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RESEARCH ARTICLE

Sagebrush treatments influence annual population change for greater sage-grouse

Kurt T. Smith[1,2], Jeffrey L. Beck[1]

Vegetation management practices have been applied worldwide to enhance habitats for a variety of wildlife species. Big sagebrush (*Artemisia tridentata* spp.) communities, iconic to western North America, have been treated to restore herbaceous understories through chemical, mechanical, and prescribed burning practices thought to improve habitat conditions for greater sage-grouse (*Centrocercus urophasianus*) and other species. Although the response of structural attributes of sagebrush communities to treatments is well understood, there is a need to identify how treatments influence wildlife population dynamics. We investigated the influence of vegetation treatments occurring in Wyoming, United States, from 1994 to 2012 on annual sage-grouse population change using yearly male sage-grouse lek counts. We investigated this response across 1, 3, 5, and 10-year post-treatment lags to evaluate how the amount of treated sagebrush communities and time since treatment influenced population change, while accounting for climate, wildfire, and anthropogenic factors. With the exception of chemical treatments exhibiting a positive association with sage-grouse population change 11 years after implementation, population response to treatments was either neutral or negative for at least 11 years following treatments. Our work supports a growing body of research advocating against treating big sagebrush habitats for sage-grouse, particularly in Wyoming big sagebrush (*A. t. wyomingensis*). Loss and fragmentation of sagebrush habitats has been identified as a significant threat for remaining sage-grouse populations. Because sagebrush may take decades to recover following treatments, we recommend practitioners use caution when designing projects to alter remaining habitats, especially when focused on habitat requirements for one life stage and a single species.

Key words: ***Centrocercus urophasianus*, herbicide application, mechanical treatment, population change, prescribed burning, wildfire**

Implications for Practice

- Practitioners should expect lower male sage-grouse lek counts following prescribed burning and mechanical treatments in sagebrush communities for up to 11 years post-treatment.
- Wildfire has an immediate and persistent negative influence on sage-grouse population change.
- Herbicide treatments to reduce sagebrush, but maintain structure, may positively influence sage-grouse population change, but not until 11 years or longer after implementation.
- As post-treatment recovery of sagebrush communities is slow, managers should use extreme caution when altering remaining big sagebrush communities to avoid long-term declines in sage-grouse.

Introduction

Habitat management practices that mimic natural disturbances are increasingly applied as conservation strategies to maintain or increase species diversity and abundance (Hunter 1993; Hobson & Schieck 1999). Vegetation treatments have been implemented by wildlife managers to restore habitats for an array of wildlife species worldwide in attempts to shift plant communities to conditions thought to increase species abundance (e.g. Hancock et al. 2011; Bergman et al. 2014; Peters et al. 2015). Mismanagement has degraded big sagebrush (*Artemisia tridentata* spp.) communities throughout the western United States, depleting herbaceous understory resources used by wildlife for food and cover (Knick et al. 2003; Davies et al. 2011). Treatments have been implemented to transition big sagebrush communities by diversifying the age structure of sagebrush plants and increase herbaceous production for livestock and wildlife (Davies et al. 2011; Beck et al. 2012). Treatments in Wyoming big sagebrush (*A. t. wyomingensis*) may result in increased total herbaceous cover (Lesica et al. 2007; Davies et al. 2012*a*), but perennial forb abundance exhibits little difference between treatments and reference areas 1–5 years following treatments (Fischer et al. 1996; Nelle et al. 2000; Davies et al. 2007, 2012*a*). Forb

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[1]Department of Ecosystem Science and Management, College of Agriculture and Natural Resources, University of Wyoming, Department No. 3354, 1000 E. University Avenue, Laramie, WY 82071, U.S.A.
[2]Address correspondence to, K. T. Smith, email ksmith94@uwyo.edu

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abundance is more likely to increase in mountain big sagebrush (*A. t. vaseyana*) communities following treatment (Dahlgren et al. 2006; Davies et al. 2012*b*). Responses of sagebrush communities following treatments have been variable, indicating that clear definitions and goals need be applied to habitat management practices to identify appropriate indicators of success (Wortley et al. 2013).

