Greater Sage-Grouse Response to Conifer Encroachment and Removal

A Dissertation
Presented in Partial Fulfillment of the Requirements for the
Degree of Doctorate of Philosophy
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Major in Natural Resources
in the
College of Graduate Studies
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by
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AUTHORIZATION TO SUBMIT DISSERTATION

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ABSTRACT

Conifer woodlands expanding into sagebrush (*Artemisia* spp.) ecosystems are a threat to sagebrush obligate species including the imperiled greater sage-grouse (*Centrocercus urophasianus*). Sage-grouse are an obligate sagebrush species that have decreased in abundance and distribution amidst the declining sagebrush biome. Conifer removal has been recommended as a conservation strategy and is accelerating rapidly despite a lack of empirical evidence on outcomes to grouse. My objective was to assess the spatial and temporal effects of conifer encroachment and removal on sage-grouse ecology including nest-site selection, seasonal habitat selection, nesting habitat succession, nest survival, and annual female survival in the northern Great Basin from 2009–2014. Land management agencies removed ~10,000 ha of encroached conifer from 2012–2014. I monitored >350 female sage-grouse and nests in both a treatment area and a control area before and after treatments.

I estimated reduced nest-site selection above a threshold of 3% conifer canopy cover at a scale of 800 m, while a before-after-control-impact (BACI) analysis of conifer removal showed increased nesting in treated areas through time indicating increased nesting habitat availability. I assessed effects of conifer encroachment and removal on nesting habitat characteristics including shrub and herbaceous abundance and richness. Increased conifer cover negatively impacted several key nesting characteristics, while conifer removal increased the suitability of nesting habitat. Additionally, assessment of female habitat selection showed conifer avoidance throughout the year at a scale of 400 m around telemetry locations. Conifer removal increased habitat availability most in the summer when sage-grouse and their broods move higher in elevation during the hot, dry weather to more productive sites that are also most susceptible to conifer encroachment. Model averaged estimates of female survival and nest survival in a BACI analysis showed some indication of increases through time in the treatment area relative to the control.

This is the first study to evaluate effects of conifer encroachment and removal on habitat selection and survival throughout multiple life history stages of sage-grouse. I observed negative effects of conifer encroachment on habitat selection. Conifer removal increased habitat availability at a landscape scale, potentially resulting in increases in demographic parameters important to population growth. This study will be crucial in evaluating the efficacy of conifer removal for sage-grouse conservation and how management can be focused to maximize benefits.

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CHAPTER 1

CONIFER ENCROACHMENT EFFECTS ON SAGE-GROUSE NEST-SITE SELECTION IN SOUTHEASTERN OREGON

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ABSTRACT Conifer woodlands have expanded 6-fold in the Great Basin and their expansion is considered a primary threat to the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) and the larger sagebrush (*Artemisia* spp.) ecosystem. Conservationists are increasingly removing trees to restore sage-grouse habitats without a full understanding of the effects of conifer encroachment on sage-grouse habitat selection. Our objective was to assess conifer encroachment on nest-site selection at the landscape level to estimate the direction, magnitude, and scale of the effect. We assessed conifer characteristics at multiple scales in conjunction with other vegetation and topographic covariates at 160 nests and 167 random points on nest-site selection in southeastern Oregon, 2010–2011. Nest-site selection was negatively associated with >3% conifer cover within 800 m of nests. Where trees were present within 800 m of nests, sage-grouse selected nest sites in areas where the trees were clustered rather than dispersed, potentially indicating preference for more open habitat. Other vegetation and topographic characteristics indicate selection for nest sites that are susceptible to conifer encroachment. Consequently, conifer encroachment may restrict otherwise high quality nesting habitat which suggests proactive management to remove trees in these areas may potentially increase desirable nesting habitat and produce population-wide benefits where nest habitat is a limiting factor.

KEY WORDS *Centrocercus urophasianus*, conifer encroachment, Great Basin, *Juniperus occidentalis*, sagebrush, sage-grouse, western juniper

Greater sage-grouse require large, contiguous tracts of sagebrush (*Artemisia* spp.)-dominated shrub-steppe in western North America (Knick and Connelly 2011, U.S. Fish and Wildlife Service [USFWS] 2015). Sage-grouse distribution has declined ~50% since European settlement of North America (Schroeder et al. 2004, Knick and Connelly 2011) with a myriad of threats contributing to habitat conversion, degradation, and fragmentation. These continuing impacts include altered fire regimes (Miller et al. 2005, 2011), invasive species (Davies et al. 2011), energy development (Walker et al. 2007, Tack 2009, Holloran et al. 2010), improper grazing, and climate change, and the interaction among these factors (Knick and Connelly 2011, Miller et al. 2011, USFWS 2015). Consequently, sage-grouse have been considered multiple times for protection under the Endangered Species Act (ESA; Stiver 2011, USFWS 2015), most recently prompting an unprecedented rangewide conservation response to reverse long-term trends and obviate the need for additional regulation (USFWS 2015).

Expansion of coniferous trees into sagebrush habitats is one primary threat that has been a focus of increasing conservation concern and restoration (Baruch-Mordo et al. 2013), yet little is known about the actual effects of conifer encroachment and management on sage-grouse (USFWS 2015). Juniper (*Juniperus* spp.) woodland along with the piñon (*Pinus* spp.)/juniper association are native plant communities estimated to have expanded in extent up to 625% (Miller and Tausch 2001, Miller et al. 2008) and are now considered one of the biggest threats to sagebrush ecosystems (Davies et al. 2011). For example, western juniper (*J. occidentalis*), the most abundant conifer in the northern Great Basin shrub-steppe, has increased 10-fold in the past 130 years in the intermountain west and currently occupies 3.6 million ha in California, Nevada, Idaho, Oregon, and Washington (Miller and Tausch 2001, Miller et al. 2005). These expansions have largely occurred at the expense of sagebrush ecosystems (Miller et al. 2011). There is an inverse relationship between sagebrush and conifer cover (Miller et al. 2011), which has implications for sage-grouse and other species dependent upon sagebrush habitats. As conifer begins to dominate, shrub and herbaceous vegetation abundance and diversity decreases due to limitation of nutrients, water, sunlight, and space, thereby increasing surface water runoff and erosion (Buckhouse and Gaither 1982, Gaither and Buckhouse 1983, Miller et al. 2005). Additionally, because increased conifer can lower the water table and affect soil water availability (Miller et al. 2005, Roundy et al. 2014), mesic riparian and meadow areas may become less prevalent in encroached areas as the land becomes more xeric.

Tree encroachment can also impact wildlife directly by increasing perch availability for avian predators (Paton 1994, Wolff et al. 1999, Manzer and Hannon 2005) which may increase predation risk. Although some guilds of birds may increase, grassland and sagebrush obligates tend to decline with increasing conifer encroachment (Coppedge et al. 2001, Rosenstock and Van Riper 2001, Grant et al. 2004, Cunninham and Johnson 2006, Noson et al. 2006, Reinkensmeyer et al. 2007)

Several studies have considered conifer trees as covariates in sage-grouse habitat selection and demographic studies. Sage-grouse did not nest in juniper habitat in southeastern Oregon (Gregg 1992) and avoided nesting within 100 m of conifers in Montana (Doherty et al. 2010). In Nevada, sage-grouse broods avoided piñon-juniper and had decreased survival in areas with higher piñon-juniper coverage (Atamian et al. 2010, Casazza et al. 2011). Sage-grouse also avoided conifers during winter in Montana and Oregon (Doherty et al. 2008, Freese 2009). Furthermore, increasing conifer abundance was associated with decreased lek occupancy in Oregon (Baruch-Mordo et al. 2013). While these studies indicate potential negative relationships between conifer and sage-grouse, no studies have systematically assessed the effects of conifer encroachment on sage-grouse habitat selection.

