Short-Term Response of Sage-Grouse Nesting to Conifer Removal in the Northern Great Basin ☆

Authors: Severson, John P., Hagen, Christian A., Maestas, Jeremy D., Naugle, David E., Forbes, J. Todd, et al.

Short-Term Response of Sage-Grouse Nesting to Conifer Removal in the Northern Great Basin ☆

John P. Severson [a],*, Christian A. Hagen [b], Jeremy D. Maestas [c], David E. Naugle [d], J. Todd Forbes [e], Kerry P. Reese [a]

[a] Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID 83844, USA
[b] Department of Fisheries and Wildlife, Oregon State University, Bend, OR 97702, USA
[c] United States Department of Agriculture, Natural Resources Conservation Service, Redmond, OR 97756, USA
[d] Wildlife Biology Program, University of Montana, Missoula, MT, 59812, USA
[e] Lakeview District, Bureau of Land Management, Lakeview, OR 97630, USA

ARTICLE INFO

ABSTRACT

Conifer woodlands expanding into sage-steppe (*Artemisia* spp.) are a threat to sagebrush obligate species including the imperiled greater sage-grouse *(Centrocercus urophasianus)*. Conifer removal is accelerating rapidly despite a lack of empirical evidence to assess outcomes to grouse. Using a before-after-control-impact design, we evaluated short-term effects of conifer removal on nesting habitat use by monitoring 262 sage-grouse nests in the northern Great Basin during 2010–2014. Tree removal made available for nesting an additional 28% of the treatment landscape by expanding habitat an estimated 9603 ha (3201 ha [±480 SE] annually). Relative probability of nesting in newly restored sites increased by 22% annually, and females were 43% more likely to nest within 1000 m of treatments. From 2011 (pretreatment) to 2014 (3 yr after treatments began), 29% of the marked population (9.5% [±1.2 SE] annually) had shifted its nesting activities into mountain big sagebrush habitats that were cleared of encroaching conifer. Grouping treatments likely contributed to beneficial outcomes for grouse as individual removal projects averaged just 87 ha in size but cumulatively covered a fifth of the study area. Collaboratively identifying future priority watersheds and implementing treatments across public and private ownerships is vital to effectively restore the sage-steppe ecosystem for nesting sage-grouse.

Introduction

Conifer woodlands have been expanding into sagebrush (*Artemisia* spp.) and grassland ecosystems throughout the western United States since European-American settlement and are considered a major threat to sagebrush and grassland obligate species (Bragg and Hulbert, 1976; Miller and Tausch, 2001; Briggs et al., 2002; Grant et al., 2004; Miller et al., 2005, 2011; Davies et al., 2011). For example, the most abundant encroaching conifer species in the northern Great Basin, western juniper *(Juniperus occidentalis),* has expanded ~10-fold during the past 130 years and currently occupies ~3.6 million ha in California, Nevada, Oregon, Idaho, and Washington (Miller and Tausch, 2001; Miller et al., 2005). In addition, various other species of juniper (*Juniperus* spp.) and piñon pine (*Pinus* spp.) are increasing threats throughout sagebrush

systems (Miller et al., 2011; United States Fish and Wildlife Service [USFWS], 2015).

Conifer expansion and infill reduce grass and forb abundance and diversity by limiting nutrients, water, sunlight, and space and increasing surface water runoff and erosion (Buckhouse and Gaither, 1982; Gaither and Buckhouse, 1983; Miller et al., 2011). Increased runoff, interception of rainfall, and increased transpiration of conifers often lower the water table and reduce springflow and streamflow (Baker, 1984; Wilcox, 2002). Conifer encroachment is categorized into three successional phases (Miller et al., 2005). Initially, conifers are present with shrubs and herbaceous plants still dominant (phase I), followed by a stage in which conifers codominate the vegetation community (phase II). Finally, the landscape is dominated by conifers with decreased understory (phase III).

Phase I and phase II transitional woodland habitats support a high diversity of shrub, grass, and forest animal species (O'Meara et al., 1981; Maser et al., 1984a, 1984b; Sedgewick, 1987; Miller et al., 2005); however, most are generalist or forest-dependent species, which flourish while sagebrush-obligate birds and mammals decline (Lloyd et al., 1998; Coppedge et al., 2004; Grant et al., 2004; Horncastle et al., 2005; Woods et al., 2013). Recent studies report negative impacts from conifer expansion to lek occupancy in greater sage-grouse

(*Centrocercus urophasianus,* hereafter sage-grouse; Baruch-Mordo et al., 2013) and declines in habitat quality for nesting (Gregg, 1992; Doherty et al., 2010), brood rearing (Atamian et al., 2010; Casazza et al., 2011), and wintering (Doherty et al., 2008; Freese, 2009). Tree encroachment can increase perch availability for corvids and raptors that prey on sage-grouse (Paton, 1994; Wolff et al., 1999; Manzer and Hannon, 2005), which may be one of the underlying mechanisms affecting sage-grouse populations.

Growing concern for sage-grouse, an obligate sagebrush species requiring large, contiguous tracts of habitat (Knick and Connelly, 2011), has led to an unprecedented rangewide conservation response to reduce threats to the species and ecosystems on which they depend (USFWS, 2015). A combination of land management policy revisions and conservation efforts has been undertaken to address a wide range of threats from energy development to wildfire (USFWS, 2015). Among the suite of conservation actions, removal of encroaching conifers at landscape scales has become an increasingly important strategy for maintaining extant populations (Baruch-Mordo et al., 2013). In Oregon alone, the amount of conifer-encroached lands treated by partners through the Sage Grouse Initiative (SGI) grew 1411% from 2010 to 2014, addressing roughly two-thirds of the phase I encroachment on priority private lands (Natural Resources Conservation Service [NRCS], 2015).

While sage-grouse biologists have long recommended conifer removal to benefit sage-grouse (Connelly et al., 2000), little research has examined the spatial and temporal effects of conifer management on sage-grouse populations and behavior (USFWS, 2015). Commons et al. (1999) reported increased lek counts of Gunnison sage-grouse (*Centrocercus minimus*) after piñon-juniper removal in Colorado. Frey et al. (2013) documented increased use of sagebrush habitats following conifer removal. While both studies increased knowledge of treatment effects, additional research with more rigorous designs is needed to further validate the results and expand inference to other areas.

Using a before-after-control-impact (BACI) framework, we evaluated the effects of conifer management on nest-site selection across landscape-scale treatment and control sites in southern Oregon. Our objective was to evaluate spatial and temporal treatment effects to inform management decisions and outcomes of ongoing conservation efforts. Specifically, we predicted that conifer removal would result in 1) additional nests within and nearer to cut areas, 2) increased available nesting habitat, and 3) greater posttreatment nesting in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*; MBS), the habitat type most impacted by conifer encroachment (Miller and Eddleman, 2001).