Evaluation of management success often includes measures such as vegetation change or increased use of targeted wildlife species, which are often inadequate surrogates for demographic response of wildlife to vegetation treatments (Block et al. 2001; Bergman et al. 2015). A particular need in evaluating treatments for wildlife is to examine effects of treatments on species response and population changes (Archer et al. 2011). Unfortunately, relatively little information exists on how sagebrush-occurring wildlife populations respond to habitat treatments in big sagebrush habitats (Knick et al. 2003; Beck et al. 2012; but see Bergman et al. 2014; Dahlgren et al. 2015). Greater sage-grouse (*Centrocercus urophasianus*) have received unprecedented conservation efforts in recent years leading the U.S. Fish and Wildlife Service to determine that greater sage-grouse (hereafter "sage-grouse") were not warranted for protection under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 2015). In Wyoming, the Core Area policy was implemented in 2008 to limit habitat loss and fragmentation in areas of high sage-grouse population densities in crucial breeding habitats (State of Wyoming Executive Order 2011). Core Areas may reduce projected long-term sage-grouse declines (Copeland et al. 2013; Gamo & Beck 2017) and suggest that mitigation practices have potential to prevent further declines (Doherty et al. 2010*a*). Treating sage-grouse habitats is thought to improve important food resources for adult and chick sage-grouse during the breeding season, potentially supplementing local populations and offsetting declines in more disturbed habitats.

For treatments to increase sage-grouse populations, habitat conditions must improve adult and chick survival, nest success, or a combination of these important vital rates. Female survival is among the most influential vital rates for sage-grouse populations, yet process variation in adult female survival is lower than that for nesting success or chick survival (Johnson & Braun 1999; Taylor et al. 2012). Vital rates most influential of population change often have lower temporal variability and may not be readily influenced by management actions (Raithel et al. 2007; Mills et al. 1999). Improved foraging resources in treated habitats adjacent to intact nesting cover could potentially improve availability of important nutritional resources for females during the pre-laying period, which may benefit reproduction (Barnett & Crawford 1994; Gregg et al. 2006). During early brood-rearing, brooding females select intermediate sagebrush cover with greater herbaceous understories compared to available habitats (Hagen et al. 2007). Brood-rearing females may utilize treated areas in close proximity to edges of intact sagebrush habitats (Dahlgren et al. 2006); however, abundance of critical insect and forb foods often does not exhibit positive response following treatments in Wyoming big sagebrush (Fischer et al. 1996; Nelle et al. 2000; Davies et al. 2007, 2012*a*; Hess & Beck 2014). Furthermore, the potential benefit of treatments for one seasonal habitat could be offset if treatment negatively alters the quality of other important seasonal habitats.

Sagebrush communities recover slowly following disturbances (e.g. Watts & Wambolt 1996; Beck et al. 2009; Hess & Beck 2012), making it difficult to estimate demographic responses in sage-grouse populations without evaluating long-term associations between population trends and habitat conditions. We used a retrospective study to evaluate sage-grouse population response to sagebrush reduction treatments occurring across different spatial and temporal scales in Wyoming. The objective of our study was to determine if treatments intended to improve herbaceous understories in sagebrush influenced annual sage-grouse population change. We thus evaluated annual population change of male sage-grouse using lek censuses across a range of vegetation treatments occurring in Wyoming from 1994 to 2012, while accounting for environmental and anthropogenic factors that have been previously shown to influence sage-grouse populations. Sage-grouse congregate at leks, communal breeding, or strutting grounds, in spring, providing opportunities to estimate relative sage-grouse population abundance (Connelly et al. 2004; Johnson & Rowland 2007). Previous studies have demonstrated that male lek counts and lek persistence may be influenced by environmental and anthropogenic activities across a range of scales in proximity to leks and population responses often exhibit lag effects following development (Harju et al. 2010; Holloran et al. 2010; Gregory & Beck 2014); we thus reasoned that sage-grouse populations may respond similarly to habitat treatments. We evaluated the relationship between male sage-grouse lek counts as an indicator of population change, and treated habitats in proximity to the lek. For this reason, our results do not evaluate how treatments targeting seasonal habitats (e.g. nesting or brood-rearing) influence specific vital rates, but rather the influence of treatments on overall population change.