We evaluated the influence of conifer characteristics at multiple scales on nest-site selection in southeastern Oregon. Our objectives were to determine effects of conifer encroachment on nesting habitat at multiple scales. We predicted that increased conifer cover would reduce nest-site selection. Additionally, because spatial configuration may change the birds' perception of available open habitat, we predicted that, clustering of individual trees would increase nest-site selection, while more dispersed trees would decrease selection (Baruch-Mordo et al. 2013). We evaluated conifer in areas of 50 to 1200 m around nests and, due to the landscape use by sage-grouse, we predicted that the greatest effects would occur at broader extents. Our research seeks to reveal nuances of conifer encroachment impacts on sage-grouse, inform adaptive management strategies for alleviating the threat, and provide insight on potential biological outcomes of ongoing conservation investments to address conifers.

STUDY AREA

Our study area was located in Oregon where western juniper encroachment is considered one of the most important factors threatening sage-grouse populations (Hagen 2011). We collected data in an area 20 km by 100 km in Lake County, south-central Oregon between the Warner Mountains and the Warner Valley extending into Modoc County, California and into Washoe County, Nevada (Figure 1.1). The study area ranged in elevation from 1360 m to 2180 m with an average of 1700 m above sea level. The dominant species was low sagebrush (*Artemisia arbuscula*), but other important species included mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) at higher elevations (~>1700 m), Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) at lower elevations (~<1500 m), and other interspersed shrub species including antelope bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* spp.), saltbrush (*Atriplex* spp.), and mountain mahogany (*Cercocarpus* spp.). Western juniper tended to occur in a patchy distribution from mid to high elevation.

METHODS

Nest and Random Locations

We captured sage-grouse hens in winter and spring 2009–2011 using spotlighting techniques (Geisen et al. 1982, Wakkinen et al. 1992) near leks and within known wintering habitats and fitted them with radio collars (22-g VHF radio-collars, Advanced Telemetry Systems, Isanti, MN, USA). Capture and handling methods were approved by the Oregon Department of Fish and Wildlife (Permit #008-12). We monitored marked hens using radio telemetry twice per week during the potential nesting seasons 2010 and 2011 until they began to occupy nesting habitat and were observed in the same place on 2 consecutive locations. We then visually observed nesting hens without flushing, and the nests were subsequently monitored twice per week until incubation was terminated (e.g., hatched, depredated).

When all nest locations were known each year, we produced fixed kernel probability distributions using the median nearest neighbor distance between nests as the bandwidth with the package adehabitatHR (Calenge 2006) in the R computing environment (R Core Team 2015). A number of random points approximately equal to the number of nests (slightly higher to account for potential late nests) were populated in the area between the 75% and 95% probability distribution, while restricting the points to greater than the minimum nearest neighbor distance of nests using ARCMAP 10.0 (Environmental Systems Research Institute, Redlands, CA, USA). This method was used as an approximation to unused/minimally used habitat by sampling in available (95% utilization distribution) but low probability habitat (between 75% and 95% utilization distribution). We assessed selection using both patch-scale vegetation variables measured at nests and random sites as well as landscape-scale variables measured using remote sensed data (Brennan et al. 2002).

We calculated median nearest neighbor distances between nests, random points, and all points combined for the reader's information, but could not separate autocorrelation-induced clustering from a habitat-induced inhomogeneous process, and therefore treated nests as independent replicates. We believed the major driver was habitat selection resulting in an inhomogeneous process that could be modeled with habitat covariates. Regardless of potential autocorrelation, our hens were representative of the population, and consequently, approximated population-wide selection.

Shrub Data

We surveyed vegetation at nests and random points between late May and early July each year after nest termination. We positioned an array of two 10-m orthogonal transects in a random orientation centered on the nest bowl or random point. We used the line intercept method (Canfield 1941) to estimate the percent cover for each shrub species and divided shrub cover into <40 cm and >40 cm tall (Connelly et al. 2000). We omitted overstory juniper cover (>2 m) from the analysis because it was not part of the shrub community, while shorter juniper (<2 m) was included in the analysis. Data within 1 m of the center of the crossed transects was removed from the shrub cover estimate to reduce bias induced from centering on the nest shrub (Musil 2011). We summarized the data into total shrub cover, total sagebrush cover, shrub cover >40 cm tall, and sagebrush cover >40 cm tall because 40 cm was reported as an important threshold for nesting (Connelly et al. 2000).

Herbaceous Data

We measured grass and forbs using ten 20 × 50-cm frames placed at 1, 3, 5, 7, and 9 m along each transect (Daubenmire 1959). In each frame, we estimated percent cover of all forbs and of 16 key forbs known to be important for nesting grouse and broods in the area (Barnett and

Crawford 1994, Drut et al. 1994, Gregg 2006). Key forbs included *Lomatium* spp., *Crepis* spp., *Agoseris* spp., *Astragalus* spp., *Orobanche* spp., *Trifolium* spp., *Phlox gracilis*, *Erigeron* spp., *Taraxacum officinale*, *Tragopogon dubius*, *Achillea millefolium*, *Aster* spp., *Mimulus* spp., *Gayophytum* spp., *Antennaria* spp., and *Blepharipappus* spp. We also estimated total grass cover, total herbaceous cover, and herbaceous cover >18 cm tall (Connelly et al. 2000). Herbaceous variables in the analysis included key forb richness, key forb cover, total forb cover, total grass cover, total herbaceous cover, and tall herbaceous cover.

Geospatial Data

We acquired remotely-sensed, 1-m resolution conifer data from the Natural Resources Conservation Service (M. J. Falkowski and J. S. Evans, U.S. Natural Resources Conservation Service, unpublished report; Poznanovic et al. 2014) consisting of a location and estimated crown diameter of individual conifer trees determined by spatial wavelet analysis (Falkowski et al. 2006, 2008; Strand et al. 2006). We calculated percent canopy cover within each of several circular buffers including radii of 50, 100, 200, 400, 800, and 1200 m around nests and random points which encompassed extents found in previous studies to be important in various sage-grouse life history stages (Doherty et al. 2010, Casazza et al. 2011, Baruch-Mordo et al. 2013). The smallest buffer was chosen because we believed it was the smallest reasonable size to evaluate given the resolution of the conifer layer. Doubling the radii in each successive buffer provided biologically meaningful size increases for sage-grouse, and quadrupled the area, minimizing spatial autocorrelation among buffers. The largest buffer was 1200 m because it was the smallest maximum distance from sampling points to the edge of the available conifer layer. We calculated a clustering index in each buffer by dividing the average nearest neighbor distance among trees in the buffer by the expected nearest neighbor distance with random dispersion. Therefore, an index of 1 was random while <1 was increasingly clustered and >1 was increasingly dispersed.

We calculated topographic characteristics to control for additional variation in the model. We used a 10-m resolution digital elevation model (DEM) to assign elevation, slope, and aspect values to each nest and random point in ARCMAP. Additionally, we calculated terrain ruggedness and landform (terrain curvature) within 100-, 400-, and 1200-m buffers using the Geomorphometry and Gradient Metrics Toolbox (version 2.0, http://evansmurphy.wix.com, accessed 2 December 2014) in ARCMAP. Ruggedness represents the variability in elevation (Riley et al. 1999), while landform represents the concavity (depression) or convexity (ridge; McNab 1989, Bolstad and Lillesand 1992). Ruggedness index units are arbitrary, but 0 indicates flat terrain and increasing values indicate more rugged terrain. Landform units are also arbitrary, but 0 is flat, while <0 is a depression and >0 is a ridge.

Data Analysis

We used random forest classification to discriminate between nests and random sites (Breiman 2001). Random forest classifiers are more resistant to collinearity of covariates than parametric models (Cutler et al. 2007), but variable reduction may decrease error and improve interpretation (Liaw and Wiener 2002, Murphy et al. 2010, Evans et al. 2010). We assessed related groups of variables for collinearity and compared variables within groups to the response to preliminarily select variables for the random forest model. Groups included the buffers of conifer canopy cover, conifer clustering, ruggedness, and landform as well as the shrub variables and the herbaceous variables. Information criteria and amount of variance explained in the response can be used to select the most appropriate scale size (Brennan et al.

