aparente ( $\hat{\lambda}$ ) en áreas quemadas y no quemadas antes y después del incendio y derivamos las relaciones BACIP, que proveen de una evidencia controlada del impacto del fuego. Encontramos que  $\hat{\lambda}$  en los lugares de apareo (*leks*) dentro del perímetro del fuego, decrecieron aproximadamente un 16% en relación con los leks en los sitios de control. Estimamos además que en un 98,5% de probabilidad, el cambio observado en  $\hat{\lambda}$  puede ser atribuido al efecto del incendio.

**Conclusiones:** Demostramos los efectos adversos del fuego en el crecimiento de las poblaciones del gallo de salvia usando el diseño experimental BACIP, el cual separa los efectos del disturbio fuego de las fluctuaciones naturales de las poblaciones de este gallo. Nuestros resultados subrayan la importancia de acciones de manejo activas y comprensivas inmediatamente posteriores a un evento de fuego (i.e., sembrado junto con el plantado de artemisia), que pueden compensar los impactos inmediatos del fuego mediante la sincronización de una rápida recuperación de artemisia, para alcanzar los requerimientos de hábitat de la especie en el corto plazo. Los lugares de apareo quemados tienen un impacto sustancial inmediato que puede extenderse más allá de los límites del incendio, especialmente si algunos lugares críticos del hábitat son eliminados. Estos impactos pueden fragmentar el hábitat e interrumpir la conectividad, afectando por lo tanto a poblaciones más grandes y contribuyendo a un mayor descenso en las poblaciones del gallo de salvia.

## Abbreviations

- BACI: Before-After-Control-Impact analysis design
- BACIP: Before-After-Control-Impact analysis design using Paired datasets
- BLM: Bureau of Land Management
- CDFW: California Department of Fish and Wildlife
- CI: Control-Impact
- CRI: CRedible Interval
- PMU: Population Management Unit
- QA: Quality Assurance
- QC: Quality Control
- SSM: State-Space Model
- USFS: United States Forest Service
- USGS: United States Geological Survey
- WAFWA: Western Association of Fish and Wildlife Agencies

## Background

Wildfire frequency has increased throughout western North America, with large-scale wildfires becoming increasingly common (D'Antonio and Vitousek 1992;

Baker 2006; Pechony and Shindell 2010; Pilliod et al. 2017). In the sagebrush (*Artemisia L. spp.*) steppe ecosystem of the Great Basin region of the United States, this phenomenon has been exacerbated by the spread of exotic annual grasses, such as cheatgrass (*Bromus tectorum L.*; Knapp 1996; Brooks et al. 2004; Chambers et al. 2014; Brooks et al. 2015) and medusahead wildrye (*Taeniatherum caput-medusae* [L.] Nevski; Young 1992). Wildfire and annual grass presence interact to form a positive feedback loop, by which grass invasion is promoted by fires and subsequently senesces early, producing continuous fine fuel beds that increase the likelihood and spread of future wildfire (Miller et al. 2011; Balch et al. 2013; Chambers et al. 2014). After wildfire, the existing sagebrush community is slow to regenerate through natural seed dispersal, and many common sagebrush species in the Great Basin do not resprout (Bunting et al. 1987; Beck et al. 2009). Thus, this annual grass–wildfire feedback cycle often results in the elimination of sagebrush on the landscape, promoting

replacement by annual grasses (Shultz 2006; Miller et al. 2013), and subsequently leading to alternative ecosystem states (Hobbs et al. 2006; Shriver et al. 2019).

The altered wildfire regime and associated state transitions of sagebrush to annual grasses in sagebrush steppe ecosystems is a major threat to species, such as the greater sage-grouse (*Centrocercus urophasianus*, Bonaparte, 1827, hereafter sage-grouse; Nelle et al. 2000; US Fish and Wildlife Service 2015; Coates et al. 2016), that require intact sagebrush communities for certain life stages. Sage-grouse populations were predicted to decline to ~43% of their current population size within the next 30 years within the Great Basin if the grass–fire cycle is left unabated (Coates et al. 2016). Sage-grouse are a gallinaceous bird species with elaborate courtship rituals that exhibit strong lek and site fidelity (Fischer et al. 1993; Schroeder and Robb 2003; Connelly et al. 2011a). Individuals will often return to the same breeding area as used in previous years, and females often nest near previous nest sites (Fischer et al. 1993; Schroeder and Robb 2003; O’Neil et al. 2020). Such behavioral rigidity following disturbance events could negatively influence population dynamics (Schroeder and Robb 2003; Carroll et al. 2017), whereby historically beneficial behaviors become maladaptive in an altered ecosystem (Battin 2004; Robertson et al. 2013; O’Neil et al. 2020).

Pervading evidence suggests that sage-grouse continue to occupy burned areas in years immediately following wildfire, instead of seeking out unburned albeit novel alternatives (Lockyer et al. 2015; Foster et al. 2019; Dudley 2020; O’Neil et al. 2020). Wildfire has been known to alter habitat composition (Hess and Beck 2012; Davis and Crawford 2015) and food resources (Rhodes et al. 2010), and may reduce nest and adult survival (Lockyer et al. 2015; Foster et al. 2019; Dudley 2020) with potentially negative impacts on lek attendance (Steenvoorden et al. 2019). This implies that wildfire is likely to have short-term negative impacts on sage-grouse population growth and may also reduce long-term habitat population capacity when permanent state transitions of habitat patches to annual grass occur (Miller et al. 2011). However, because multiple stressors may affect populations simultaneously and sage-grouse populations tend to be cyclical (Garton et al. 2015; Coates et al. 2018; Coates et al. 2019), it is often difficult to attribute short-term population decline to a single, specific cause. Under these circumstances, paired study designs that facilitate comparisons between affected and unaffected areas are especially useful for understanding the influence of localized disturbances on populations of conservation concern (Conner et al. 2016). Within the Great Basin, for example, a better understanding of the impacts of changing wildfire regimes on sage-grouse populations has become an important resource

management objective (US Fish and Wildlife Service 2015; WAFWA 2015; Ricca and Coates 2020).