Methods

Study Area

Our study occurred in Sage-Grouse Core Areas within the Wyoming portion of the Western Association of Fish and Wildlife Agencies Wyoming Basins Sage-Grouse Management Zone II (MZ II; Stiver et al. 2006; Fig. 1). This area encompassed all or portions of 25 (approximately 81%) of Wyoming's 31 Core Areas. We restricted our analyses to this area because data collected on sagebrush treatments were limited to Core Areas (described below), evidence suggests that sage-grouse populations respond differently to energy development (and conceivably other habitat alterations) between Sage-Grouse Management Zones I and II within Wyoming (Doherty et al. 2010*a*; Gamo & Beck 2017), and treatments are generally not recommended in Sage-Grouse Management Zone I due to limited big sagebrush cover (WGFD 2011). Our study area encompassed 50,957 km^2 and individual Core Areas ranged in size from 41 to 18,567 km^2. The region was dominated by Wyoming big sagebrush communities interspersed with black sagebrush

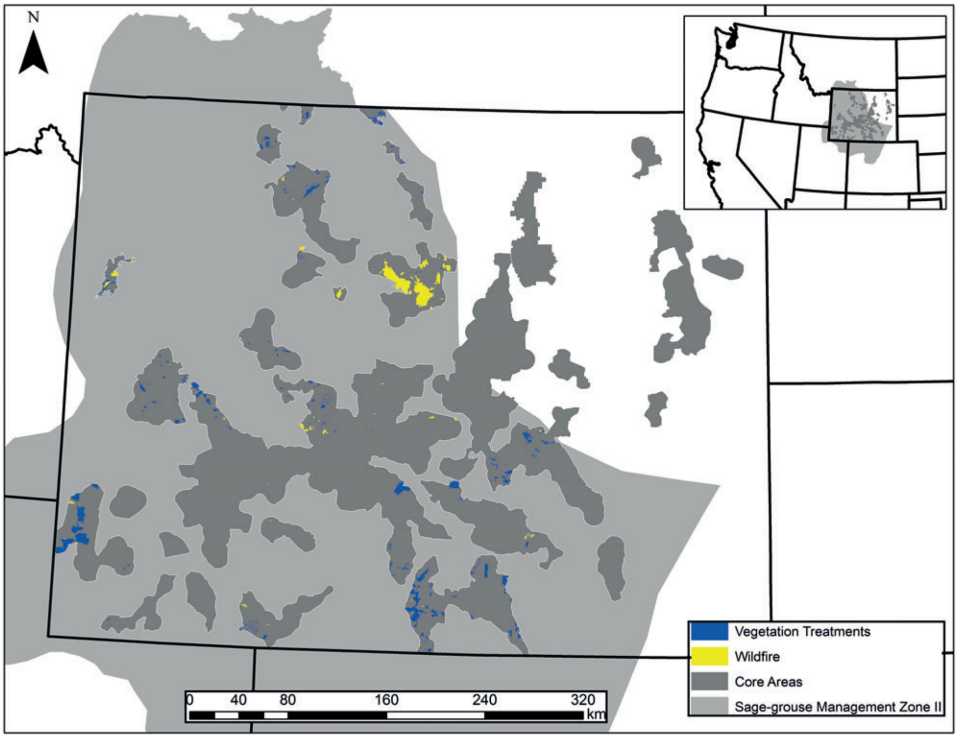

Figure 1. Map of the study area depicting vegetation treatments and wildfires occurring from 1994 to 2012 in Wyoming's Core Areas within Sage-Grouse Management Zone II, Wyoming, United States.