2002, Jackson and Fahrig 2015) and we used these criteria with a combination of linear and nonlinear methods to select variables in each group. We calculated pairwise Pearson correlation coefficients between each pair of variables in each group as well as between each variable and the response (nest = 1, random = 0) to determine potential strength and direction of response. Additionally, to assess potential nonlinear associations, we fit logistic generalized additive models (GAM) between each covariate and the response in R (R Core Team 2015) using the mgcv package (Wood 2006). We fit smooths with cubic regression splines with an optimal smoothing term calculated using generalized cross-validation. We then assessed the deviance explained by the GAM and the associated Akaike's information criterion (AIC) along with the correlation coefficients to select the variables to be used in the final model. The values within the different variable groups and buffers were highly correlated (e.g., correlation coefficient for conifer cover ranged from 0.67 to 0.96 among buffers). When variables within groups were compared to the response (nest/random), there was agreement among the linear correlation and the univariate nonlinear deviance and AIC about which variable most influenced the response in all cases except in the landform group where 2 buffer sizes with opposite effects were selected. We applied the random forest classifier with function rfsrc in the randomForestSRC package (version 1.6.0, www.cran.r-project.org, accessed 20 February 2015) to these variables with nest versus random as the response and then used the var.select function in package rfsrc to apply minimal depth variable selection to determine if additional variables needed to be removed (Ishwaran et al. 2010). We produced 3000 classification trees in the random forest and used default values for the other parameters.

We assessed the accuracy of the final model with the out-of-bag error rate and the confusion matrix to ensure balanced nest and random site classification. Additionally, we used 30 iterations of 10-fold cross-validation using the errorest function in the ipred package (version 0.9-3, www.cran.r-project.com, accessed 20 February 2015) to produce an additional estimate of error rate as recommended by Evans et al. (2010). We also calculated the relative importance of each variable in the model and produced partial dependence plots to assess the marginal selection response to each variable, standardizing the response axis between 0 and 1 to aid in interpretation. To verify our buffer size choice for the conifer characteristics, we calculated the error of 30 iterations of 10-fold cross-validation of the random forest model for each buffer size of canopy cover and clustering in turn, while maintaining all other variables in the model, and calculated the median error for each buffer size.

To explore the results of the random forest further, we produced box plots comparing nests to random shrub and conifer cover in various habitat types including Wyoming big sagebrush (WBS), WBS/low sagebrush (LS) association, LS, LS/bitterbrush (BB) association, mountain big sagebrush (MBS), and mountain shrub which included associations among MBS and other shrubs such as BB, mahogany, and/or snowberry (*Symphoricarpos* spp.). We compared shrub and conifer canopy cover at nest and random sites in each habitat type using one-way analysis of variance (ANOVA) to aid in interpretation of primary effects in the predictive model.

RESULTS

We located and surveyed 160 nests and 167 random points in 2010 and 2011 (Figure 1.1). The median nearest neighbor distance between nest points, random points, and all points combined was 405 m, 652 m, and 502 m, respectively. Variables selected based on correlation, deviance, and AIC included percent shrub and forb cover, conifer cover and clustering at 800 m, ruggedness at 100 m, landform at 100 m and 1200 m, elevation, slope, and aspect. The nonlinear deviance and AIC indicated the 100-m buffer of landform was most influential while the linear correlation indicated the 1200-m buffer was most influential. Additionally, the linear correlations of the 2 buffers with the response indicated opposite effects (i.e., the 100-m buffer had a negative effect). Therefore, both buffers were retained in the final model. When we applied the random forest with minimal depth selection, no additional variables were removed. Because the conifer clustering index was undefined with no trees present, only sites with conifers within 800 m could be used in the analysis, resulting in a sample size of 153 nests and 152 random sites.

The random forest error stabilized at 2000 classification trees indicating that maximum achievable predictive accuracy had been achieved. The final model had 23.3% out of bag error indicating adequate classification success. The predicted error rate was 22.7% for nests and 23.9% for random sites indicating a balance in classification of the response classes. The 10-fold cross-validation error was 24.9%. Shrub cover was the most important variable affecting nest-site selection, followed by conifer clustering within 800 m, forb cover, elevation, and conifer cover within 800 m, while 5 of the 6 terrain features (i.e., aspect, landform within 100 m and 1200, ruggedness within 100 m, and slope) were less important (Figure 1.2). The correlation between canopy cover and clustering of trees was high ($r = 0.65$). However, removing each of these variables in turn increased predictive error by 3–4 percentage points, indicating that both variables improved the model. When we substituted each buffer size for conifer canopy cover and clustering, the 800-m buffer was justified as the best scale producing the lowest error rates (Figure 1.3). The clustering index in the 50-m buffer produced a slightly lower error rate (Figure 1.3), but due to the index being undefined in the absence of trees, only 50 nests were assessed potentially inducing imprecision and bias, and therefore was not selected. The buffer size for conifer cover had lower influence on the results than clustering due to high correlation of canopy cover among buffers (Figure 1.3).

The probability of nest-site selection had a monotonically increasing response to increasing shrub cover along the 10-m transects but became asymptotic above ~30% shrub cover (Figure 1.4A). The response to forb cover increased sharply to ~3% cover and then leveled off (Figure 1.4B). The response to conifer clustering within an 800-m radius was high at low to mid values of clustering (<0.6; i.e., clustered), but dropped off sharply at ~0.7 and remained low at values >1 (i.e., random to dispersed; Figure 1.4C). The probability of nest-site selection was high with conifer cover up to ~3% but dropped off sharply by 4% and remained low at higher percent cover (Figure 1.4D). There was a low probability of selection at low elevations, but the probability increased at mid to high elevations (Figure 1.5A). Nesting hens selected northeast, east and southeast slopes (Figure 1.5B). For the landform variable, they selected ridges at large scale (1200 m, Figure 1.5C), but depressions at small scale (100 m, Figure 1.5D). Furthermore, they selected less rugged terrain at the 100-m scale (Figure 1.5E) and moderate slopes (5–20 degrees, Figure 1.5F).

There was low conifer cover in the WBS (nests [N]: 0.17% ± 0.10 SE, random [R]: 0.45% ± 0.22 SE, $F_{1,18} = 0.66$, $p = 0.428$) and WBS/LS (N: 0.24% ± 0.16 SE, R: 0.21% ± 0.12 SE, $F_{1,15} = 0.02$, $p = 0.893$) habitat types and the differences between nests and random were not significant (Figure 1.6A). There was slightly more conifer cover in LS (N: 1.40% ± 0.21 SE, R: 1.84% ± 0.30 SE, $F_{1,148} = 1.34$, $p = 0.249$), but there was not a significant difference between nests and random sites. There was more conifer cover at the random sites in the

LS/BB, MBS, and mountain shrub habitat types, but nests generally occurred in areas of less conifer cover than random sites although the difference in MBS was not significant (LS/BB N: 1.20% ± 0.26 SE, R: 3.73% ± 0.76 SE, $F_{1,39} = 12.78$, $p < 0.001$; MBS N: 2.64% ± 1.88 SE, R: 5.52% ± 0.77 SE, $F_{1,8} = 2.64$, $p = 0.143$; mountain shrub N: 2.16% ± 0.32 SE, R: 3.87% ± 0.61 SE, $F_{1,59} = 7.37$, $p = 0.009$; Figure 1.6A). Additionally, nests in WBS generally occurred in areas with less shrub cover than random (N: 20.6% ± 2.1 SE, R: 28.8% ± 3.4 SE, $F_{1,18} = 2.26$, $p = 0.150$), while shrub cover was greater at nests than random sites in all other habitat types, although the only significant differences were in LS (N: 27.9% ± 1.4 SE, R: 18.7% ± 1.3 SE, $F_{1,148} = 23.10$, $p < 0.001$), LS/BB (N: 39.7% ± .3 SE, R: 28.5% ± 3.5, $F_{1,39} = 5.08$, $p = 0.029$), and MBS (N: 37.3% ± 9.5, R: 13.3% ± 4.4 SE, $F_{1,8} = 6.60$, $p = 0.033$), while nests in WBS/LS (N: 22.5% ± 3.1 SE, R: 21.2% ± 4.2 SE, $F_{1,15} = 0.06$, $p = 0.812$) and mountain shrub (N: 37.3% ± 2.3 SE, R: 33.9% ± 3.7 SE, $F_{1,59} = 0.68$, $p = 0.414$) were not significantly different than random (Figure 1.6B).