Recent wildfires that burned substantial areas of sagebrush in northeastern California and northwestern Nevada, USA, have created both opportunity and urgency to evaluate short-term impacts on important sage-grouse breeding concentration areas occurring near the periphery of current sage-grouse distribution. In 2012, a large wildfire (hereafter, the Rush Fire) burned approximately 124 000 ha of sagebrush in Lassen County, California, and Washoe County, Nevada (Bureau of Land Management 2012), an area that supported a breeding population of 1500 to 4500 sage-grouse between 1987 and 2003 (Armentrout and Hall 2005). To evaluate the impact of the Rush Fire on estimated rate of change in apparent sage-grouse population abundance ( $\hat{\lambda}$ ) in this region, we proposed and implemented a paired study design contrasting  $\hat{\lambda}$  within and outside areas that burned using sage-grouse lek count data that were recorded before and after a large fire event. For wildlife and resource managers, the continued use of lek sites by sage-grouse for courtship provides opportunity for annual monitoring of sage-grouse populations. Lek counts are the most common and cost-effective method for tracking sage-grouse abundance at various spatial scales (Patterson 1952; Connelly and Schroeder 2007; Blomberg and Hagen 2020). Lek counts were implemented as early as the 1930s (Johnson and Rowland 2007), so in many cases long-term population trends can be established from these datasets. Lek counts are a direct measure of male lek attendance and are generally assumed to track overall abundance and population trends (Blomberg et al. 2013a; Monroe et al. 2016; Wann et al. 2019). Lek counts have been used to evaluate effects of a variety of impacts within the species’ range, stemming from energy development (Green et al. 2017), agriculture (Doherty et al. 2016), livestock grazing (Monroe et al. 2017), and conifer expansion (Baruch-Mordo et al. 2013), as well as prescribed fire (Connelly et al. 2000) and wildfire (Coates et al. 2016; Steenvoorden et al. 2019).

The long-term lek count datasets used in our study facilitated a before-after-control-impact (BACI) analysis design using paired datasets (BACIP; Stewart-Oaten et al. 1986), which are used to make inference about impacts of a treatment or disturbance (Queen et al. 2002) relative to controls. In this case, count data collected from leks inside and outside the known fire perimeter provided a robust BACIP dataset spanning breeding years prior to and after the Rush Fire (2007 to 2012 and 2013 to 2018, respectively). The primary purpose of the BACIP study design is to compare the state of a system after the impact of a disturbance to the state of the same

system where the disturbance did not occur, while accounting for pre-existing spatial heterogeneity and natural temporal change (Green 1979; Stewart-Oaten et al. 1986; Underwood 1992). Applying a BACI analysis to sage-grouse lek count data provides an empirically based framework to quantify the effects of this large-scale wildfire on the population dynamics of a peripheral population of sage-grouse. We hypothesized that population growth rates of leks located inside the Rush Fire perimeter would be more adversely affected than leks located outside the fire perimeter.

## Methods

### Study area

Our study took place within the Buffalo-Skedaddle Population Management Unit (PMU) in eastern Lassen County of northeastern California, and Washoe County in northwestern Nevada (hereinafter, Susanville study area). The Buffalo-Skedaddle PMU encompasses an area of approximately 1 172 260 ha. The study site, which occupied most of the Buffalo-Skedaddle PMU, ranged in elevation from 1350 to 2400 m and consisted predominantly of public land administered by the Bureau of Land Management, or private lands. During the study period (2007 to 2018) the area experienced a mean annual precipitation of 27.17 cm ( $SD = 14.11$ ) and a mean annual temperature of 10.6 °C ( $SD = 0.74$ ; Susanville Municipal Airport, Western Regional Climate Center; <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca8702>). The Rush Fire took place in August 2012 (post breeding season) and burned approximately 124 000 ha. Most of the burn (>97%) occurred within the Buffalo-Skedaddle PMU (~18% of PMU area burned), extending from Skedaddle Mountain to Madeline Plains along the western side of the California–Nevada state border (Fig. 1).

Throughout the study area, cheatgrass and medusa-head wildrye were common understory vegetation components, but were more prevalent inside the fire perimeter, post-fire (P. Coates, US Geological Survey, Dixon, California, USA, unpublished data). Outside the Rush Fire perimeter, the plant community was a cold desert shrub steppe dominated big sagebrush (*Artemesia tridentata* Nutt.), dwarf sagebrush (*A. arbuscula* Nutt.), and antelope bitterbrush (*Purshia tridentata* Curran). Silver sagebrush (*A. cana* Pursh) was common in the northwest area of the study site. The primary land uses were livestock grazing (sheep and cattle) and irrigated agriculture. US Highway 395 and a network of smaller paved, improved gravel, and unimproved two-track roads provided access throughout the study area. The study area included 80 sage-grouse leks, with 30 considered active ( $\geq 2$  males observed on at least two separate occasions during the previous ten years; WAFWA 2015). Local breeding abundance estimates for this sub-

population (PMU-level) ranged from 1500 to 4000 individuals between 1987 and 2003 (Armentrout and Hall 2005).