(*Artemisia nova*) and low sagebrush (*Artemisia arbuscula*), with communities of mountain big sagebrush at higher elevations (Rowland & Leu 2011; Knight et al. 2014).

Lek Count Data

We used maximum male lek count data from the Wyoming Game and Fish Department (WGFD) annual sage-grouse lek survey database from 1995 to 2012 to assess population change in response to treatments occurring from 1994 to 2012. Annual counts of male sage-grouse attending leks are performed range-wide by federal, state, and provincial wildlife agencies and provide estimates of relative population abundance when conducted across sufficient spatial and temporal scales (Fedy & Aldridge 2011; Blomberg et al. 2013). We followed WGFD definitions to classify leks as occupied or unoccupied (WGFD Sage-grouse definitions 2010) and restricted leks to Wyoming's Core Areas within Sage-Grouse MZ II to match the extent of vegetation treatment data. In addition, we removed consecutive annual lek counts of zero to minimize spurious estimates of no population change when zero males were present for more than 2 years, following methods of Coates et al. (2015). We estimated intrinsic annual rate of change for each lek, with the form:

$$r_{it} = \ln[N_{it}] - \ln[N_{it-1}]$$

where N was the maximum male lek count at lek i, during year t. We refer to this metric of intrinsic annual rate of change as population change. We added a constant of 0.1 to all lek counts when no males were recorded to avoid zero counts (Coates et al. 2015).

Predictor Variables

We assessed the influence of density dependence on population change with Gompertz methods. Gompertz density dependence estimates population change with logarithmic abundance (Dennis et al. 2006). We evaluated Gompertz density dependence with no time lag ($\ln[N_t]$) and 1-year time lags ($\ln[N_{t-1}]$) as these have been supported in regional sage-grouse population growth models (Garton et al. 2011, 2015; Coates et al. 2015).

To account for potential confounding effects of anthropogenic disturbance, we obtained well data from the Wyoming Oil and Gas Conservation Commission from 1995 through 2012 and used spud date to determine the year when drilling began (WOGCC 2012). We obtained monthly precipitation data from 1994 through 2012 (4-km resolution; PRISM Climate Group 2016) to account for precipitation on annual population change. We estimated annual, winter (1 November–30 April), early summer (1 May–30 June), late summer (1 July–30 August), and precipitation during May, June, and July individually.

Sagebrush treatments and wildfire occurring from 1994 to 2012 in Sage-grouse Core Areas were compiled by the WGFD and the Conservation Research Center of Teton Science School (CRCTSS 2012). Treatments were defined as activities that reduced sagebrush canopy cover in sage-grouse habitats of 0.4 ha or larger and included chemical applications (2,4-D and tebuthiuron), mechanical thinning (mowing and other forms of mastication), and prescribed burning. Wildfires were defined similarly when their spatial footprints were 0.4 ha or larger. Treatment polygons were originally clipped to state or federally administered lands to protect the privacy of deeded landowners; however, we obtained raw treatment data and followed methods of CRCTSS (2012) to digitize treatments that occurred on private lands in Core Areas with available data. We used the Monitoring Trends in Burn Severity database to include any wildfires that were not included in the CRCTSS dataset during the same time period (Eidenshink et al. 2007). We classified treatments into four categories: chemical, mechanical, prescribed fire, and cumulative (total) treatments. We calculated the total area of treatments and wildfires within circular analysis regions around each lek (scales described below). In some cases, treatments or wildfire occurred across the same spatial footprint during subsequent years. For example, a theoretical treatment occurred during 1994 and was followed by another treatment that covered a portion of the previous treatment footprint in 1996. In these instances, treatments or wildfire were reclassified to reflect the most recent treatment or wildfire following its implementation. The original treatment or wildfire was maintained, but truncated to reflect the remaining area that was not influenced by the most recent activity.