Methods

Study Area

Data were collected in a treatment area in southern Lake County in south-central Oregon between the Warner Mountains and the Warner Valley and a control area in southern Lake County south of Warner Valley extending into Modoc County, California north of Cowhead Lake and into Washoe County, Nevada north of Mosquito Lake (Fig. 1). We delineated discrete boundaries for treatment and control study areas guided by natural barriers (e.g., canyons, cliffs, forest), as well as observed sage-grouse movements (see Fig. 1). The treatment area totaled 34 000 ha and ranged in elevation from 1490 m to 2100 m with an average of 1770 m above sea level. The control area totaled 40 000 ha and ranged in elevation from 1360 m to 2180 m with an average of 1680 m above sea level. Pretreatment conifer cover was 3.0% and 3.9% throughout the treatment and control areas, respectively, calculated from data acquired from the NRCS (Falkowski and Evans, 2012; Poznanovic et al., 2014). Mean monthly temperature from 2000 to 2014 was 8.7°C (min: 6.4°C, max: 10.7°C). Mean annual precipitation from 2000 to 2014 was 17.8 cm (min: 11.0 cm, max: 33.0 cm). Both areas were dominated by low sagebrush (*Artemisia arbuscula*) habitat, but other dominant species included MBS at higher elevations,
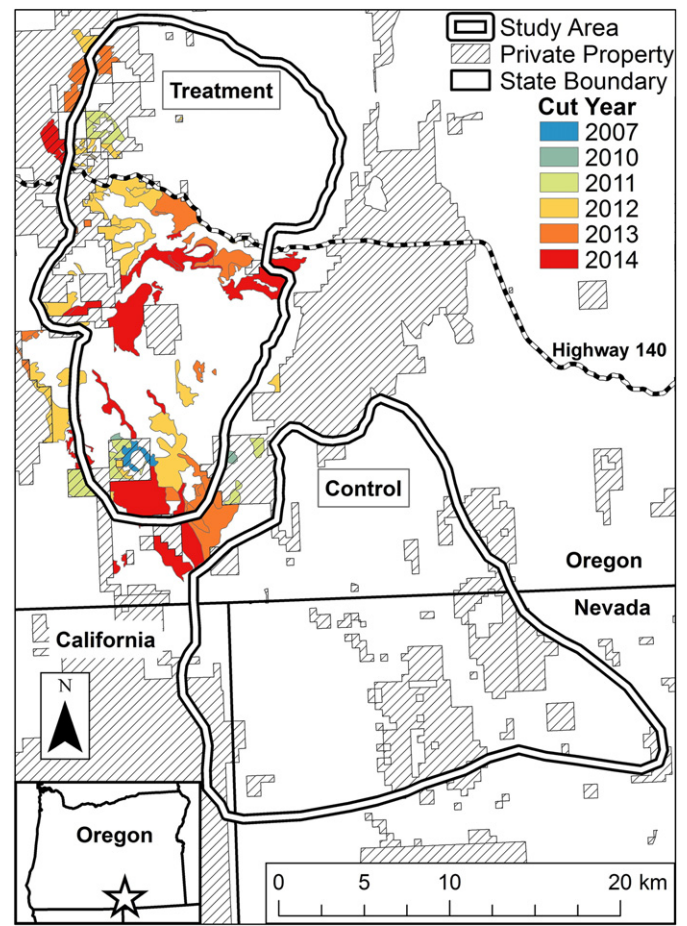

Figure 1. Treatment and control study areas in (star in inset) used to assess greater sage-grouse response to conifer management in Lake County, Oregon, 2010–2014. Colored polygons delimit years of conifer removal. Although some removal began as early as 2007, a majority of the cutting began in 2012.

Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) at lower elevations, and other interspersed shrubs including antelope bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* spp.), saltbrush (*Atriplex* spp.), and mountain mahogany (*Cercocarpus* spp.). We also identified mountain shrub habitat, which was generally codominated by MBS and other shrubs such as antelope bitterbrush and mountain mahogany. We combined mountain shrub with the MBS habitat type for analysis. Western juniper occurred in patchy distributions from mid to high elevation.

Conifer Management

The Bureau of Land Management (BLM) removed juniper on federal land while the NRCS, in association with the Oregon Department of Fish and Wildlife, assisted landowners with juniper removal on private land within and surrounding the treatment area (see Fig. 1). Treatments generally occurred from late fall to early spring and were designed to maximize shrub retention. Most of the treated areas were phase I to phase II encroachment (Miller et al., 2005) with generally intact understory herbaceous and shrub vegetation. Most treatments were conducted by hand-cutting with brushsaws and chainsaws, but 444 ha were machine cut (e.g., feller-buncher) in fall 2013 to spring 2014. Additional slash treatment of cut conifers was conducted where necessary to reduce woody fuels and a vertical structure. Various treatments were implemented depending on tree size and density, understory, and landowner preference [on private land] but mostly consisted of cut-leave, cut-lop, cut-burn, and cut-pile-burn. Cut-leave involved cutting trees without

additional slash treatment and generally occurred in areas with trees of low size and density. Cut-lop consisted of felling trees and removing tall branches from tree boles to reduce vertical structure and avian predator perches. Cut-burn occurred with larger, denser trees to expose the understory and encourage growth. Generally, cut trees were left to dry for ~1 yr and then burned individually. Effort was made to burn only individual trees to reduce shrub mortality and burn scars. Cut-pile-burn involved felling trees, cutting into manageable pieces, and stacking in small piles for burning when soils were frozen. This technique was used less often due to cost but was deemed necessary in some areas of high tree density to reduce area impacted by slash burning. Across all treatments, the objective was complete conifer removal, but an attempt was made to leave "presettlement" trees in locations that historically supported juniper, so some areas still had standing trees after treatment (BLM, 2011). BLM biologists identified "presettlement" trees using criteria such as size, leader growth, crown form, bark, and habitat (Miller et al., 2005). Although specific treatments were thought to influence management effects, we grouped treatments into two categories to simplify the analysis and interpretation: 1) cutting without slash burning and 2) cutting with slash burning.

We defined year as the first year of the nesting season following treatment. Treatments from January to May were designated with the current year, while treatments from June to December were designated with the following year. Although some treatments occurred from 2007 to 2011 (<10%), most occurred from 2012 to 2014 and slash burning began in 2012. Within the study area, 6488 ha of trees were cut and 2277 ha of trees were burned, while 9443 ha and 3540 ha were cut and slash burned, respectively, in and around the study area with an average treatment size of 87 ha (Table 1; see Fig. 1).