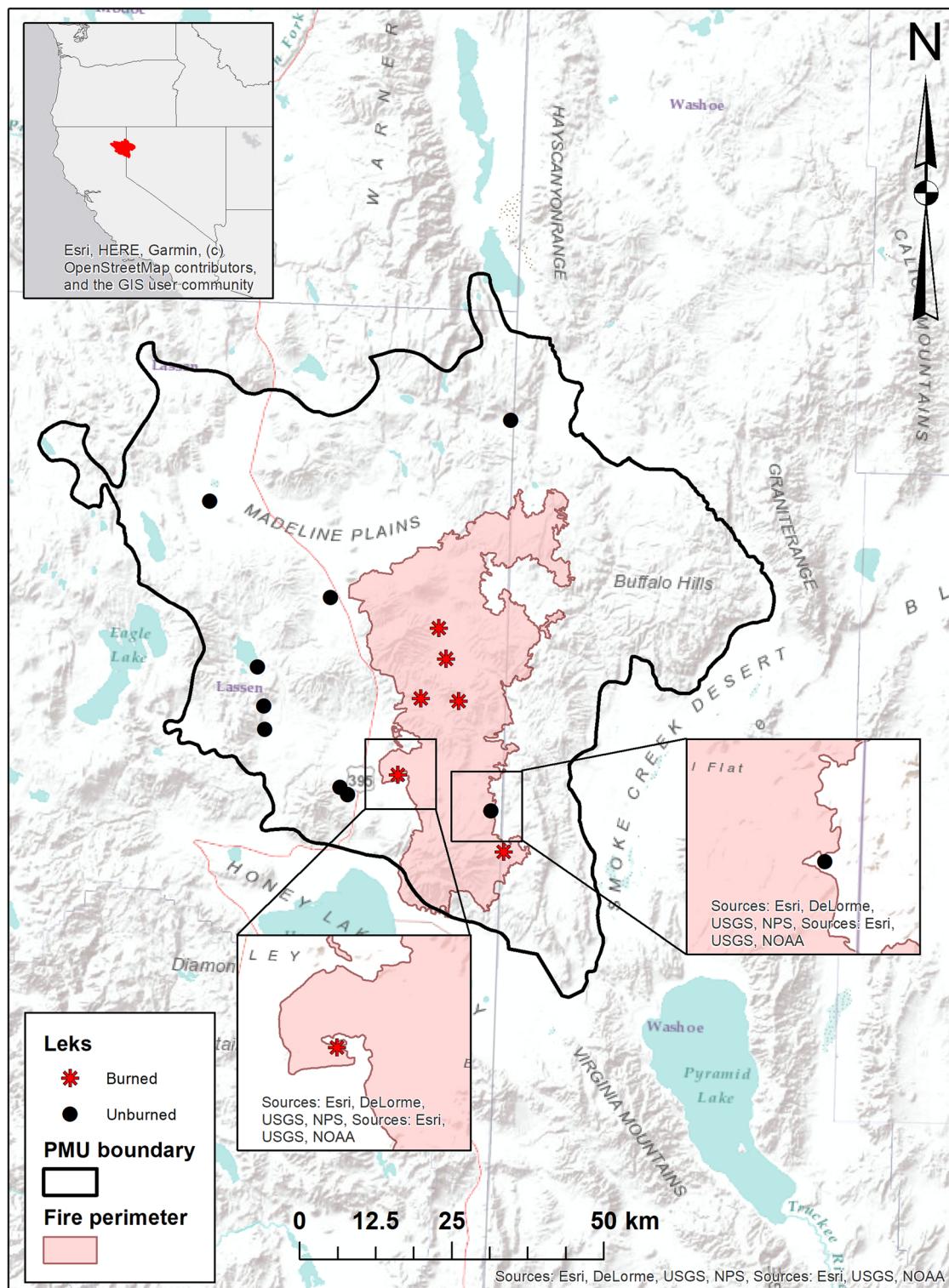
### Lek counts

Personnel from California Department of Fish and Wildlife (CDFW), Bureau of Land Management (BLM), US Forest Service (USFS), and US Geological Survey (USGS) used established protocols (Connelly et al. 2003) to count sage-grouse leks within the Susanville study area from early March to late April, spanning the period of peak lek attendance by males in this region (Wann et al. 2019). Lek counts were conducted between 30 min before and 90 min after sunrise by ground observers using binoculars, spotting scopes, or both, from suitable observation locations. Three lek counts were conducted during a single survey and the highest male count was recorded. Each lek was counted multiple times during the breeding season and the maximum male count was assumed to represent peak male attendance for each lek from 2007 to 2018. All lek count data used for analyses were obtained from the Western Association of Fish and Wildlife Agencies dataset and were subject to QA and QC measures (WAFWA 2015) prior to analysis.

To estimate the impact of the Rush Fire on  $\hat{\lambda}$ , we used count data from 15 active leks located within the Buffalo-Skedaddle PMU (Fig. 1). Leks used in the analysis had to have an active status within the WAFWA dataset, and fewer than five missing counts over the 12-year study period. We overlaid leks that met those criteria with wildfire spatial data collected from the Monitoring Trends in Burn Severity (Eidenshink et al. 2007) database and assigned a categorical fire affiliation of inside ( $n = 6$ ; impact) or outside ( $n = 9$ ; control) based on their location relative to the Rush Fire perimeter (Fig. 1). Leks located outside the fire perimeter had an average distance of 12.3 km ( $SD = 8.4$  km) to the nearest fire perimeter edge and ranged from 0.3 to 27.0 km outside the fire perimeter. Leks located inside the fire perimeter had an average distance of 4.7 km ( $SD = 3.5$  km) to the nearest fire perimeter edge and ranged from 0.2 to 9.0 km inside the fire perimeter.