Data Analysis

We modeled population change with generalized estimating equations (GEE) using package "geepack" in R (Yan & Fine 2004; Hojsgaard et al. 2006; R Development Core Team 2015), where we assigned individual leks to clusters with an autoregressive correlation structure appropriate for longitudinal data (Wang & Carey 2003). Annual rate of change followed a normal distribution. To assess spatial scales and lag effects, we evaluated the area of habitat treatments and wildfires within 1.0, 2.5, 5.0, 6.4, 8.4, and 10.0-km radii scales around leks to build four separate models assessing 1, 3, 5, and 10-year time lags. We calculated the perimeter-to-area ratio of each treatment to determine the relative size of the average treatment within each scale. We included oil and gas well density (number of wells/km^2) within the intermediate scale (5.0 km) of each lek for all wells present during year $t-1$ in all models. The resolution of precipitation data (4 km) did not allow us to precisely match these scales, therefore we evaluated precipitation at the raster cell containing the lek (cell) and at approximately 5 and 10 km around each lek (5 and 10 km scales), during year $t-1$ in all models. In addition, we assessed the potential relationship between population change and precipitation occurring when treatments were implemented for each lag model (described below). We estimated time lags in response to vegetation treatments and wildfire by allowing at least one full growing season following implementation of treatments. For example, we evaluated a 1-year time lag for population change in response to treatments that occurred 2 years prior to N_t. We used a sequential approach with the quasi-likelihood information criterion (QIC; Pan 2001; Burnham & Anderson 2002) to evaluate predictor variables within variable subsets.

Well density, precipitation, wildfire, and treatment variables were centered and Z-transformed to facilitate direct comparison between variables and ensure model convergence (Becker et al. 1988). For each lag model, we carried forward the Gompertz density dependence (no lag or 1-year lag) with the most model support and well density variable if univariate models had QIC values lower than the null model and 85% confidence intervals (CIs) of parameter estimates did not overlap zero (Arnold 2010). We performed variable screening for precipitation, wildfire, and treatment models by determining the most predictive of the three analysis scales for precipitation variables and the most predictive of the six analysis scales for wildfire and treatment variables by retaining the scale with the lowest QIC value when 85% CIs did not overlap zero. The most supported scale for area of wildfire was brought forward to final modeling. For remaining precipitation and treatment variables, we retained the variable with the lowest QIC value if correlation coefficients $|r| \geq 0.6$. We brought forward remaining variables within each variable subset if model support indicated an improvement over the null model. Remaining variables within density dependence, well density, precipitation, and wildfire subsets were combined and assessed relative to the best Gompertz density dependence only model. We refer to this model as the base model. We then assessed model improvement by including vegetation treatment variables that were retained following initial variable screening. We refer to this model as the treatment model. Treatment models within four QIC of the base model were considered competitive (Arnold 2010). We performed post hoc evaluation of final lag models to evaluate possible interactions with elevation (as a surrogate for vegetation type where mountain big sagebrush would be expected to grow at higher elevations and Wyoming big sagebrush at lower [Davies et al. 2011; Knight et al. 2014]) and the perimeter-to-area ratio of treatments when treatments were present in the most predictive model and were informative (85% CIs surrounding parameter estimates that did not include zero).

Results

Approximately 3% (1,511 km^2) of our 50,957 km^2 study area was treated from 1994 to 2012; 270 km^2 (17.8% of total area treated) were treated with chemical applications, mechanical treatments occurred across 196 km^2 (13.0% of total), and 1,045 km^2 (69.2% of total) were treated with prescribed fire. In addition, wildfire occurred across 676 km^2 of sagebrush habitats from 1994 to 2012. Treatments occurred at elevations ranging from 1,359 to 2,631 m (mean ± SE [chemical, 2011 ± 2.8 m; mechanical, 1,816 ± 7.0 m; prescribed fire, 2,144 ± 6.1 m]; Fig. S1, Supporting Information) and treatment size ranged from 0.004 to 79 km^2 (mean ± SE [chemical, 0.11 ± 0.02 km^2; mechanical, 0.15 ± 0.02 km^2; prescribed fire 0.74 ± 0.11 km^2]; Fig. S1).