Nest and Random Locations

Sage-grouse females were captured during winter to spring 2009–2014 in the treatment area and 2010–2014 in the control area using spotlighting techniques (Giesen et al., 1982; Wakkinen et al., 1992) near leks and wintering habitat. Capture effort and locations were similar among years. We strived for sample sizes of ~40 radioed (22-g VHF radio-collars, model #A4060, Advanced Telemetry Systems, Isanti, MN) females at the start of nesting (~1 April) in each of the two areas. To minimize the potential for spatial bias in our sample, we trapped in similar areas each year and female capture locations were on average 818 m (standard deviation [SD] = 69 m) from the nearest past or present cut. Additionally, we made every effort to capture females in advance of nest-site selection. In the treatment area, 93% of females ($n = 129$) were captured before the onset of nest initiation (1 April), and 100% were captured well in advance of median nest initiation (29 April).

We monitored radio-marked females twice per week during the potential nesting seasons from 2010 to 2014. When a female was observed in the same place on two consecutive locations, she was then observed visually, without flushing, to verify nesting. Nests were subsequently monitored twice per week until incubation was terminated (e.g., hatched, depredated), after which the location was recorded for spatial analysis. To describe available habitat, we generated random

points within the treatment area boundary totaling 20 times the number of treatment area nests for each year in ArcMap 10.0 (ESRI, 2011). All nests were included as independent replicates for the analyses, even though some females nested in multiple years ($n = 33$) or renested after failure during the same year ($n = 19$). Models with an individual female as a random effect did not converge due to most females having only one nest. Because of nest-area fidelity (Fischer et al., 1993), some autocorrelation in these instances likely exists, but we believe including all data was more beneficial than disregarding these pseudo-replicates. The median distance between consecutive within-year nests in our study was 507 m (mean: 940 m, maximum: 6652 m), and thus we believe sage-grouse are plastic enough to choose nest sites on the basis of habitat covariates in addition to area fidelity.

Defining Nesting Areas

We used kernel density estimates of nest locations to calculate 95% nesting areas as a response for our BACI analysis. We calculated the annual kernel density estimate in both the treatment and control areas using nest locations as a point pattern. We calculated the bandwidth by minimizing the mean-square error criterion (Diggle, 1985) using the bw.diggle function in the spatstat package (Baddeley and Turner, 2005) within the R 3.1.2 environment (R Core Team, 2014). We then calculated the kernel estimate with this bandwidth using the kernelUD function and extracted the 95% distribution with the getverticeshr function in the adehabitatHR package (Calenge, 2006) in R.

Geospatial Data

We derived from treatments four variables whose estimates were assigned to each nest and random point. The variables were recalculated annually to account for changing availability. Age of the treatment polygons was calculated as number of years since treatment and was zero for not treated. Cut age or slash burn age represented the number of years since cutting or slash burning when a point occurred within the treatment polygon and was 0 if not in a treatment. Cut proportion was the proportion of an 800-m radius circle around nests and random points that was treated. Previous analyses had revealed that 800 m was an important scale for nest-site selection relative to juniper in this study area (Severson, 2016). Distance to closest cut was the distance in meters to the nearest treated area.

Habitat Selection

We compared nest and random locations in the treatment area using logistic generalized additive mixed models (GAMs) with function gam in package mgcv (Wood, 2006) in the R environment (R Core Team, 2014) using year as a random effect. We used GAMs because we anticipated nonlinearity in the cut age or slash burn age variables due to time lags or, potentially, an initial decline in habitat suitability after treatment. We used only nests and random points within 5000 m of treatments because farther distances were unlikely to affect selection of treated areas and a majority of sage-grouse travel < 5000 m from leks

Table 1
Annual areal estimates of cut and slash-burned conifer in the treatment study area used to assess greater sage-grouse response to conifer removal in Lake County, Oregon, 2007–2014. The greater treatment area included the treatment area, as well as the immediate surrounding area (see Fig. 1)

Yr	Treatment area			Greater treatment area			Average size (ha)
	Cut (ha)	Cumulative cut (ha)	Slash burn (ha)	Cut (ha)	Cumulative cut (ha)	Slash burn (ha)	
2007	143	143	—	143	143	—	72
2010	17	160	—	57	200	—	29
2011	432	592	—	781	981	—	71
2012	2073	2665	95	2709	3690	97	68
2013	1331	3996	991	2288	5978	1989	76
2014	2492	6488	1191	3465	9443	1454	144
Total	6488	6488	2277	9443	9443	3540	87

Table 2
Model specification and selection criteria in logistic generalized additive mixed model habitat selection analysis for nesting greater sage-grouse in Lake County, Oregon, 2010–2014. Intercept and random effects omitted for brevity

		Selection criteria		
Model[1]		MCE	AUC	AIC
6[2]	CutAge + Distance	0.392	0.653	7164.9
5	CutAge + BurnAge + Distance	0.393	0.650	7160.1
4[3]	CutAge + BurnAge + Proportion + Distance	0.394	0.646	7159.8
7	Distance	0.394	0.643	7207.5
3	s(CutAge) + s(BurnAge) + Proportion + Distance	0.399	0.633	7140.9
1	s(CutAge) + s(BurnAge) + s(Proportion) + s(Distance)	0.402	0.630	7009.1
2	s(CutAge) + s(BurnAge) + s(Proportion) + Distance	0.406	0.621	7134.0

AIC indicates Akaike's information criterion; AUC, cross-validated area under the curve; MCE, cross-validated mean class error; "s," smoothed terms.
[1] Proportion = proportion cut within 800 m, Distance = distance to closest cut.
[2] Selected best model.
[3] Global model selected for variable selection.

to nest (Holloran and Anderson, 2005). Because decisions on the random sample size in a used-available analysis can affect parameter estimates, relative variable importance, and, therefore, interpretation, we optimized the model weighting parameter using cross-validation before model selection to maximize estimation accuracy of covariate effects and predictive power of the models (see Appendix A).

In a GAM, the optimal smoothness of the nonlinear response must be determined (Wood, 2006). The package mgcv can automatically select the smoothing parameter (number of knots) for each variable using generalized cross-validation (GCV; Wood, 2004), which is an efficient approximation of leave-one-out-cross-validation (LOOCV) and is closely related to Akaike's information criterion (AIC; Golub et al., 1979; Anderson, 2008). However, this close association with AIC may lead to overfitting (see Murtaugh, 2009 and Arnold, 2010 for discussions on AIC overfitting) because LOOCV selects models with low bias but high variance, which can lead to unnecessary complexity (Hastie et al., 2009), thereby reducing predictive capability. We used 30 iterations of 10-fold cross validation (CV; Breiman and Spector, 1992; Kohavi, 1995) in the GAM from a minimum of 2 (linear; i.e., GLM) to a maximum of 5 knots. We used the CV mean class error (MCE) and the CV area under the receiver operating characteristics (ROC) curve (AUC) to select among fully linear, fully nonlinear, and partial linear models (Table 2). AIC scores were also included for completeness but were not used in the selection. When we selected the best global model form, we systematically removed variables with the lowest *P* values until the cross-validated MCE stopped declining. We plotted the response curves as the relative classification probability ± 95% confidence interval of each variable holding all other variables at their median.