DISCUSSION

Our study represents the first empirical evidence of sage-grouse avoidance of conifer for nesting at landscape scales. We observed negative effects of encroaching conifer on sage-grouse nesting habitat at a broad scale (800 m) with relatively low canopy cover (~4%). Previous work has demonstrated similarly low tolerance levels of conifers both on breeding areas (Baruch-Mordo et al. 2013) and in wintering areas (Freese 2009). Incorporating data on spatial configuration, we found sage-grouse nesting where trees were more clustered as opposed to dispersed. This selection may be driven by open space availability in the interspaces between tree clusters. Likewise, Baruch-Mordo et al. (2013) observed decreasing lek occupancy as trees become more dispersed rather than clustered.

Shrub cover was the most important variable in nest-site selection in our study which is consistent with the results of a meta-analysis showing total shrub cover had a larger effect size than sagebrush cover, grass cover, forb cover, and grass height (Hagen et al. 2007). Because shrub cover is inversely related to conifer cover (Miller et al. 2011), direct negative effects of conifer encroachment on nesting habitat would be expected to increase through time as woodland succession progresses. When we considered shrub cover by habitat, sage-grouse selected the greatest shrub cover in LS, LS/BB, MBS, and possibly mountain shrub (Figure 1.6B). Low sagebrush/BB, MBS, and mountain shrub are also the habitat types that are most impacted by conifer encroachment (Figure 1.6A, Davies et al. 2011). Strong selection for shrub cover may override avoidance of conifers of short height and low cover, which may explain why selection was not impacted until >3% conifer canopy cover (Figure 1.4D). Hens may perceive these low-density areas in the early stages of encroachment as suitable habitat due to the vegetation cover, but research is needed to determine if nest success is affected by avian predators due to increased available perch sites, thereby producing a possible ecological trap. However, as conifer cover surpasses a threshold (i.e., >3%), selection decreases regardless of shrub cover. It is currently unknown if removing conifers in these areas can increase habitat availability and quality to potentially improve nest success and increase populations (Taylor et al. 2012). Although lacking adequate study designs to conclusively attribute observed responses to conifer removal, previous research has indicated potential benefits, including increased populations and habitat selection, as a result of removing conifer in sage-grouse habitat (Commons et al. 1999, Frey et al. 2013).

Previous studies have found effects of topographic features on sage-grouse habitat selection (Yost et al. 2008, Doherty et al. 2010, Aldridge et al. 2012, Baruch-Mordo et al.

2013), but while important in our study, we found vegetation characteristics to be more influential in nest-site selection. It is possible that these terrain features may be merely indicators of or surrogates for habitat variables that were not measured. For example, better quality habitat types (e.g., MBS, mountain shrub) and greater conifer abundance occur at higher elevations due to increased available moisture (Miller and Eddleman 2001, Miller et al. 2005), while lower quality habitat types (e.g., WBS) and less conifer occur at lower elevations. Landform was not correlated with the other variables, but by definition, the greater landform index at 1200 m (ridges), which we observed to be selected, was slightly higher in elevation than the immediate area. An inspection of landform index at 100 m overlaid on an aerial photograph revealed that many of the low index areas where we observed nests often delineated areas of MBS and mountain shrub habitat as well as encroaching conifer indicating greater moisture and nutrient availability (McNab 1993). Sage-grouse hens in our study area selected nest sites in depressions on high-elevation ridges in or near MBS or mountain shrub sites. These community types have a greater chance of being invaded by conifers (Miller and Eddleman 2001, Miller et al. 2005), potentially causing a tradeoff between higher quality habitat near trees compared to lower quality habitat further from trees.

We encourage some caution with interpretation of exact threshold values from our work because conifer covariates were derived from modeled surfaces in GIS. The data were produced using spatial wavelet analysis on the normalized difference vegetation index of 4-band, 1-m resolution aerial imagery (Falkowski et al. 2006, Strand et al. 2006). Ground- based estimates of cover using traditional methods, such as line intercept, would likely yield different cover estimates than remote sensing data (Ko et al. 2009). Poznanovic et al. (2014) reported high correlation between the wavelet data and reference plots, but the wavelet data slightly underestimated canopy cover because smaller trees may not be detected (Strand et al. 2006). However, larger trees may have more impact on the habitat and sage-grouse behavior than smaller trees (Baruch-Mordo et al. 2013), potentially because smaller trees often resemble the size structure of the rest of the shrub community and provide limited perches for avian predators. These remotely sensed data are increasingly being used by land managers and researchers as they become available, thereby allowing our results to be comparable to their assessments.

Our results complement a growing body of research on grassland and sagebrush obligate bird species which have shown varying tolerances to tree encroachment. Grassland bird species occurrence was reduced to ~0% with 20–60% canopy cover at 500-m scale (Grant et al. 2004), while Cunningham and Johnson (2006) found multiple important scales up to 1600 m with ~0% occurrence at <20% cover for some bird species. Generally, thresholds of sagebrush obligate songbirds were <50% cover at 1000-m scale (Noson et al. 2006). Counts of lesser prairie-chickens (*Tympanuchus pallidicinctus*) were negatively associated with increasing tree cover within 4.8 km of leks (Fuhlendorf et al. 2002). Additionally, no lesser prairie-chicken nests were found in habitat with >2 trees/ha (Lautenbach 2015). In sum, these studies indicate general negative effects of tree encroachment at large scales on a wide variety of grassland and sagebrush obligate birds, illustrating the importance of this fundamental shift in habitat structure in determining habitat suitability for a host of species dependent upon grass and shrub-dominated systems.

MANAGEMENT IMPLICATIONS

Our results further confirm the negative effects of conifer encroachment on sage-grouse habitat and support the inclusion of conifer removal as a key strategy in rangewide efforts to conserve sage-grouse (Natural Resources Conservation Service [NRCS] 2015, USFWS 2015). To maintain suitable nesting habitat, conifer should be reduced to well below 4% canopy cover over at least a 200-ha area (i.e., 800-m radius around potential nest sites). In areas where conifer cover has been reduced to <4% but it is necessary to leave some trees on the landscape for other resource purposes, priority should be placed on removing dispersed trees and leaving few, larger stands of clustered trees in the more rugged terrain to minimize impacts on nesting habitat potential. Targeted conifer removal efforts are clearly needed to maintain existing nesting habitats affected by encroachment and may increase available nesting habitat in areas currently unsuitable, collectively resulting in population-wide benefits where nest habitat is a limiting factor.

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Associate Editor:

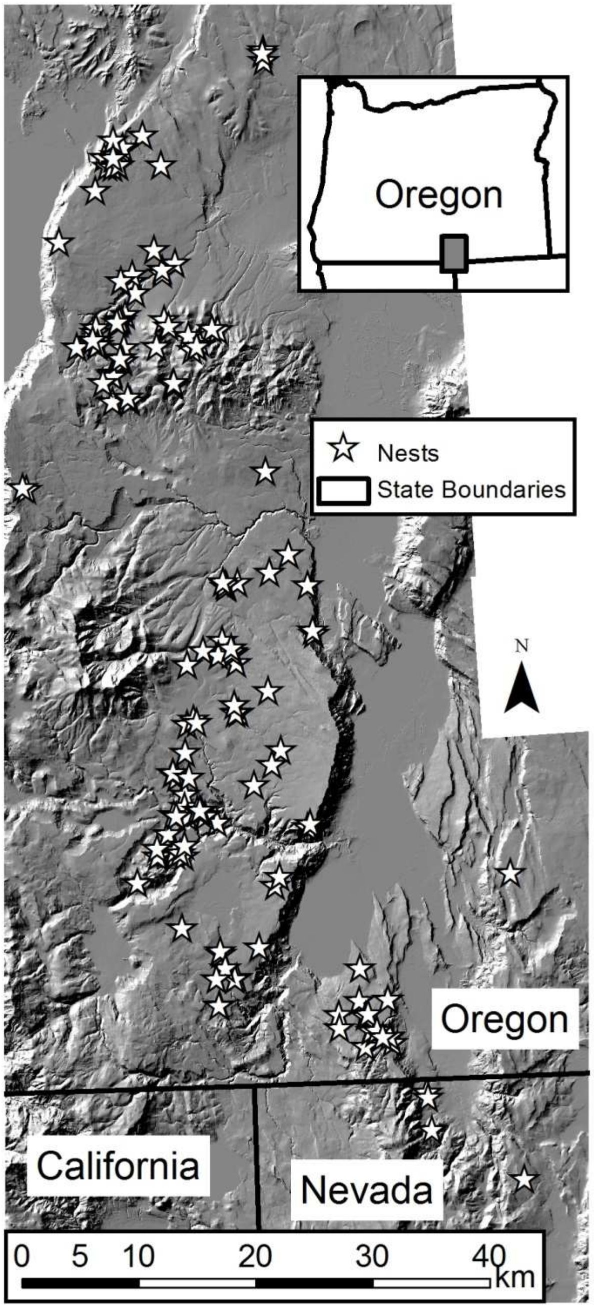

Figure 1.1. Map of the study area in southeastern Oregon with the Warner Mountains on the left and Warner Valley on the right and nests of greater sage-grouse from 2010–2011 depicted as stars. The base map is a hillshade showing the terrain. Inset shows study area location in Oregon.

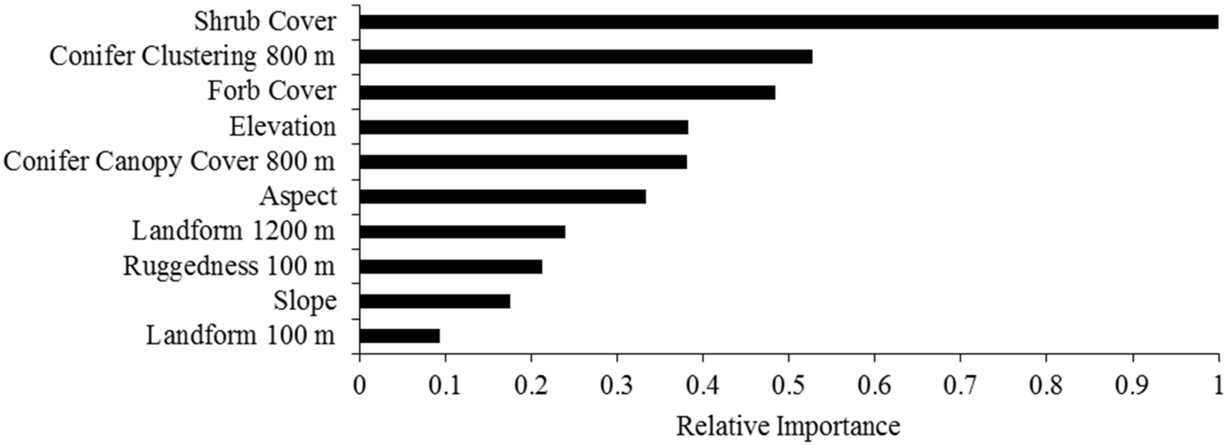

Figure 1.2. Relative importance (standardized to 1) of variables in random forest model of greater sage-grouse nest-site selection in southeastern Oregon from 2010–2011. The number in the variable represents the selected scale (radius in m) around the points, while shrub and forb cover were measured within 5 m of the point, and elevation, aspect, and slope were measured from the 10-m resolution digital elevation model.

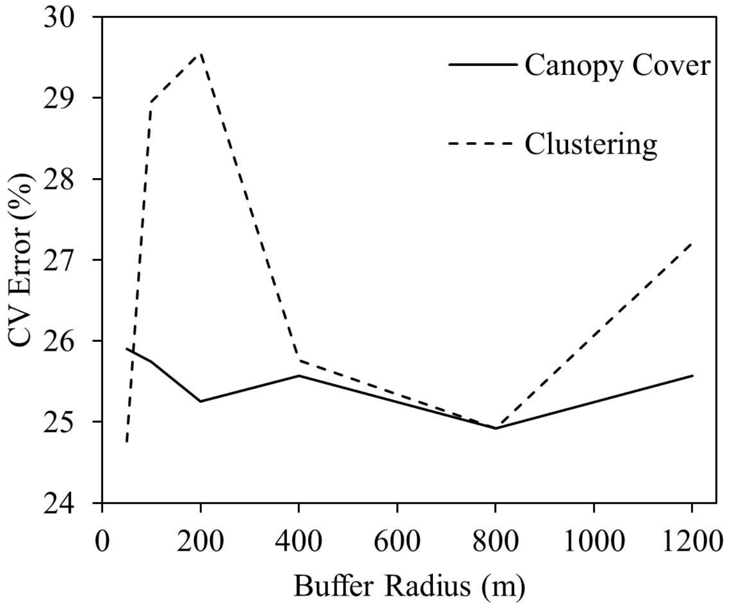

Figure 1.3. Effects of varying buffer sizes from 50–1200 m on cross-validated (CV) random forest error of conifer characteristics on greater sage-grouse nest-site selection in southeastern Oregon from 2010–2011.