Our 1-year lag models included 8,293 estimates of population change from 945 leks from 1996 to 2012. We modeled population change with 7,779 estimates from 942 leks from 1998 to 2012 in 3-year lag models and used 7,180 estimates of population change from 936 leks during 2000–2012 in 5-year lag models. Our 10-year lag model included 5,515 estimates of population change from 925 leks from 2005 to 2012.

In all models, Gompertz with no time lag, well density, precipitation, and wildfire variables were consistently correlated with population change (Tables S1–S5). For the 1-year time lag model, vegetation treatments that were brought forward following initial variable screening included chemical and mechanical treatments within 10.0 km. The treatment model was competitive with the full model (Tables S1 & S5). Chemical treatments within 10.0 km ($\widehat{\beta}_1 = -0.017 \pm 0.016$ SE) and mechanical treatments ($\widehat{\beta}_1 = -0.015 \pm 0.016$ SE) were negatively associated with population change; however, 85% CIs for both treatment types included zero. The final 3-year lag model including vegetation treatments was 13.14 QIC points lower than the full model (Table S2). Mechanical treatments within 1.0 km of a lek were negatively associated with population change ($\widehat{\beta}_1 = -0.037 \pm 0.015$ SE; Table S5). We found no support for interactive effects between mechanical treatments and perimeter-to-area ratio of treatments ($\widehat{\beta}_1 = 0.014$, 85% CI −0.004 to 0.033) or mechanical treatments and elevation ($\widehat{\beta}_1 = -0.050$, 85% CI −0.152 to 0.052).

Treatment variables in the final 5-year time lag model included mechanical treatments within 10.0 km. The model including mechanical treatments was competitive with the full model (Table S3); mechanical treatments within 10.0 km were negatively associated with population change ($\widehat{\beta}_1 = -0.025 \pm 0.018$ SE; Table S5). However, 85% CIs of the parameter estimate for mechanical treatments overlapped zero. The final 10-year lag model including vegetation treatments was 17.32 QIC points lower than the full model (Table S4). Chemical treatments within 10.0 km ($\widehat{\beta}_1 = 0.036 \pm 0.014$ SE) and mechanical treatments within 10.0 km ($\widehat{\beta}_1 = 0.004 \pm 0.021$ SE) were positively correlated with population change; however, 85% CIs of the parameter estimate for mechanical treatments within 10.0 km overlapped zero. Prescribed fire within 2.5 km was negatively associated with population change in the 10-year lag model ($\widehat{\beta}_1 = -0.042 \pm 0.017$ SE). We found no support for interactive effects between chemical treatments and the perimeter-to-area ratio of treatments ($\widehat{\beta}_1 = 0.007$, 85% CI −0.027 to 0.040) or elevation ($\widehat{\beta}_1 = -0.044$, 85% CI −0.112 to 0.025). Similarly, we found no support for interactive effects between prescribed fire and the perimeter-to-area ratio ($\widehat{\beta}_1 = 0.011$, 85% CI −0.020 to 0.042) or elevation of treatments ($\widehat{\beta}_1 = -0.017$, 85% CI = 0.039–0.005).

Discussion

The primary objective of our study was to evaluate how sagebrush treatments influenced annual sage-grouse population change. We incorporated demographic factors (density dependence), environmental conditions (precipitation and wildfire), and anthropogenic disturbance (well density) to account for factors that have been attributed to sage-grouse population dynamics, prior to assessing the influence of sagebrush treatments on sage-grouse population growth. We found negative associations between the amount of mechanically treated sagebrush within 1.0 km and prescribed fire within 2.5 km on sage-grouse population change in our 3 and 10-year lag models, respectively. Chemical treatments within 10.0 km were positively associated with sage-grouse population change 11 years after treatment. We found no relationship with treatments and population change in our 1 and 5-year lag models, indicating a neutral population response to treatments at these temporal scales. Furthermore, the influence of treatments on population change did not vary with the size of individual treatments or elevation. However, the majority of treatments were small (<2 km^2), potentially reducing our ability to detect an effect of treatment size on population growth. Although we lacked fine scale demographic information to identify specific mechanisms to support our findings, annual counts provide suitable estimates to track trends in abundance through time (Connelly et al. 2004; Johnson & Rowland 2007).