### Modeling approach

We used a state-space modeling (hereafter, SSM) approach in a Bayesian framework (Royle and Dorazio 2008; Kéry and Schaub 2011) to estimate  $\hat{\lambda}$  from lek count data collected from a population of sage-grouse within the Susanville study area. The advantage of SSM over other methods is that it accounts for observation error ( $\epsilon$ ; i.e., detections are imperfect), and it is inherently Markovian, which was appropriate for these time series data. We bifurcated the modeling process based



**Fig. 1** Map of greater sage-grouse (*Centrocercus urophasianus*) study site (Buffalo-Skedaddle PMU) in northeastern Lassen County, California, and northwestern Washoe County, Nevada, USA, between 2007 to 2018. The solid black line represents the Buffalo-Skedaddle PMU boundary (red polygon in inset map). The pink shaded polygon indicates the extent of the 2012 Rush Fire. Leks assigned to the control group (unburned leks; black dots) were located between 0.3 to 27.0 km outside the fire perimeter. Leks assigned to the impact group (burned leks; red asterisks) were located between 0.2 to 9.0 km inside the fire perimeter

on fire category (*i.e.*, inside perimeter, outside perimeter) and applied a set of hierarchical equations to the lek time series data, referred to as the process (true, but latent state) and observation (relationship of observation data to latent state) components of the SSM. For both fire categories, the process component of this model was expressed as:

$$\log(\hat{N}_{l,j+1}) = \log(\hat{N}_{l,j}) + \hat{r}_{lj}, \quad (1)$$

$$\hat{r}_{lj} \sim \text{Normal}(\bar{r}_l, \sigma_{r_l}^2), \quad (2)$$

and the observation component was expressed as:

$$\log(y_{lj}) = \log(\hat{N}_{l,j}) + \varepsilon_{lj}, \quad (3)$$

$$\varepsilon_{lj} \sim \text{Normal}(0, \sigma_{y_l}^2), \quad (4)$$

$$\log(\hat{N}_{l,1}) \sim \text{Uniform}(-5, 5) \quad (5)$$

We used log-transformed lek counts within the modeling process and used intrinsic growth rate ( $\hat{r}$ ) as a population rate of change parameter for each lek ( $l$ ) and each year ( $j$ ) with normally distributed mean intrinsic growth rate with variance parameter ( $\sigma_{r_l}^2$ ) (Kéry and Schaub 2011; Green et al. 2017). We assigned a vague prior to the mean intrinsic growth rate ( $\bar{r}_l$ ) for each lek. A vague prior was also specified for the initial population size ( $\hat{N}_{l,1}$ ) using a uniform distribution with lower (-5) and upper (5) limits, which approximated a range of 0 to 150 on a linear scale. The upper limit was approximately twice the maximum observed initial lek count for the population and thus provided ample space for estimating  $\hat{N}_{l,1}$ . We derived the finite rate of increase ( $\hat{\lambda}$ ) from  $\hat{r}$  using the equation:

$$\hat{\lambda}_{lj} = \exp(\hat{r}_{lj}). \quad (6)$$

We sampled 100 000 model iterations from three independent chains after a burn in of 50 000 iterations. Posterior samples saved for inference were thinned by a factor of five. Statistical analyses were conducted using program JAGS version 4.3 (Plummer 2017) run through program R version 3.4.0 (R Core Team 2017) using packing `rjags` (Plummer 2019).

### BACI ratios and control-impact measures

To evaluate the effect of the Rush Fire on population growth of sage-grouse, we applied BACI ratio methodologies (Conner et al. 2016) and two control-impact (CI) measures (Chevalier et al. 2019) to the posterior distributions of estimated growth rates at leks categorized by fire impact versus control.

We assigned posterior distributions of population growth rate estimates ( $\hat{\lambda}_{jg}$ ) to a year ( $j$ ) and group ( $g$ ), where the group-level index was categorized as either inside (*i.e.*, impact,  $i$ ) or outside (*i.e.*, control,  $c$ ) the Rush Fire perimeter. Population growth rate ratios ( $R_{\hat{\lambda}_{ijc}}$ ) were calculated on an annual basis:

$$R_{\hat{\lambda}_{ijc}} = \frac{\hat{\lambda}_{ji}}{\hat{\lambda}_{jc}}, \quad (7)$$

where the rate of change at impact sites ( $\hat{\lambda}_{ji}$ ) served as the numerator and the rate of change at control sites ( $\hat{\lambda}_{jc}$ ) served as the denominator. We averaged annual rate of change ratios across two time periods corresponding to either before (2007 to 2008 : 2011 to 2012;  $\bar{R}_{\hat{\lambda}_{ijc} \text{ before}}$ ) or after (2012 to 2013 : 2017 to 2018;  $\bar{R}_{\hat{\lambda}_{ijc} \text{ after}}$ ) the wildfire event. Because  $\hat{\lambda}$  in year  $j$  was calculated as the change in abundance from year  $j$  to  $j+1$ , and because the Rush Fire occurred between population counts in 2012 and 2013, we assigned the  $\hat{\lambda}$  and  $\bar{R}$  values for 2012 to the after period. To estimate the relative wildfire effect on population rate of change ( $R_{\hat{\lambda}_{BACI}}$ ), we divided the rate of change ratio of the after period by the before period:

$$R_{\hat{\lambda}_{BACI}} = \frac{\bar{R}_{\hat{\lambda}_{ijc} \text{ after}}}{\bar{R}_{\hat{\lambda}_{ijc} \text{ before}}}. \quad (8)$$