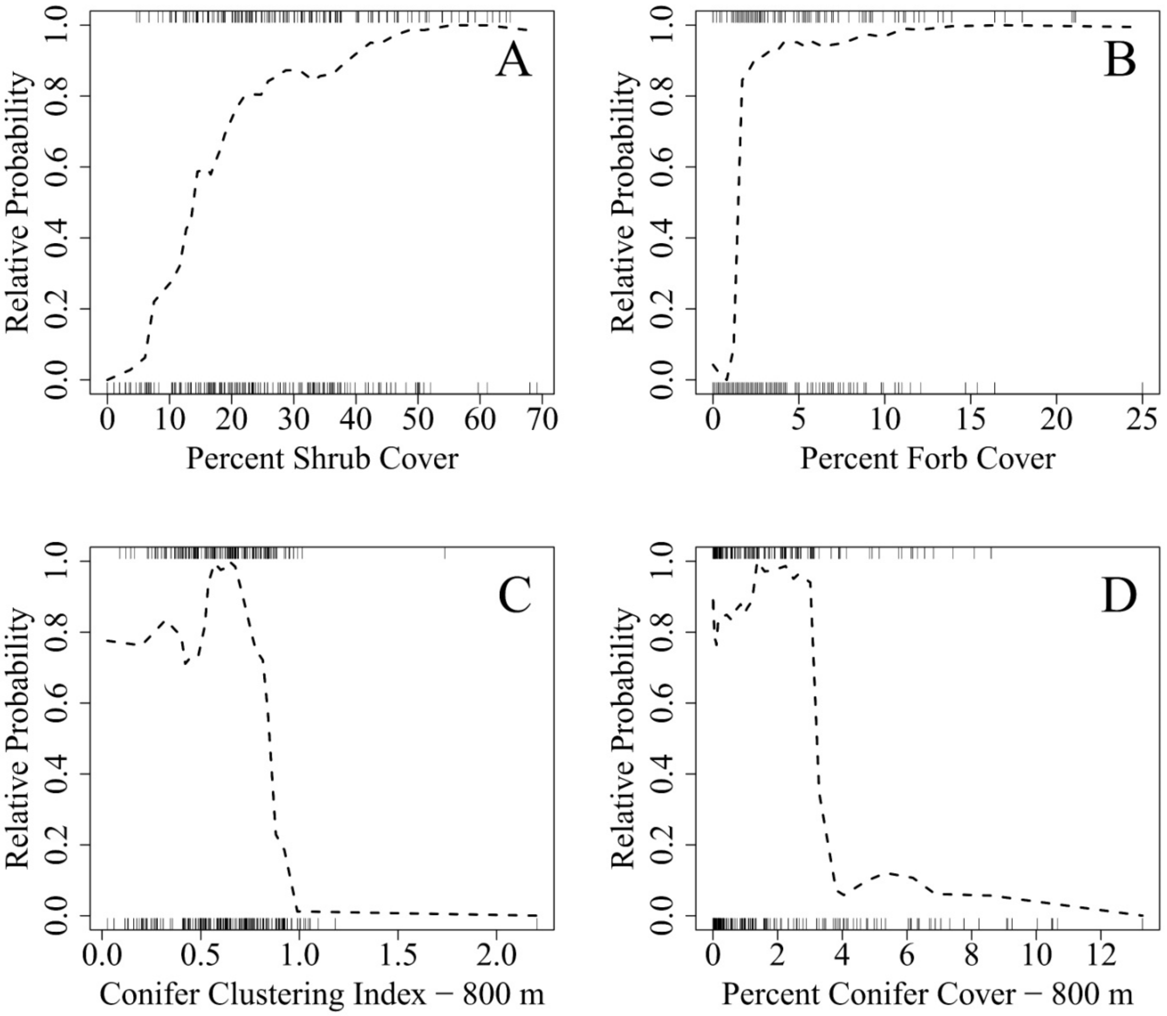

Figure 1.4. Partial dependence plots for vegetation and conifer characteristics with standardized probability of greater sage-grouse nest-site selection in southeastern Oregon from 2010–2011. Tick marks at the top of the plots are data at nests and tick marks at the bottom are data at random sites. A) Percent shrub cover within 5 m. B) Percent forb cover within 5 m. C) Conifer clustering index within 800-m buffer. D) Percent conifer canopy cover within 800-m buffer.

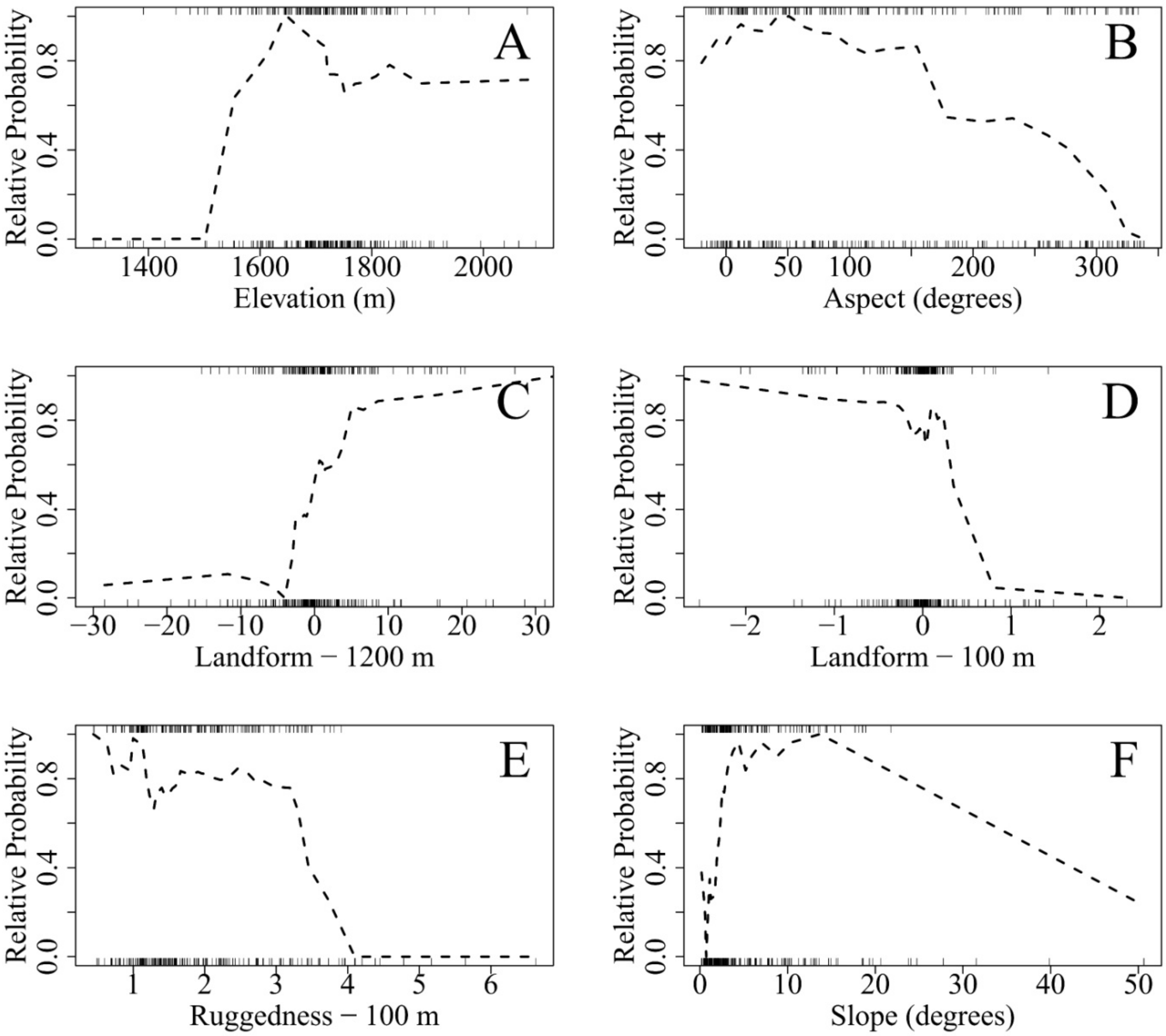

Figure 1.5. Partial dependence plots for terrain characteristics with standardized probability of greater sage-grouse nest-site selection in southeastern Oregon from 2010–2011. Tick marks at the top of the plots are data at nests and tick marks at the bottom are data at random sites. A) Elevation. B) Aspect. C) Landform within 1200-m buffer. D) Landform within 100-m buffer. E) Terrain ruggedness within 100-m buffer. F) Slope.