BACI Analysis

To assess study area-wide treatment effects, nest data response variables from 2011 to 2014 were analyzed in a BACI framework (Stewart-Oaten et al., 1986), with 2011 representing effectively before data because there were few treatments completed before the 2011 nesting season (< 10% of total). The response variables in the models included nesting area calculated from the 95% kernel density and proportion of nests in mountain shrub and MBS communities. Previous research in this study area observed greater conifer cover in MBS (5.52%) and mountain shrub (3.87%) habitats than in low sagebrush (1.84%) and Wyoming big sagebrush (0.45%) habitats (Severson, 2016). MBS and mountain shrub also received ~80% of the conifer removal treatments (BLM, 2011). Thus, we hypothesized a shift in nesting to these habitats after treatment. Because amount of treated area increased through time (see Table 1), the BACI design was an impact trend-by-time interaction (Weins and Parker, 1995), wherein we used year as a continuous time variable rather than the factor, before-after treatment. We used linear mixed-effects models (function lme) in the nlme package (Pinheiro

et al., 2014) in the R environment (R Core Team, 2014) to assess the study area × year interactive fixed effect with year as a random effect. The interaction described the treatment effect, and the main effects were not important. Because we had few years, we were unable to assess a more complicated model structure (e.g., autoregressive correlation). We produced interaction plots and plots of the estimated relative treatment effect. The latter plots were produced by taking the difference between the control and the treatment area for each year and setting the first year (2011; ~pretreatment) to zero.

Results

Habitat Selection

We captured and fitted transmitters to 129 and 114 females in treatment and control areas and resulted in locating 153 (2010–2014) and 109 (2011–2014) nests in these areas, respectively (Table 3). Of the 153 treatment area nests and 3060 random points, 118 nests and 2263 random points were within 5000 m of cut areas and therefore used in the habitat selection analysis. The fully linear model (Model 4 in Table 2) had the lowest CV MCE and highest CV AUC of all full models and was used as the global model for variable selection (see Table 2). The model with the variables cut age and distance to the closest cut (Model 6 in Table 2) had the lowest CV MCE (0.392) and highest CV AUC (0.653; see Table 2), explained 7.9% of the deviance, and was selected as the best model. Both effects were significant ($P < 0.001$), but age of cut area had a positive effect (coefficient = 0.203; Fig. 2A) while distance to nearest cut area had a negative effect (coefficient = −0.00056; Fig. 2B) on nest-site selection. The odds ratio for the age of cut was 1.22 (95% CI: 1.15–1.31) annually or a 22% increase in probability of use each year following treatment. The odds ratio for distance to nearest treatment was 0.99944 (95% CI: 0.99938–0.99950) per meter equating to a 5.5% decrease in probability of use for every 100 m from a treatment or 43% decline for every 1000 m from a treatment.

Table 3
Summarized greater sage-grouse nest data, nest area (95% kernel density estimate of nest locations), and proportion of nests in mountain big sagebrush (MBS) for each study area in Lake County, Oregon, 2010–2014

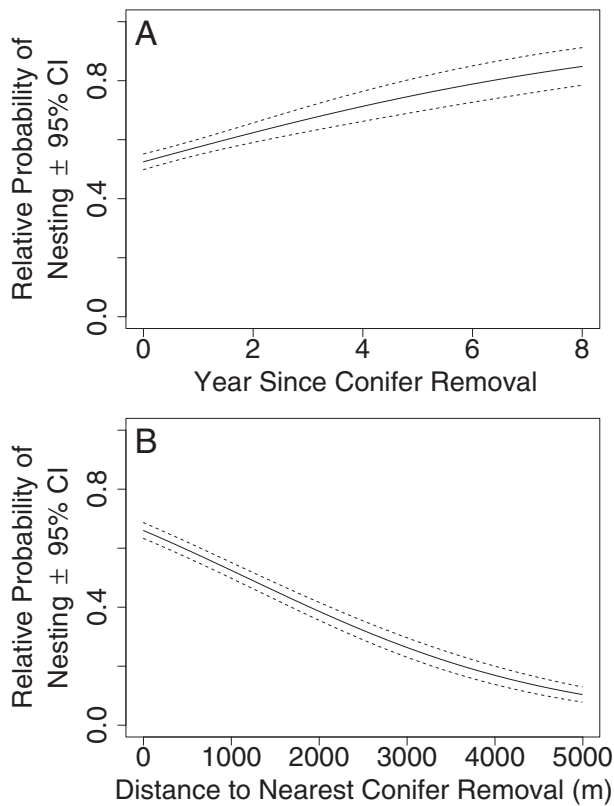|	Nests		Area (ha)		MBS proportion	
Yr	Treatment	Control	Treatment	Control	Treatment	Control
2010	28	—	2597	—	0.54	—
2011	21	19	3669	7994	0.14	0.11
2012	30	26	3124	5633	0.40	0.31
2013	38	36	15 883	13 153	0.50	0.31
2014	36	28	13 475	8875	0.50	0.18
Average	30.6	27.3	7749	8914	0.42	0.23

Figure 2. Response plots for relative probability of greater sage-grouse nesting in relation to conifer removal areas in Lake County, Oregon, 2010–2014. Relative probability of nesting: **A,** in a treated area as a function of time since cut and **B,** near a treated area as a function of distance to nearest removal area.

Standardized coefficients were 0.169 and –0.766, respectively, indicating that distance to nearest treatment was ~4.5 times more influential than age of treatment. Slash burn age and proportion of treated area within 800 m were not selected.

BACI Treatment Effects

Trends in nesting area and proportion of nests in MBS both increased with conifer removal (Fig. 3). Time × area interactions were positively related to increasing amount of available nesting area ($P = 0.022$, $F = 44.4$, $df = 2$) and a greater number of nests in MBS habitat ($P = 0.015$, $F = 66.6$, $df = 2$). By 2014, models predict that treatments resulted in an estimated 3201 ha ($\pm$ 480 SE) of additional nesting area annually and a 9.5% ($\pm$ 1.2 SE) annual increase in nests in MBS habitat (see Table 3; Fig. 3C, D).