We calculated two additional CI measures (CI-contribution and CI-divergence) to provide greater insight into not only the magnitude but also the direction (*i.e.*, source) of variability among the four BACI groups (Chevalier et al. 2019). CI-contribution measures relative change in the impact area to the control area and was expressed as:

$$CI - \text{contribution} = \left| \hat{\lambda}_{i,\text{after}} - \hat{\lambda}_{i,\text{before}} \right| - \left| \hat{\lambda}_{c,\text{after}} - \hat{\lambda}_{c,\text{before}} \right|, \quad (9)$$

where positive values indicate that changes in the impact areas are driving overall system observed changes.

Conversely, negative values indicate that changes in the control area are driving overall observed changes.

CI-divergence measures the dissimilarity of impact and control areas after the wildfire relative to before the wildfire and was expressed as:

$$CI\text{-}divergence = \hat{\lambda}_{i,\text{after}} - \hat{\lambda}_{c,\text{after}} - |\hat{\lambda}_{i,\text{before}} - \hat{\lambda}_{c,\text{before}}|. \quad (10)$$

Positive CI-divergence values indicate that differences between control and impact population growth rates have increased (*i.e.*, are more dissimilar) after the wildfire as compared to before the wildfire. Negative values indicate that control and impact population growth rates after the wildfire are more similar as compared to before the wildfire.

## Results

We used count data from six leks located inside and nine leks located outside the Rush Fire perimeter (Fig. 1). Before the Rush Fire,  $\hat{\lambda}$  at leks that later burned (*i.e.*, occurred inside the Rush Fire perimeter; impact group) were generally higher (1.08; 95% Credible Interval [CRI]; Lee 1997] = 0.99 to 1.14) than leks that did not burn (0.97; 95% CRI = 0.88 to 1.03). Conversely, after the Rush Fire,  $\hat{\lambda}$  at burned leks was generally lower (0.88; 95% CRI = 0.84 to 0.95) than for unburned leks (0.95; 95% CRI = 0.91 to 1.04; Fig. 2). Using a BACI ratio approach, we found that the mean  $\hat{\lambda}$  ratio after the Rush Fire ( $\bar{R}_{\hat{\lambda}_{i|c}\text{ after}}$ ) had a median value of 0.94 (95% CRI = 0.86 to 1.03) and was less than the mean  $\hat{\lambda}$  ratio before the fire ( $\bar{R}_{\hat{\lambda}_{i|c}\text{ before}}$ ), which had a median value of 1.13 (95% CRI = 1.02 to 1.27; Fig. 2). In terms of posterior evidence, we found that  $\bar{R}_{\hat{\lambda}_{i|c}\text{ after}}$  had nearly 73 times as many posterior samples below 1 (~91.0%) as compared to  $\bar{R}_{\hat{\lambda}_{i|c}\text{ before}}$  (~1.3% of posterior samples). This suggests little evidence of a lower  $\hat{\lambda}$  value across leks inside the fire compared to leks outside the fire prior to the fire event. Conversely, there was strong evidence for lower  $\hat{\lambda}$  values across leks inside the fire compared to leks outside the fire, following the fire event.

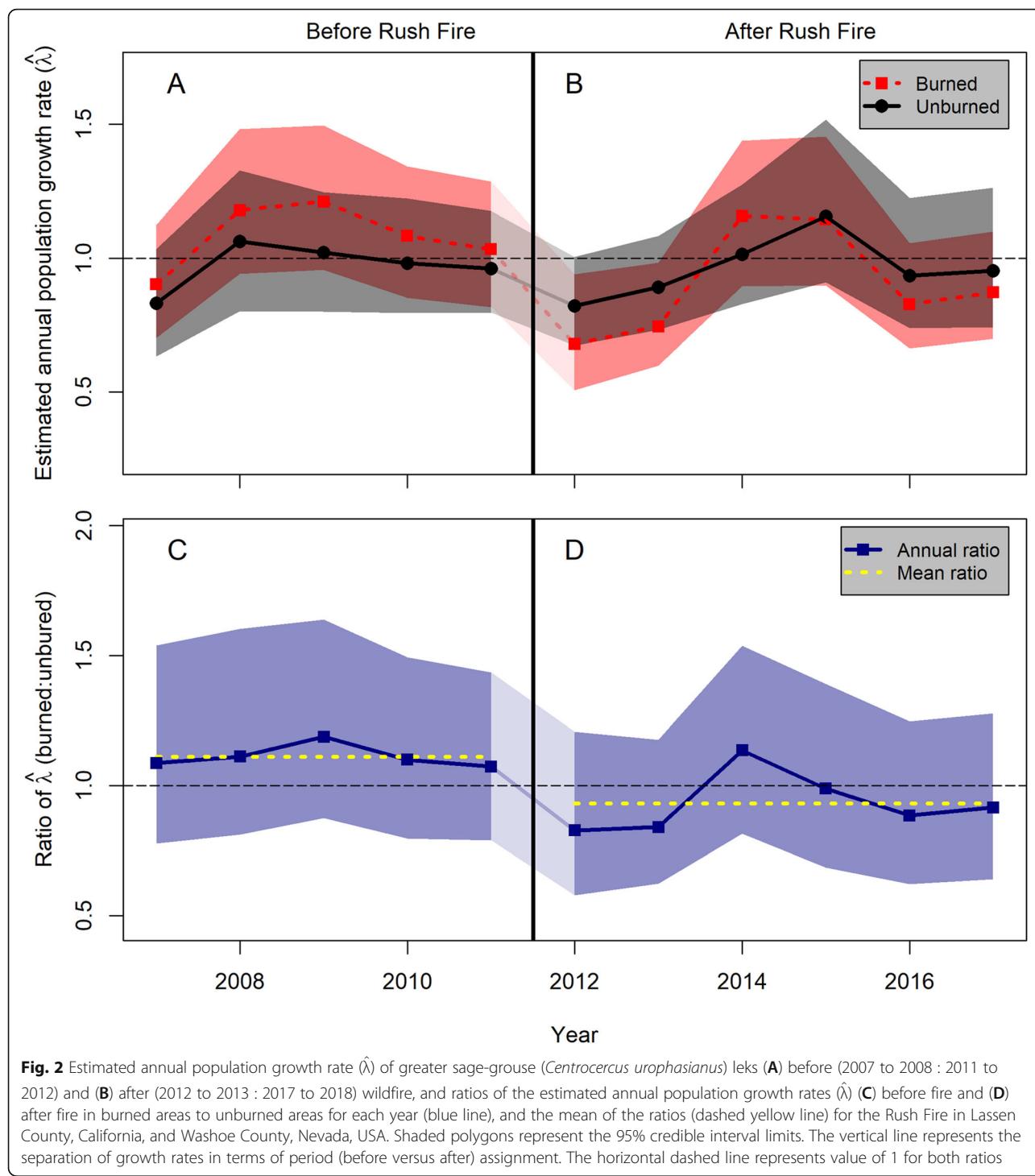
The overall, median effect ( $R_{\hat{\lambda}_{BACI}}$ ) was 0.84, indicating that  $\hat{\lambda}$  at burned leks decreased approximately 16% (95% CRI = 0.71 to 0.98) relative to  $\hat{\lambda}$  at unburned leks following the Rush Fire. Moreover, approximately 98.5% of the posterior distribution of the ratio estimate was <1, indicating substantial evidence of negative rate of change (Fig. 3). CI measures indicate that the observed change in  $\hat{\lambda}$  after the Rush Fire