A myriad of studies have demonstrated the importance of structural cover of sagebrush communities used yearlong by sage-grouse to provide concealment cover (Schroeder et al. 1999; Gregg & Crawford 2009; Dinkins et al. 2016) as well as meeting the nutritional requirements of adults and chicks (Johnson & Boyce 1990; Barnett & Crawford 1994). Because sagebrush treatments typically reduce sagebrush cover and height (with the potential exception of chemical treatments) to levels lower than sage-grouse use for nesting or brood-rearing sites, treated habitats may not be suitable habitat for sage-grouse until treated sagebrush recovers to sufficient levels to provide cover (Hess & Beck 2012). If herbaceous production is limiting sage-grouse populations, benefits of vegetation treatments may be achieved if treatments provide increased foraging opportunities while concurrently maintaining landscapes of suitable and intact sagebrush structural cover important for sage-grouse seasonal habitats. However, the juxtaposition and variability of unaltered sagebrush often meet guidelines for sage-grouse habitats (Doherty et al. 2010*b*). If vegetation treatments near leks result in functional habitat loss, it is conceivable that both juvenile males and females may be less likely to establish breeding territories near leks with greater amounts of treatments (e.g. Holloran et al. 2010).

Studies that have evaluated sage-grouse response to treatments in big sagebrush have reported mixed results (see Beck et al. 2012). For instance, Connelly et al. (2000) found a reduction in male lek attendance 1–5 years after prescribed burning in Wyoming big sagebrush habitats in the Big Desert of southeastern Idaho. Fischer et al. (1996) found similar sage-grouse abundance on burned and unburned areas in Wyoming big sagebrush in the same study area 1–3 years after burning. In contrast, sage-grouse pellet densities, total grouse abundance, and brood abundance were greater in tebuthiuron treated sites relative to mechanical treatments or control areas in mountain big sagebrush in south-central Utah (Dahlgren et al. 2006). Dahlgren et al. (2006) attributed increased use of tebuthiuron treated sites by sage-grouse to increased forb production; however, shrub cover was still relatively high in treated sites (approximately 20%). Furthermore, some evidence exists for increased male lek counts associated with small treatments (<200 ha) in high elevation mountain big sagebrush and mid-elevation basin big sagebrush (*A. t. tridentata*) communities compared to leks in surrounding areas (Dahlgren et al. 2015).

Our finding that prescribed fire within 2.5 km was negatively associated with rates of population change up to 11 years following treatments provide further evidence that prescribed fire has limited utility in treating Wyoming big sagebrush habitats for sage-grouse (Beck et al. 2009, 2012). Furthermore, prescribed fire may promote exotic annual grass invasion in Wyoming big sagebrush communities (Chambers et al. 2007; Davies et al. 2016). In addition, general lack of herbaceous response and concomitant reduction in sagebrush cover following mechanical treatments (e.g. Davies et al. 2012*a*) may not improve habitat quality for sage-grouse. Chemical treatments such as tebuthiuron do not kill all sagebrush plants (Olson & Whitson 2002) and leave behind shrub skeletons that sage-grouse may use for cover (Dahlgren et al. 2006). Increased herbaceous cover while maintaining intact cover of sagebrush may explain our findings that chemical treatments were positively associated with rates of population change 11 years after treatments.