Discussion

Although tree removal has long been suggested for conserving prairie and sage-grouse (Grange, 1948; Hamerstrom et al., 1952; Connelly et al., 2000; Hagen et al., 2004), few studies have actually quantified effects of conifer management on those grouse species and their habitats (Hagen et al., 2004; USFWS, 2015). Many studies have documented negative effects of woody encroachment on prairie grouse (Freese, 2009; Casazza et al., 2011; McNew et al., 2012; Lautenbach, 2015), but our study represents a major step forward in evaluating the effects of landscape-scale habitat restoration for sage-grouse and prairie grouse in general.

We observed increased nesting in and near treatments through time after conifer removal. At the landscape scale, area of nesting habitat and propensity of nesting in MBS habitats also increased through time in the treatment area relative to the control area, which we attributed to the
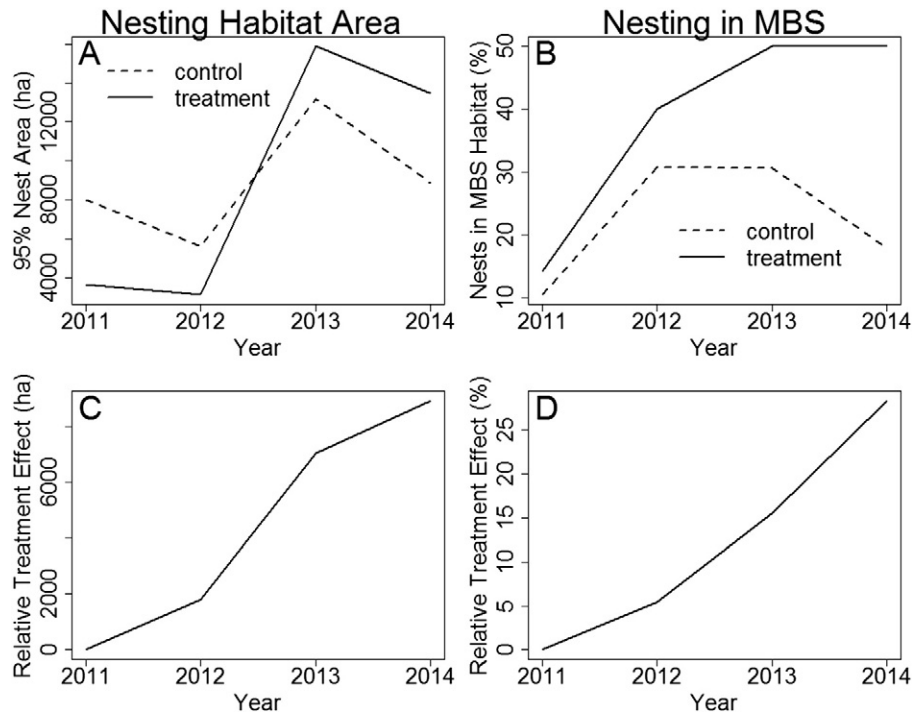

Figure 3. A, Interaction ($P = 0.022$) between time and study area with estimated greater sage-grouse nesting area calculated from 95% kernel density as the response in Lake County, Oregon, 2010–2014. Treatments primarily started in 2012 and continued through 2014. **B,** Interaction ($P = 0.015$) between proportion sage-grouse nests in mountain big sagebrush (MBS) habitat and study area. Change in **C,** amount of nesting area and **D,** proportion of nests in MBS, calculated as the difference between control and treatment minus the 2011 difference to standardize for ~before treatment difference.

conifer removal as this was the landscape-scale change between these two areas that occurred during our study. Ours is the first time-controlled BACI experiment to document the restorative benefits of conifer removal to sage-grouse, and results support previous claims of its utility as a conservation strategy (Connelly et al., 2000; Baruch-Mordo et al., 2013). We would expect landscape-scale nest habitat availability to increase through time on the basis of known lag effects in population response to other habitat changes (Harju et al., 2010). However, habitat is not static and benefits would diminish as conifers reinvade and cover reaches intolerable thresholds (Severson, 2016), which may occur within ~50–100 years without removals depending on soils, seed sources, and weather/climatic conditions (Miller et al., 2005). Further monitoring will be needed to fully evaluate long-term effects of conifer removal on sage-grouse and longevity of various treatment techniques (Boyd et al. 2017 this issue).

Our habitat selection model and BACI analysis indicated that sage-grouse nesting habitat availability increased following restorative treatments. Furthermore, the BACI analysis revealed increased nesting in higher-elevation sagebrush habitats (MBS and mountain shrub) where conifer encroachment was greatest and most removal occurred. Because we did not have a detailed map of shrubs in the area, we were unable to assess the shift in habitat use more directly. However, vegetation data at nests supported the idea of nests shifting more into MBS communities after treatments. We believe that available nesting habitat may be limited because much of the productive habitat in this area was conifer encroached. Conifer removal in these areas appeared to increase the relative probability of nesting in previously unavailable habitat. Such shifts in space use may lead to population increases if the habitat is suitable and not a potential ecological trap (Coates et al. 2017 this issue; Severson, 2016). MBS communities are disproportionately affected by encroachment due to favorable site conditions for tree growth (Miller et al., 2005), so conifer removal in these areas could be beneficial under changing climate patterns as sage-grouse may need to shift their distributions to higher elevations (Miller and Eddleman, 2001).

Our results suggest that conifer removal may increase the probability of nesting by sage-grouse. We used an 800-m radius to calculate the proportion of treatment area based on our previous research (Severson, 2016), but treatment effects may occur at other unassessed scales. We found a strong monotonically decreasing trend in selection with distance to treatments out to 5000 m. Thus, treatments may have an effect from small to large extents. The importance of distance to conifer removal area implies that the ecological footprint of conifer stands on sage-grouse is larger than the actual area of the stand. Consequently, targeted removal of conifer may have a larger positive benefit than the actual area removed; thus, more nesting habitat would be produced than the size of the treatments. Our treatments averaged 87 ha in size ranging up to 665 ha and totaled 6488 ha in a 34 000-ha study area (~20%) possibly indicating large conifer removal projects on the landscape may be needed to benefit sage-grouse, but more research is needed to assess scales of selection and effects of treatment size.

Surprisingly, we observed positive effects in a relatively short time period (~2–4 years). Sage-grouse are long-lived species typically exhibiting high nest-area fidelity (Fischer et al., 1993; Connelly et al., 2011). Nest-area fidelity behavior varies depending on habitat and other factors, and distance between consecutive nests has ranged from < 1 km to > 30 km (Fischer et al., 1993; Schroeder and Robb, 2003). Fidelity could cause a lag in the observed treatment effect, but the length of our study incorporating multiple generations and the potential plasticity in nest-site selection could account for the observed treatment effect. While we did not assess nest fidelity directly, our results indicate a shift in habitat use following treatments. Nearly a third (29%) of nesting females in the treatment area relative to the control increased use of mountain big sagebrush habitats in and around treated areas. Birds may have nested in treatments soon after restoration because sage-grouse already occupied nearby unencroached habitats.