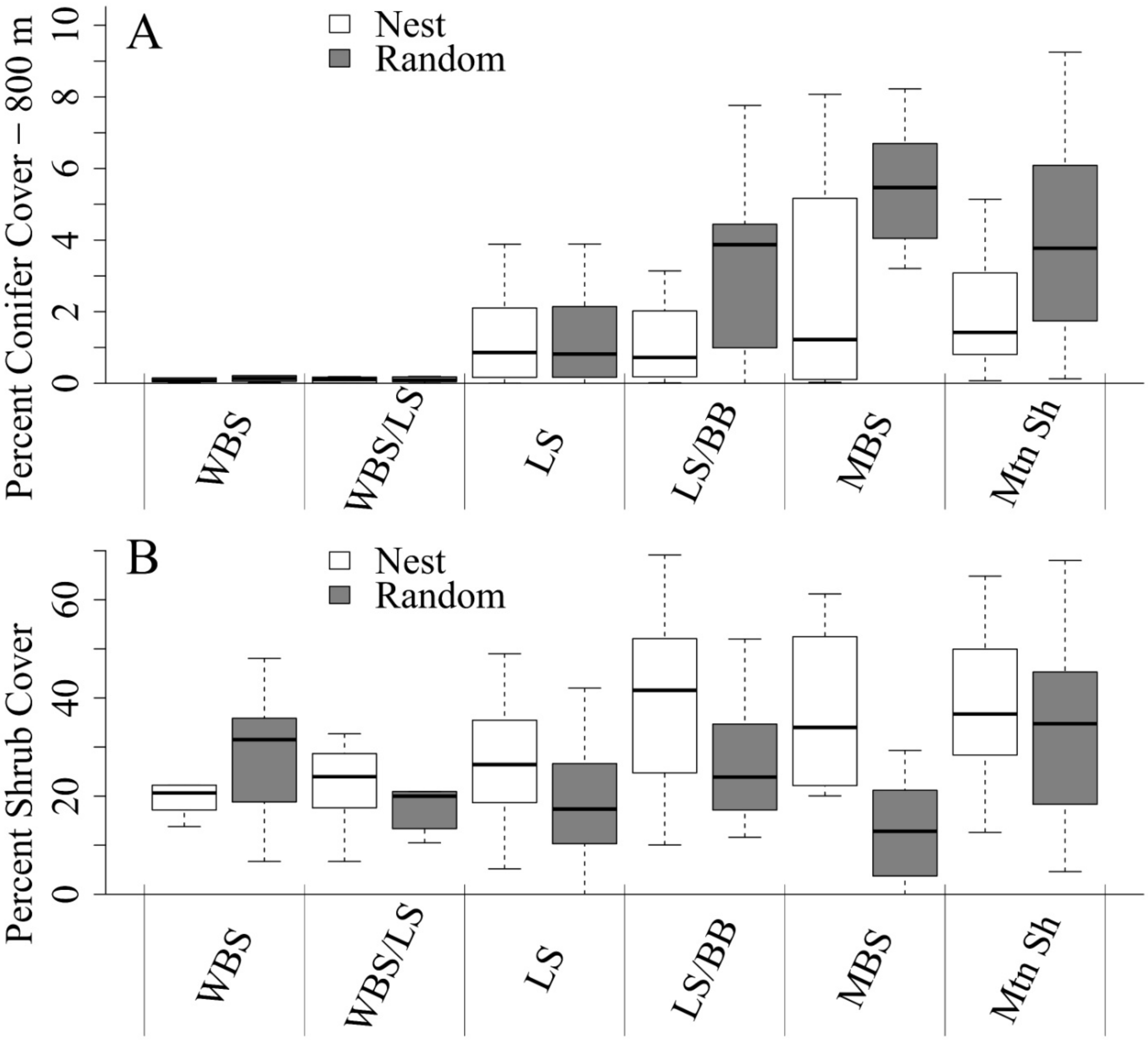

Figure 1.6. Comparison of A) conifer cover and B) shrub cover between greater sage-grouse nests and random sites in different habitat types of southeastern Oregon from 2010–2011. The boxes represent the interquartile range (IQR) with median. The whiskers are the lesser of either the IQR or the difference between the median and the minimum or maximum. WBS = Wyoming big sagebrush; LS = low sagebrush; BB = bitterbrush; MBS = mountain big sagebrush; Mtn Sh = mountain shrub.

CHAPTER 2

SHORT-TERM RESPONSE OF SAGE-GROUSE NESTING TO CONIFER REMOVAL IN THE NORTHERN GREAT BASIN

Submitted to Rangeland Ecology and Management

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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 (BACI) 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 years 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.

Keywords: conifer management, encroachment, Great Basin, sagebrush steppe, sage-grouse, western juniper

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, Briggs et al. 2002, Davies et al. 2011, Grant et al. 2004, Miller et al. 2005, Miller et al. 2011, Miller and Tausch 2001). 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 et al. 2005, Miller ant Tausch 2001). 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 reduces grass and forb abundance and diversity by limiting of 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 lowers the water table and reduces spring and stream-flows (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 where conifers co-dominate the vegetation community (Phase-II), and ending with a landscape 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 (Maser et al. 1984a, 1984b; Miller et al. 2005; O'Meara et al. 1981; Sedgewick 1987); however, most are generalist or forest-dependent species which flourish while sagebrush-obligate birds and mammals decline (Coppedge et al. 2004, Grant et al. 2004, Horncastle et al. 2005, Lloyd et al. 1998, 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 (Doherty et al. 2010, Gregg 1992), 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 (Manzer and Hannon 2005, Paton 1994, Wolff et al. 1999), 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 upon which they depend (USFWS 2015). A combination of land management policy revisions and restoration 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 during 2010–2014, the amount of conifer-encroached lands treated by partners through the Sage Grouse Initiative (SGI) grew 1411%, 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 (*C. 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 help 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.

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. 2.1). We delineated discrete boundaries for treatment and control study areas guided by natural barriers (e.g., canyons, cliffs, and forest) as well as observed sage-grouse movements (Fig. 2.1). 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. Both areas were dominated by low sagebrush (*Artemisia arbuscula*) habitat, but other dominant species included MBS at higher elevations, 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 dominated by MBS but also included 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

Bureau of Land Management (BLM) removed juniper on federal land while the Natural Resources Conservation Service in association with the Oregon Department of Fish and Wildlife assisted landowners with juniper removal on private land within and surrounding the treatment area (Fig. 2.1). 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 brush- 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 year 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 pre-settlement trees in locations that historically supported juniper, thus some areas still had standing trees after treatment (BLM 2011). BLM biologists identified pre-settlement 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 2007–2011 (<10%), most occurred from 2012–2014 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 2.1; Fig. 2.1).

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 (Geisen et al. 1982, Wakkinen et al. 1992) near leks and wintering habitat. We strived for sample sizes of ~40 radioed (22-g VHF radio-collars, model #A4060, Advanced Telemetry Systems, Isanti, MN, USA) females at start of nesting (~1 April) in each of the two areas. We monitored radio-marked females twice per week during the potential nesting seasons from 2010–2014. 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 re-nested after failure during the same year (n = 19). Although autocorrelation in these instances likely exists, we believe including all data was more beneficial than disregarding these pseudo-replicates.

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. Age of the treatment polygons was calculated as number of years since treatment. 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 (see Chapter 1). 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 (GAM) 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 further distances were unlikely to affect selection of treated areas. 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 prior to 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; Anderson 2008, Golub et al. 1979). 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 10-fold cross validation (CV; Breiman and

Specter 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 2.2). 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 classification probability ±1.96 standard errors 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 2012 (<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. Because amount of treated area increased through time (Table 2.1), 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 by 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 as well as 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 153 and 117 females in treatment and control areas. Marked females enabled us to locate 153 (2010–2014) and 109 (2011–2014) nests in the treatment and control areas, respectively (Table 2.3). 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 2.2) had the lowest CV MCE and highest CV AUC of all full models and was used as the global model for variable selection (Table 2.2). The model with the variables cut age and distance to the closest cut (Model 6 in Table 2.2) had the lowest CV MCE (0.392) and highest CV AUC (0.653; Table 2.2) 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. 2.2A) while distance to nearest cut area had a negative effect (coefficient = –0.00056; Fig. 2.2B) on nest-site selection. The odds ratio for the age of cut was 1.22463 annually or a 22% increase in probability of use each year following treatment. Odds ratio for distance to nearest treatment was 0.99944 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. 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. 2.3). 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 (±480 SE) of additional nesting area annually and a 9.5% (±1.2 SE) annual increase in nests in MBS habitat (Table 2.3; Fig. 2.3C, 2.3D).

Discussion

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 population-level benefits to increase through time based on 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 re-invade and cover reaches intolerable thresholds (see Chapter 1), 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. this issue).

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). An indicator of nest fidelity, median distance between consecutive sage-grouse nests in Idaho was 0.7 km and ranged >2.0 km for adults and >2.5 km for juveniles (Fischer et al. 1993). Nesting fidelity can vary widely as evidenced in fragmented habitats of Washington state where average distance between re-nesting females was 2.6 km and ranged up to 26.6 km, and the same measure between consecutive year nests was 3.0 km and ranged up to 32.9 km (Schroeder and Robb 2003). Birds may have nested in treatments soon after restoration because sage-grouse already occupied nearby un-encroached habitats; we caution that restorative cuts placed further from occupied habitats may take longer to be used. In southeast Idaho, nesting females remained faithful to areas despite losing 25% of available habitat to wildfire (Fischer et al. 1993). In contrast, nearly a third (29%) of nesting females readily shifted into mountain big sagebrush habitats once cleared of encroaching conifer in our area. More research may be needed to learn how shifting habitat mosaics affect nest-area fidelity.

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 vegetation map of the area, we were unable to assess the shift in habitat use more directly, but our evidence supports the idea of a shifting habitat mosaic. We believe that available nesting habitat may be a limiting factor because much of the high quality habitat in this area was conifer encroached. Conifer removal in these areas appears to reduce avoidance of otherwise suitable nesting habitat, and should theoretically lead to population increases, although demographics should be assessed for potential ecological traps (Coates et al., this issue). MBS communities are disproportionately affected by encroachment due to favorable site conditions for tree growth (Miller et al. 2005), thus conifer removal in these areas could be beneficial under changing climate patterns as sage-grouse may need to shift their distributions to higher elevations.