Our results do come with caveats. First, we were unable to evaluate the potential influence of post-treatment grazing rest on treatment response and population change in sage-grouse. Information on livestock utilization is generally restricted to the scale of allotments (e.g. Monroe et al. 2017) making it difficult to infer grazing pressure at individual treatments. Federal land management agencies typically restrict grazing from treatments for two growing seasons where possible and regulate grazing pressure on treated and untreated areas. Limited information on post-treatment grazing response suggests that herbaceous cover response did not differ between grazed and ungrazed prescribed fire treatments up to 4 years following treatments (Bates et al. 2009). The spatial and temporal scales of our analysis limited our ability to detect uneven grazing pressure for livestock that may have preferentially selected treated sites, thus altering herbaceous understory composition and potentially sage-grouse responses. Future research should evaluate how grazing may influence vegetation response following treatments over longer time periods. Secondly, we evaluated a relatively short-term sage-grouse response following treatments, compared to long-term recovery rates of big sagebrush following treatments (Watts & Wambolt 1996). However, a 1–10-year response (negative or neutral) could have lasting effects on sagebrush communities and sage-grouse populations. While the short-term negative responses we found could be premature, no information exists on whether these treatments may improve rates of population change as treated areas mature. Furthermore, it is necessary to determine the time frame in which a positive association with population change following chemical treatments can be expected.

Restoration practices must align with localized threats influencing wildlife populations (Barnas et al. 2015) and be based on practical solutions that can be afforded to sage-grouse populations through management actions (Boyd et al. 2014). Further research is needed to identify the mechanisms associated with habitat use and demographic responses of sage-grouse to these habitat manipulations. Nevertheless, a general lack of vegetative response following treatment, particularly in Wyoming big sagebrush communities in MZ II, dictates that sound science and precautionary principles (Myers 1993; Connelly 2013) be applied when determining if treatments are warranted in the future. Management Zone II consists largely of sagebrush habitats classified as moderately resilient to disturbance and resistant to invasive annual grasses (Chambers et al. 2017). Thus, we can likely extend our findings to other areas across the sagebrush biome with equivalent or lower resilience and resistance. However, treatment effects on grouse populations in areas with lower or higher resilience and resistance may differ and warrant further investigation.

Loss and fragmentation of sagebrush habitats has been identified as a significant threat for remaining sage-grouse populations (Knick et al. 2003). Because sagebrush habitats recover slowly following disturbance and limited evidence suggests that habitat treatments improve herbaceous understories important for sage-grouse during the breeding season, we recommend that managers take caution and strive to maintain sufficient sagebrush cover when designing treatment projects to alter intact sagebrush habitats, particularly when management is focused on habitat requirements for one life stage (Dahlgren et al. 2006; Doherty et al. 2010*b*; Taylor et al. 2012). Without further research that supports treating sagebrush, managers may better focus their efforts on practices such as conifer removal, where increased suitable habitat and reproductive success for sage-grouse has been demonstrated (Sandford et al. 2016; Severson et al. 2016).

There is a need to evaluate and assess the single-species management approach that has been applied in many areas to sage-grouse conservation. Short-term benefits to sage-grouse populations do not necessarily provide long-term solutions that could potentially be afforded by more ecosystem focused conservation strategies (e.g. Boyd et al. 2014). In Wyoming, sagebrush rangelands provide habitat to nearly 450 avian, mammalian, herptile, and fish species (WGFD 2010) and many of these species could be influenced by treatments designed for sage-grouse habitat restoration. Efforts to maintain large, continuous sagebrush landscapes provides a more ecosystem level approach for maintaining sagebrush habitats and will likely be more beneficial to sage-grouse and other sagebrush occurring wildlife in the future.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Proportion of sagebrush treatments by size and elevation.
Table S1. Top and competing models within variable subsets and combined models explaining 1-year time lags.
Table S2. Top and competing models within variable subsets and combined models explaining 3-year time lags.
Table S3. Top and competing models within variable subsets and combined models explaining 5-year time lags.
Table S4. Top and competing models within variable subsets and combined models explaining 10-year time lags.
Table S5. Variable coefficients, standard errors, and 85% confidence intervals from top generalized estimating equation models comparing 1, 3, 5, and 10-year lag effects.

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