Because of nest-area fidelity, we caution that restorative cuts placed farther from occupied habitats may take longer to be used. The distance between consecutive nests in our area (median: 507 m, mean: 940 m) suggest that treatments within 1000 m of occupied habitat may increase the nesting probability over the short term, but more research is needed to learn how shifting habitat mosaics interact with nest-area fidelity.

While our results generally indicate positive outcomes of conifer removal on sage-grouse, much remains to be learned. We were unable to evaluate all types of removal methods separately and instead grouped methodologies. Pretreatment and posttreatment tree cover and size, as well as integrity of understory vegetation, also may influence sage-grouse habitat use. Multiscale analyses will help refine information on spatial effects, and additional monitoring of this study site, as well as other studies throughout the Great Basin, will be necessary to draw firm, long-term conclusions. Additionally, we examined only one life-history stage of sage-grouse and information is needed on other aspects of the species' ecology to more fully understand the costs and benefits of this management strategy. Although use increased after conifer removal, it is possible that risk in these areas could also increase, thereby forming an ecological trap (Van Horne, 1983). Coates et al. (2017 this issue) observed increased selection for but decreased survival in productive areas with low conifer cover, implying that if some trees remain after treatment, the habitat may appear suitable but could be risky. Future analyses will directly assess survival and habitat selection throughout the year, but this was beyond the scope of this paper.

Implications

When sage-grouse nesting habitat is limited by conifer encroachment, tree removal appears to be a viable option for improving habitat availability. Nesting habitat availability appears to increase after treatments and treated areas become more beneficial with time. Treatments should target areas thought to be nesting habitats that have been excluded by conifers. Our results suggest that nesting in these previously encroached habitats (e.g., mountain big sagebrush) can increase after treatment. Nest habitat availability in and near treated areas increases dramatically when conifer is removed, but we did not determine scales of selection here. Planning conifer removal at large scales may be important; for example, our individual treatments averaged 87 ha in size and cumulatively covered ~20% of the landscape over 4 years. With mixed land ownership patterns in the West, collaborative partnerships engaging public and private landowners to holistically treat landscapes across administrative boundaries, as done in our study area, are vital to effectively restoring sage-grouse habitats.

Appendix A

We optimized the weighting parameter before model selection because of the resource selection design we used. Unlike used-unused

designs (e.g., occupancy) where the response is relatively certain and proportions of responses are system based and estimable, used-random designs have uncertainty in the random locations and the proportion of response is design based and therefore not estimable. Because the response was categorical, we used classification errors calculated from the predicted probability with 0.5 as the cutoff between used and random. Depending on the random sample size, classification error rates could approach 100% for random and 0% for used samples or vice versa due to the imposed weighting (either number of random points or the weighting parameter). Increased number of random points increases estimation accuracy of available habitat but could overweight and therefore overfit the random data. In a used-unused design, each sample is assumed to be an actual Bernoulli trial with implied weights based on the proportion of used and unused and should therefore not have weights imposed (Venables and Ripley, 1999), but those weights are unknown in a used-random design. However, strategic weighting of the used-random samples may help account for the design-based response, as well as the uncertainty in the response. Using weights that maximize the separation between the used and available samples (i.e., minimize predictive error) seems to be a logical solution. Although a 20:1 nest-to-random weighting may seem reasonable because we used 20 times as many random samples as nests,

certainty of classification of nest samples and uncertainty in classification of random samples (i.e., a random site may be used or unused) would likely increase the optimum weighting ratio further as it may be beneficial to give more weight to samples with greater certainty. We used 10 iterations of 10-fold cross-validation (CV) for weights from 1:1 to 100:1 (nest:random) to determine the optimum weight by minimizing the CV classification error. We programmed cross-validations in the R environment for both completely linear (generalized linear model) and extremely flexible (generalized additive mixed model; max knots = 10) responses and used average class error to minimize sampling design influence on error rates. AIC could not be used because the likelihood scale changes by weight. To further evaluate the necessity of weighting and to help interpret the choice of weighting, we calculated standardized linear slopes and significance for all variables using 1:1 to 100:1 weights. Fig. A.1A shows that, in this dataset, weighting influences the significance and slope of the variables. The weighting that produced the greatest predictive power (i.e., lowest error) was ~30:1 (Fig. A.1B), which was then used in the subsequent resource selection analysis. At this weighting, nests had higher prediction accuracy than random points (Fig. A.1C), which makes sense given certainty of nests and uncertainty of random points (i.e., some random points may have nests that we did not find).
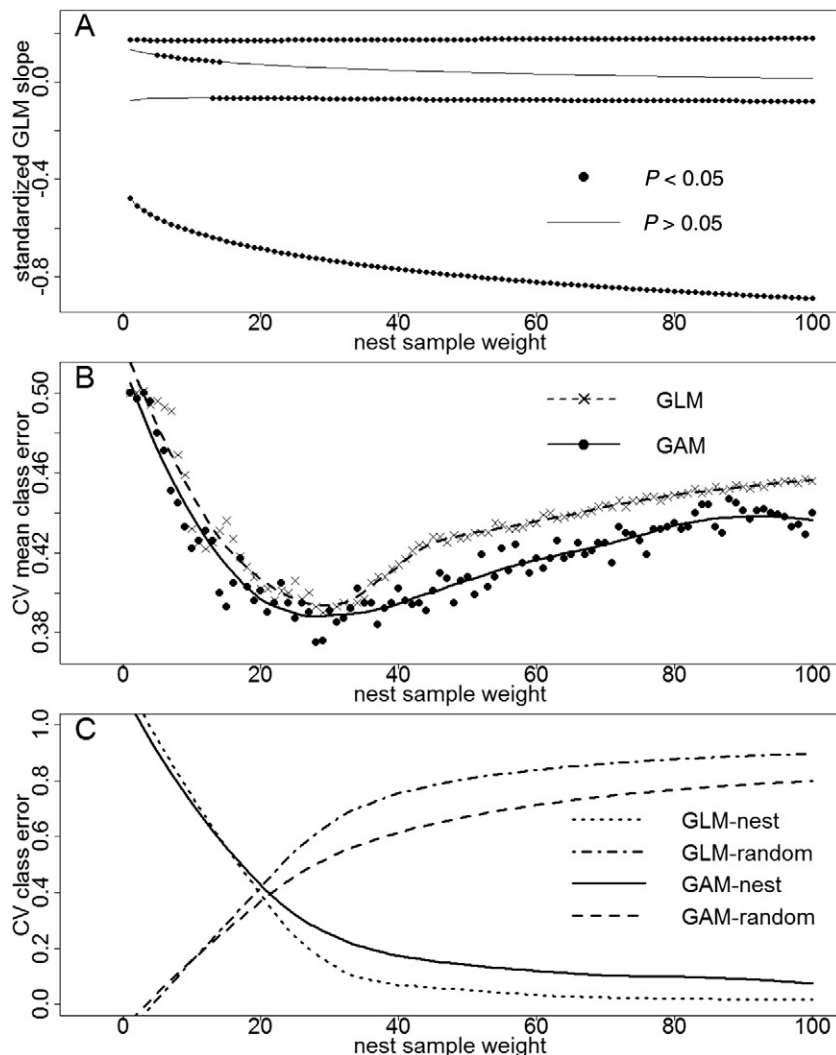
Figure A.1 Effects of class weight specification on regression outcomes in greater sage-grouse nest-site selection in Lake County, Oregon, 2010–2014. There were 20 times as many random samples as nests. X-axis represents nest-to-random weights as x:1. **A,** Change in generalized linear model (GLM) regression slope and significance for the four variables in Table 2. **B,** Cross-validated (CV) mean class error rate for GLMs and generalized additive models (GAMs). **C,** CV class error for GLMs and GAMs.