was largely due to a change in  $\hat{\lambda}$  at the burned leks (CI-contribution = 0.14; 95% CRI = -0.01 to 0.26), with moderate evidence of  $\hat{\lambda}$  between burned and unburned leks becoming more similar after the Rush Fire (median CI-divergence = -0.04; 95% CRI = -0.15 to 0.07).

## Discussion

Assessing the impacts of disturbance on wildlife populations is a cornerstone of wildlife conservation. We evaluated the localized impacts of wildfire, a dynamic disturbance type that is central to management and conservation of sage-grouse in the Great Basin (Miller et al. 2011; US Fish and Wildlife Service 2015; Coates et al. 2016). Using a robust time series of lek counts that took place before and after a major wildfire event, we were able to isolate the influence that a specific wildfire event had on the local sage-grouse population by making use of a BACIP experimental design within a Bayesian hierarchical SSM framework. Sage-grouse populations express cyclical patterns (ranging in duration from 10 to 12 years; Row and Fedy 2017) and are strongly correlated with annual changes in precipitation (Coates et al. 2018). Yet, these potential confounding influences can be accounted for by measuring the responses of sage-grouse within the same sub-populations before and after wildfire, while contrasting responses inside and outside burned areas. Applying this concept within the BACI framework (Conner et al. 2016), we observed strong evidence (98.5% probability) of negative change in  $\hat{\lambda}$  at sage-grouse leks affected by a large wildfire relative to leks that occurred outside the fire perimeter (*i.e.*, not affected). After the fire,  $\hat{\lambda}$  for leks located within the fire perimeter declined by approximately 16% relative to control leks, which was based on minimal changes observed at those leks located outside the fire perimeter (median  $\hat{\lambda}$  before fire = 0.97, median  $\hat{\lambda}$  after fire = 0.95).

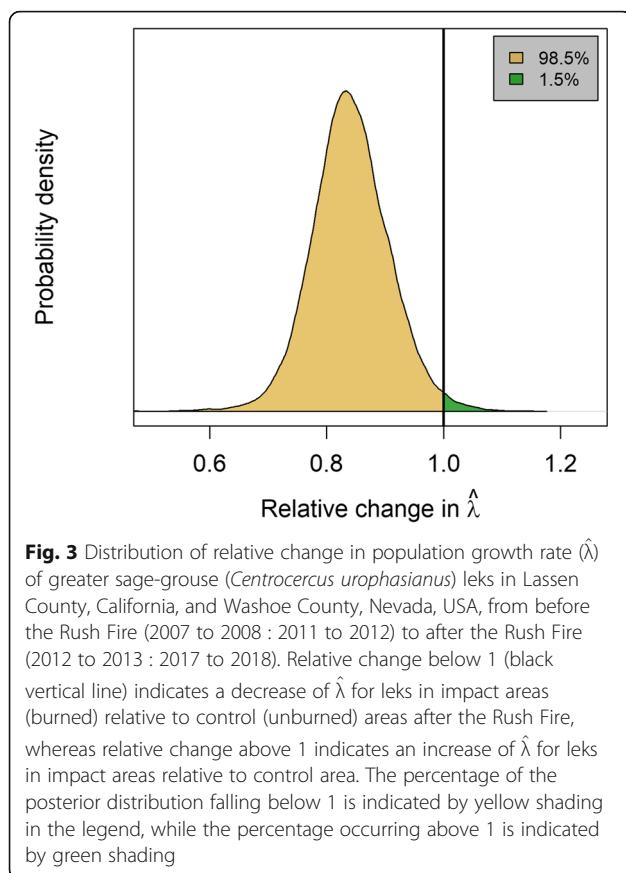
Our results indicate a meaningful shift in local sage-grouse population dynamics following wildfire. The mean  $\hat{\lambda}$  ratio of impact to control before the fire was >1 (Fig. 2C), meaning that  $\hat{\lambda}$  inside the fire perimeter was higher than  $\hat{\lambda}$  outside the fire perimeter (pre fire). After the fire, the mean  $\hat{\lambda}$  ratio was <1 (Fig. 2D), meaning that  $\hat{\lambda}$  inside the fire perimeter was lower than  $\hat{\lambda}$  outside the fire perimeter (post fire). Based on the CI-contribution measure, the observed change in  $\hat{\lambda}$  ratio in the wake of the Rush Fire was largely due to a change in  $\hat{\lambda}$  at burned leks, and the degree of dissimilarity in  $\hat{\lambda}$  among burned and unburned leks decreased (*i.e.*,  $\hat{\lambda}$  at burned and unburned leks became more similar) over the same time period. One explanation for this shift is that habitat conditions prior to wildfire were better within the burn perimeter than the more peripheral