References

Anderson, DR, 2008. Model based inference in the life sciences. Springer, New York City, NY, USA, pp. 184.

Arnold, TW, 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74, 1175–1178.

Atamian, MT, Sedinger, JS, Heaton, JS, Blomberg, EJ, 2010. Landscape-level assessment of brood rearing habitat for greater sage-grouse in Nevada. Journal of Wildlife Management 74, 1533–1543.

Baddeley, A, Turner, R, 2005. Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12, 1–42.

Baker Jr., MB, 1984. Changes in streamflow in an herbicide treated piñon-juniper watershed in Arizona. Water Resources Research 20, 1639–1642.

Baruch-Mordo, S, Evans, JS, Severson, JP, Naugle, DE, Maestas, JD, Kiesecker, JM, Falkowski, MJ, Hagen, CA, Reese, KP, 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biological Conservation 167, 233–241.

BLM [Bureau of Land Management], 2011. South Warner Juniper Removal Project Environmental Assessment (DOI-BLM-L050-2009-0037-EA). US Department of Interior, Bureau of Land Management, Lakeview, OR, USA.

Bragg, TB, Hulbert, LC, 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29, 19–24.

Breiman, L, Spector, P, 1992. Submodel selection and evaluation in regression: the x-random case. International Statistical Review 60, 291–319.

Briggs, JM, Hoch, GA, Johnson, LC, 2002. Assessing the rate, mechanisms, and consequences of tallgrass prairie to Juniperus virginiana forest. Ecosystems 5, 578–586.

Buckhouse, JC, Gaither, RE, 1982. Potential sediment production within vegetative communities in Oregon's Blue Mountains. Journal of Soil and Water Conservation 37, 120–122.

Calenge, C, 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197, 516–519.

Casazza, ML, Coates, PS, Overton, CT, 2011. Linking habitat selection and brood success in greater sage-grouse. In: Sandercock, B.K., Martin, K., Segelbacher, G. (Eds.), Ecology, conservation, and management of grouseStudies in avian biology 39. University of California Press, Berkeley, CA, USA, pp. 151–167.

Commons, M. L., R. K. Baydack, and C. E. Braun. 1999. Sage-grouse response to piñon-juniper management. In: S. B. Monson, and R. Stevens [Comps.]. Proceedings: Ecology and Management of Piñon-Juniper Communities within the Interior West, 15–18 September 1997; Provo, UT, USA. Proc. RMRS-P-9. Ogden, UT, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 238–239.

Connelly, JW, Rinkes, ET, Braun, CE, 2011. Characteristics of greater sage-grouse habitats. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitatStudies in avian biology 38. University of California Press, Berkeley, CA, USA, pp. 69–83.

Connelly, JW, Schroeder, MA, Sands, AR, Braun, CE, 2000. Guidelines to manage sage-grouse populations and their habitats. Wildlife Society Bulletin 28, 967–985.

Coppedge, BR, Engle, DM, Masters, RE, Gregory, MS, 2004. Predicting juniper encroachment and CRP effects on avian community dynamics in southern mixed-grass prairie, USA. Biological Conservation 115, 431–441.

Davies, KW, Boyd, CS, Beck, JL, Bates, JD, Svejcar, TJ, Gregg, MA, 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144, 2573–2584.

Diggle, P, 1985. A kernel method for smoothing point process data. Applied Statistics 34, 138–147.

Doherty, KE, Naugle, DE, Walker, BL, 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74, 1544–1553.

Doherty, KE, Naugle, DE, Walker, BL, Graham, JM, 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72, 187–195.

ESRI, 2011. ArcGIS Desktop: Release 10 [computer program]. Environmental Systems Research Institute, Redlands, CA, USA.

Falkowski, M. J., and J. S. Evans. 2012. Mapping conifer trees in sage-grouse habitat using spatial wavelet analysis: a tool for prioritizing treatment of conifer encroachment. Unpublished Report. Washington, DC, USA: US Department of Agriculture, Natural Resources Conservation Service.

Fischer, RA, Apa, AD, Wakkinen, WL, Reese, KP, Connelly, JW, 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95, 1038–1041.

Freese, MT, 2009. Linking greater sage-grouse habitat use and suitability across spatio-temporal scales in central Oregon [thesis]. Oregon State University, Corvallis, OR, USA.

Frey, SN, Curtis, R, Heaton, K, 2013. Response of a small population of greater sage-grouse to tree removal: implications of limiting factors. Human-Wildlife Interactions 7, 260–272.

Gaither, RE, Buckhouse, JC, 1983. Infiltration rates of various vegetative communities within the Blue Mountains of Oregon. Journal of Range Management 36, 58–60.

Giesen, KM, Schoenberg, TJ, Braun, CE, 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10, 224–231.

Golub, GH, Heath, M, Wahba, G, 1979. Generalized cross-validation as a method for choosing a good ridge parameter. Technometrics 21, 215–223.

Grange, WB, 1948. Wisconsin Grouse Problems. Publication 328 A-1948. Wisconsin Conservation Department, Madison, WI, USA.

Grant, TA, Madden, E, Berkey, GB, 2004. Tree and shrub invasion in mixed-grass prairie: implications for breeding grassland birds. Wildlife Society Bulletin 32, 807–818.

Gregg, MA, 1992. Use and selection of nesting habitat by sage-grouse in Oregon [thesis]. Oregon State University, Corvallis, OR, USA.

Hagen, CA, Jamison, BE, Giesen, KM, Riley, TZ, 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. Wildlife Society Bulletin 32, 69–82.

Hamerstrom, F, Hamerstrom, F, Mattson, OE, 1952. Sharptails into the Shadows. Wisconsin Wildlife No. 1. Wisconsin Conservation Department, Madison, WI, USA.

Harju, SM, Dzialik, MR, Taylor, RC, Hayden-Wing, LD, Winstead, JB, 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74, 437–448.

Hastie, T, Tibshirani, R, Friedman, J, 2009. The elements of statistical learning: data mining, inference, and prediction. Springer, New York, NY, USA, pp. 745.

Holloran, MJ, Anderson, SH, 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107, 742–752.

Horncastle, VJ, Hellgren, EC, Mayer, PM, Ganguli, AC, Engle, DM, Leslie Jr., DM, 2005. Implications of invasion by Juniperus virginiana on small mammals in the southern great plains. Journal Of Mammology 86, 1144–1155.

Knick, ST, Connelly, JW, 2011. Greater sage-grouse and sagebrush: an introduction to the landscape. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitatStudies in avian biology 38. University of California Press, Berkeley, CA, USA, pp. 1–12.

Kohavi, R, 1995. A study of cross-validation and bootstrap for accuracy estimation and model selection. In: Mellish, C.S. (Ed.), Proceedings of the 14th International Joint Conference on Artificial Intelligence Volume 2. Morgan Kaufmann Publishers, San Mateo, CA, USA, pp. 1137–1143.

Lautenbach, JM, 2015. Lesser-prairie chicken reproductive success, habitat selection, and response to trees [thesis]. Kansas State University, Manhattan, KS, USA.

Lloyd, J, Mannan, RW, Destafano, S, Kirkpatrick, C, 1998. The effects of mesquite invasion on a southeastern grassland bird community. Wilson Bulletin 110, 403–408.

Manzer, DL, Hannon, SJ, 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69, 110–123.

Maser, C, Thomas, JW, Anderson, RG, 1984a. Wildlife habitats in managed rangelands—the Great Basin of Southeastern Oregon: the relationship of terrestrial vertebrates to plant communities, Part 1. General Technical Report PNW-172. US Department of Agriculture Forest Service, Portland, OR, USA.

Maser, C, Thomas, JW, Anderson, RG, 1984b. Wildlife habitats in managed rangelands—the Great Basin of Southeastern Oregon: the relationship of terrestrial vertebrates to plant communities, Part 2. General Technical Report PNW-172. US Department of Agriculture Forest Service, Portland, OR, USA.

McNew, LB, Prebyl, TJ, Sandercock, BK, 2012. Effects of rangeland management on site occupancy dynamics of prairie-chickens in a protected prairie preserve. Journal of Wildlife Management 76, 38–47.

Miller, RF, Eddleman, LE, 2001. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Technical Bulletin 151. Oregon State University Agricultural Experiment Station, Corvallis, OR, USA.

Miller, RF, Tausch, RJ, 2001. The role of fire in juniper and piñon woodlands: a descriptive analysis. In: Gallery, K.E.M., Wilson, T.P. (Eds.), Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. miscellaneous publication 11. Tall Timbers Research Station, Tallahassee, FL, USA, pp. 15–30.

Miller, RF, Bates, JD, Svejcar, TJ, Pierson, FB, Eddleman, LE, 2005. Biology, ecology, and management of western juniper. Technical Bulletin 152. Oregon State University Agricultural Experiment Station, Corvallis, OR, USA.

Miller, RF, Knick, ST, Pyke, DA, Meinke, CW, Hanser, SE, Wisdom, MJ, Hild, AL, 2011. Characteristics of sagebrush habitat and limitations to long-term conservation. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitatStudies in avian biology 38. University of California Press, Berkeley, CA, USA, pp. 145–184.

Murtaugh, PA, 2009. Performance of several variable-selection methods applied to real ecological data. Ecology Letters 12, 1061–1068.

NRCS [Natural Resources Conservation Service], 2015. Outcomes in conservation: Sage Grouse Initiative. Available at: http://www.sagegrouseinitiative.com/wp-content/uploads/2015/02/NRCS_SGI_Report.pdf Accessed 14 December 2015.

O'Meara, TE, Haufler, JB, Stetler, LH, Nagy, JG, 1981. Nongame wildlife responses to chaining of piñon-juniper woodlands. Journal of Wildlife Management 45, 381–389.

Paton, PWC, 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8, 17–26.

Pinheiro, J, Bates, D, DebRoy, S, Sarkar, D, R Core Team [computer program], 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1–118. R Core Team, Vienna, Austria.

Poznanovic, AJ, Falkowski, MJ, Maclean, AL, Smith, AMS, Evans, JS, 2014. An accuracy assessment of tree detection algorithms in juniper woodlands. Photogrammatic Engineering and Remote Sensing 80, 627–637.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schroeder, MA, Robb, LA, 2003. Fidelity of greater sage-grouse Centrocercus urophasianus to breeding areas in a fragmented landscape. Wildlife Biology 9, 291–299.

Sedgewick, JA, 1987. Avian habitat relationships in piñon-juniper woodland. Wilson Bulletin 99, 413–431.

Severson, JP, 2016. Greater sage-grouse response to conifer encroachment and removal [dissertation]. University of Idaho, Moscow, ID, USA.

Stewart-Oaten, A, Murdoch, WW, Parker, KR, 1986. Environmental impact assessment: "pseudo-replication" in time? Ecology 67, 929–940.

USFWS [US Fish and Wildlife Service], 2015. 50 CFR Part 17 Endangered and Threatened Wildlife and Plants; 12-month findings for petitions to list the greater sage-grouse (Centrocercus urophasianus) as threatened or endangered. Docket No. FWS–R6–ES–2015–0146. US Department of Interior, Fish and Wildlife Service, Washington, DC, USA.

Van Horne, B, 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47, 893–901.

Venables, WN, Ripley, BD, 1999. Modern applied statistics with S-Plus. 3rd ed. Springer, New York, NY, USA, pp. 501.

Wakkinen, WL, Reese, KP, Connelly, JW, Fischer, RA, 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20, 425–426.

Weins, JA, Parker, KR, 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. Ecological Applications 5, 1069–1083.

Wilcox, BP, 2002. Shrub control and streamflow on rangelands: a process based viewpoint. Journal of Range Management 55, 318–326.

Wolff, JO, Fox, T, Skillen, RR, Wang, G, 1999. The effects of supplemental perch sites on avian predation and demography of vole populations. Canadian Journal of Zoology 77, 535–541.

Wood, SN, 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association 99, 673–686.

Wood, SN, 2006. Generalized additive models: an introduction with R. CRC Press, Boca Raton, FL, USA 410 pp.

Woods, BA, Rachlow, JL, Bunting, SC, Johnson, TR, Bocking, K, 2013. Managing high-elevation sagebrush-steppe: do conifer encroachment and prescribed fire affect habitat for pygmy rabbits? Rangeland Ecology & Management 66, 462–471.