**Fig. 2** Estimated annual population growth rate ( $\hat{\lambda}$ ) of greater sage-grouse (*Centrocercus urophasianus*) leks (A) before (2007 to 2008 : 2011 to 2012) and (B) after (2012 to 2013 : 2017 to 2018) wildfire, and ratios of the estimated annual population growth rates ( $\hat{\lambda}$ ) (C) before fire and (D) after fire in burned areas to unburned areas for each year (blue line), and the mean of the ratios (dashed yellow line) for the Rush Fire in Lassen County, California, and Washoe County, Nevada, USA. Shaded polygons represent the 95% credible interval limits. The vertical line represents the separation of growth rates in terms of period (before versus after) assignment. The horizontal dashed line represents value of 1 for both ratios

habitat outside the burn, resulting in superior sage-grouse population performance. Following the fire, however, habitat conditions were apparently degraded such that sage-grouse population responses were no longer superior within the burned area, with negative instead of positive trends in growth rate. This change in the BACI ratio, coupled with a now declining population at leks that

burned, suggests that localized extirpation within the Buffalo-Skedaddle PMU is a threat to this relatively isolated population. Sage-grouse populations on the periphery of the species distribution, such as the population in the Buffalo-Skedaddle PMU, may be at least partially dependent on dispersal from more interior populations, suggesting implications for the maintenance of lek



connectivity (Knick and Hanser 2011; Knick et al. 2013; Row et al. 2018). The Rush Fire may have isolated this local population from more interior and southern populations by fragmenting habitat, thereby leading to reduced connectivity and subsequent short-term population decline. If declines are not curbed by habitat restoration or rapid recovery efforts (Ricca and Coates 2020), acute long-term impacts become increasingly likely, especially considering natural recovery rates of a decade or more for most sagebrush communities (Pilliod et al. 2017; Pyke et al. 2020).

We found that overall population growth was reduced following wildfire. Wildfire can have a variety of impacts on the demographics of local sage-grouse populations, which has been demonstrated in several study regions and suggests mechanisms for the population declines that we observed at the Buffalo-Skedaddle PMU. The Rush Fire occurred in August 2012, which implied that most, if not all, hatch-year sage-grouse chicks were mobile and flighted, decreasing the likelihood of direct mortality caused by fire. However, the Rush Fire burned approximately 80 to 90% of the vegetation within the wildfire perimeter (Bureau of Land Management 2012). Fall and winter resources were likely substantially affected because wildfire kills sagebrush, which otherwise

provides critical forage and cover for sage-grouse during the winter season (Connelly et al. 2011b; Miller et al. 2013). For example, substantial reductions in winter survival were documented following a large wildfire in Oregon, USA (Foster 2016). Moreover, nesting vegetation was severely affected, which likely contributed to low nest survival documented after the fire, between 2015 and 2018 (Dudley 2020). After the wildfire, sage-grouse used a higher percent of non-shrub nest cover inside the fire perimeter (e.g., perennial grasses and forbs) than outside the perimeter (Dudley 2020). Increased habitat edge by way of fragmentation of sagebrush communities may also increase the occupancy and density of visual nest predators such as common ravens (*Corvus corax* Linnaeus, 1758; Howe et al. 2014; O'Neil et al. 2018; Coates et al. 2020), with greater potential impacts where shrub cover has been reduced (Coates and Delehanty 2010). Sage-grouse chicks require habitat that provides both cover and foraging opportunity, which can be characterized by a shrub overstory and herbaceous understory with an abundance of insects (Connelly et al. 2011b; Blomberg et al. 2013b; Gibson et al. 2017). Native plant communities, including shrub overstory, may be replaced by annual grasses after wildfire (Chambers et al. 2007; Beck et al. 2009; Miller et al. 2013; Chambers et al. 2014). Such habitat conversion can also negatively affect insect abundance (Beck et al. 2012). Rhodes et al. (2010) found that fire reduced the abundance of ants (Hymenoptera), an important food source for young sage-grouse chicks. While the Rush Fire occurred after critical nesting and brood rearing seasons in 2012, the local sage-grouse populations were likely subject to long-term seasonal indirect effects through impacts on cover and food resources, and could have lasting effects on the sagebrush community in areas of low ecosystem resistance and resilience (Miller et al. 2011; Chambers et al. 2014; Coates et al. 2016). Continued assessments of the sage-grouse demographic responses in this region are needed to inform post-fire mechanisms contributing to population decline.

The extent of large-scale wildfires can exceed the range of movements exhibited by typical sage-grouse populations, which may constrain adaptive behaviors such as nest foraging and lead to maladaptive selection patterns (Remeš 2000; O'Neil et al. 2020). Before the Rush Fire, female sage-grouse nested on average 3.7 km ( $SD = 2.9$ ) from the nearest lek (Davis et al. 2014), which is significantly less than the average distance between the fire perimeter edge and affected leks used in this analysis (mean = 4.7 km, range = 0.2 to 9.0 km). Hens that continue to attend fire-affected leks are less likely to access resources and nest beyond the fire perimeter due to strong patterns of site fidelity (Connelly et al. 2011a), and may instead settle in sub-optimal habitats that

contribute to poor performance (Battin 2004). Islands of unburned habitat could provide partial refuge for sage-grouse occupying areas affected by wildfire (Steenvoorden et al. 2019), which could prove to be important in areas where sage-grouse exhibit high degrees of site fidelity. However, it is unlikely that habitat in the form of islands could fully compensate for potential population declines following fire. Although further investigation is needed, intact sagebrush islands appeared to be sparse within our study area based on estimated loss of native plant communities loss (Bureau of Land Management 2012) and type conversion to cheatgrass approximately eight years following the wildfire (Dudley 2020).

Our findings are consistent with several studies showing population impacts on sage-grouse following a major wildfire event. A simulation analysis conducted by Pedersen et al. (2003) found that, under most scenarios, fire resulted in reduced sage-grouse populations, sometimes leading to local population extirpation. Results from Smith and Beck (2018) also demonstrated that wildfire was associated with immediate and enduring adverse impacts on sage-grouse population change, such that growth rates were reduced for up to 11 years post wildfire. In the Great Basin, sage-grouse populations were predicted to decline 57% by 2044 if current annual grass–wildfire cycle trends continued (Coates et al. 2016). The results from our analysis are consistent with those findings and provide a pattern-based case study that demonstrates reductions in population size and suggests a potential mechanism for species range contraction that can occur when peripheral populations are affected (e.g., Coates et al. 2019). Although not investigated as part of this study, reductions in population size following wildfire are likely a function of reduced rates of survival and recruitment (Foster et al. 2019; Anthony 2020; Dudley 2020), as well as potential emigration away from affected areas. Additional demographic studies are needed to identify mechanisms by which wildfire influences population dynamics and the long-term prevalence of such negative effects.

## Conclusions

This study contributes additional evidence that wildfire has short-term negative impacts on sage-grouse populations. Long-term impacts are also likely given the time required for sagebrush communities to recover, coupled with the existing threat of permanent state transitions to annual grassland associated with a grass–fire feedback cycle (Balch et al. 2013; Coates et al. 2016; Shriner et al. 2019). Continued monitoring of wildfire-affected populations is warranted, as lingering wildfire effects may reduce habitat quality and population capacity over an extended period (Coates et al. 2016). In addition, impacts to other sagebrush ecosystem species need

investigation to understand community-wide impacts on species diversity. Active restoration efforts that facilitate sagebrush regrowth while providing short-term cover and resources for nesting and winter foraging (Pyke et al. 2020; Ricca and Coates 2020) may be required to sustain local populations following increasingly frequent wildfire events affecting sage-grouse habitat across the extent of its range.

## Acknowledgements

We thank R. Croston, K. Miller, and T. Kimball for providing helpful comments that improved this manuscript. This research was supported by funding from the California Department of Fish and Wildlife (CDFW), Bureau of Land Management (BLM), and US Geological Survey (USGS). Collection of field data was supported by multiple federal and state agencies, including CDFW, BLM, USGS, Idaho State University, and University of Idaho. We are particularly grateful to M. Ricca (USGS), J. Atkinson (USGS), R. Kelble (USGS), J. Severson (USGS), S. Mathews (USGS), A. Johnson (BLM), K. Miller (CDFW), and K. Collum (BLM) for their contributions to field study logistics, data, and conceptual design. We thank numerous technicians who helped conduct lek counts. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

## Authors' contributions

In alphabetical order of last name: P.S.C., and D.J.D. conceived idea and design. I.F.D. and S.C.G. collected the data. B.G.P., I.F.D., and S.T.O. analyzed the data. P.S.C., D.J.D., I.F.D., S.C.G., S.T.O., and B.G.P. wrote and edited the manuscript. P.S.C., D.J.D., and S.C.G. contributed resources and funding. All authors read and approved the final manuscript.

## Funding

This research was conducted under grants from California Department of Fish and Wildlife, Bureau of Land Management, and US Geological Survey.

## Availability of data and materials

The data that support the findings of this study are available from California Department of Fish and Wildlife but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are, however, available from the authors upon reasonable request and with permission of California Department of Fish and Wildlife.

## Declarations

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The authors declare that they have no competing interests.

### Author details

<sup>1</sup>US Geological Survey, Western Ecological Research Center, Dixon Field Station, 800 Business Park Drive, Suite D, Dixon, California 95620, USA.

<sup>2</sup>Department of Biological Sciences, Idaho State University, 921 South 8th Avenue, Pocatello, Idaho 83209, USA. <sup>3</sup>California Department of Fish and Wildlife, 1010 Riverside Parkway, West Sacramento, California 95605, USA.

Received: 28 July 2020 Accepted: 9 March 2021

Published online: 10 May 2021

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