The results of our separate analyses indicate that conifer removal encourages nesting by sage-grouse. We used an 800-m radius to calculate the proportion of treatment area based on our previous research (see Chapter 1), but treatment effects may occur at other unassessed scales. We found 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 negative impact of conifer stands on sage-grouse is larger than the actual area of the stand. Consequently, removing conifer has a larger positive footprint than the actual area removed; thus more nesting habitat may 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%) indicating landscape-scale conifer removal may be needed to benefit sage-grouse.

Although tree removal has long been suggested for conserving prairie and sage-grouse (Connelly et al. 2000, Grange 1948, Hagen et al. 2004, Hamerstrom et al. 1952), few studies have actually quantified effects (Hagen et al. 2004, USFWS 2015). Many studies have documented negative effects of woody encroachment on prairie grouse (Cassaza et al. 2011, Freese 2009, Luatenbach 2015, McNew et al. 2012). Our study represents a major step forward in evaluating the effects of landscape-scale habitat restoration for sage-grouse and prairie grouse in general. 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. Pre- and posttreatment tree cover and size, and 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. Future analyses will directly assess survival and habitat selection throughout the year, but this was beyond the scope of this paper.

Implications

When nesting habitat is a limiting factor to a sage-grouse population in a conifer encroached system, tree removal appears to be a viable option for improving habitat availability. We have shown that nesting habitat increases after treatments and treated areas become more beneficial with time. Treatments should target areas which are thought to be nesting habitat that has been excluded by conifers. We showed that nesting in these previously encroached habitats (e.g., mountain big sagebrush) can increase after treatment. Nesting in and near treated areas increases dramatically when conifer is removed, but we did not determine scales of selection here. Planning conifer removal at appropriately large scales is important as 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.

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Table 2.1. Area of cut and slash burned conifer in the treatment study area each year in southern Oregon used to assess greater sage-grouse response to conifer removal. The greater treatment area included the treatment area as well as the immediate surrounding area (see Fig. 2.1).

	Treatment Area		Greater Treatment Area		Average
Year	Cut (ha)	Slash Burn (ha)	Cut (ha)	Slash Burn (ha)	Size (ha)
2007	143	—	143	—	72
2010	17	—	57	—	29
2011	432	—	781	—	71
2012	2073	95	2709	97	68
2013	1331	991	2288	1989	76
2014	2492	1191	3465	1454	144
Total	6488	2277	9443	3540	87

Table 2.2. Models and selection criteria in generalized additive mixed model habitat selection analysis for greater sage-grouse in Oregon. Values under the variable heading are number of knots used in smoothing. The maximum number of knots from burn age was 3 due to limited number of years. linear = 2 knots. Dashes represent an unused variable. MCE = cross-validated mean class error. AUC = cross-validated area under the curve. AIC = Akaike's information criterion.

	Variable				Selection Criteria		
Model	Cut Age	Burn Age	Cut Proportion	Distance Close	MCE	AUC	AIC
Model 1	5	3	5	5	0.402	0.630	7009.1
Model 2	5	3	5	linear	0.406	0.621	7134.0
Model 3	5	3	linear	linear	0.399	0.633	7140.9
Model 4[1]	linear	linear	linear	linear	0.394	0.646	7159.8
Model 5	linear	linear	—	linear	0.393	0.650	7160.1
Model 6[2]	linear	—	—	linear	0.392	0.653	7164.9
Model 7	—	—	—	linear	0.394	0.643	7207.5

[1] Global model selected for variable selection.

[2] Selected best model.

Table 2.3. Summarized greater sage-grouse nest data for each study area in southern Oregon.

	Nests		Area (ha)[1]		MBS Proportion[2]	
Year	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	15883	13153	0.50	0.31
2014	36	28	13475	8875	0.50	0.18
Average	30.6	27.3	7749	8914	0.42	0.23

[1] 95% kernel density estimate of nest locations

[2] Proportion of nests in mountain big sagebrush (MBS) and mountain shrub habitats.

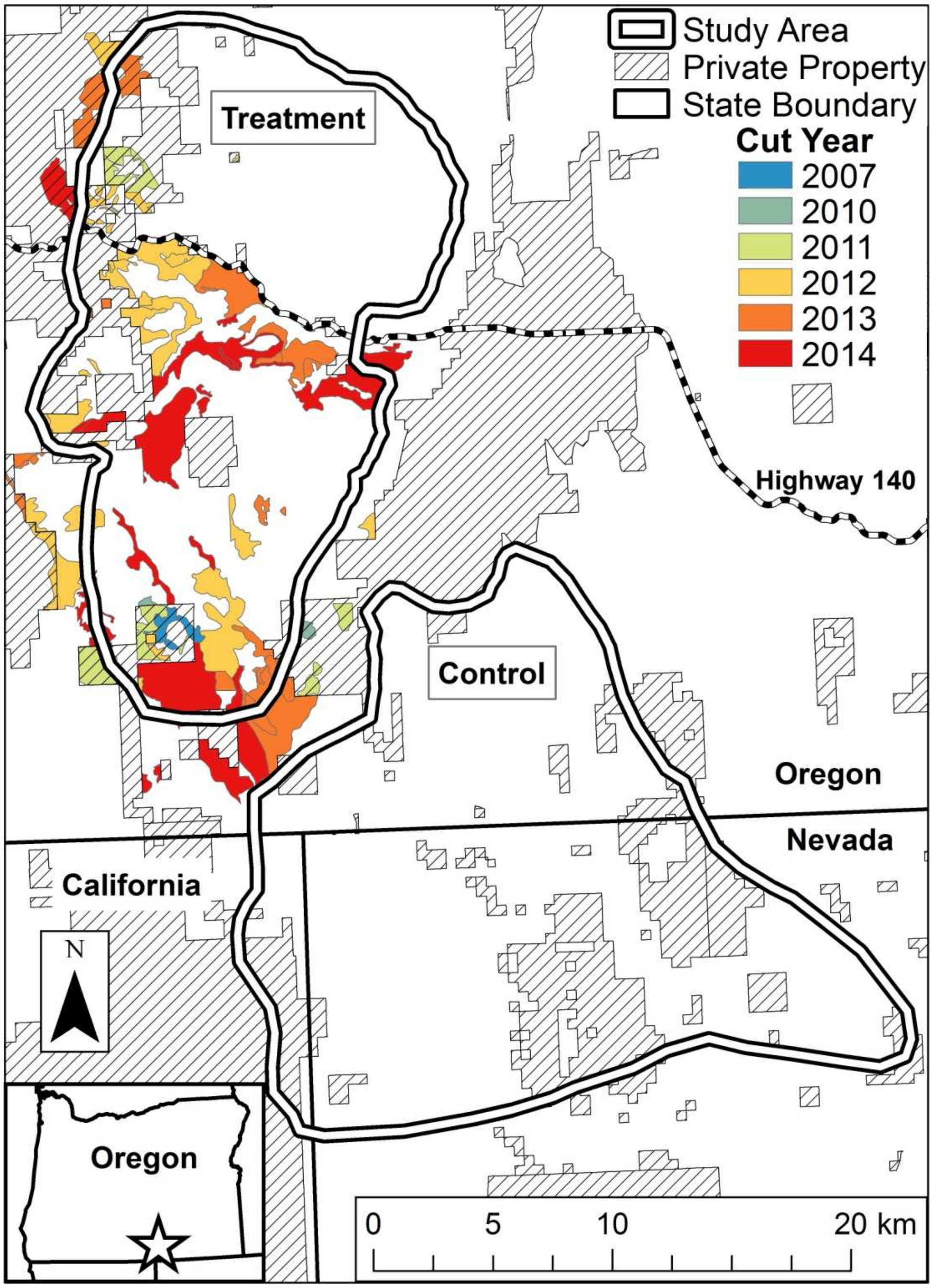

Figure 2.1. Treatment and control study areas in southern Oregon (star in inset) used to assess greater sage-grouse response to conifer management. Colored polygons delimit years of conifer removal. Although some removal began as early as 2007, a majority of the cutting began in 2012.

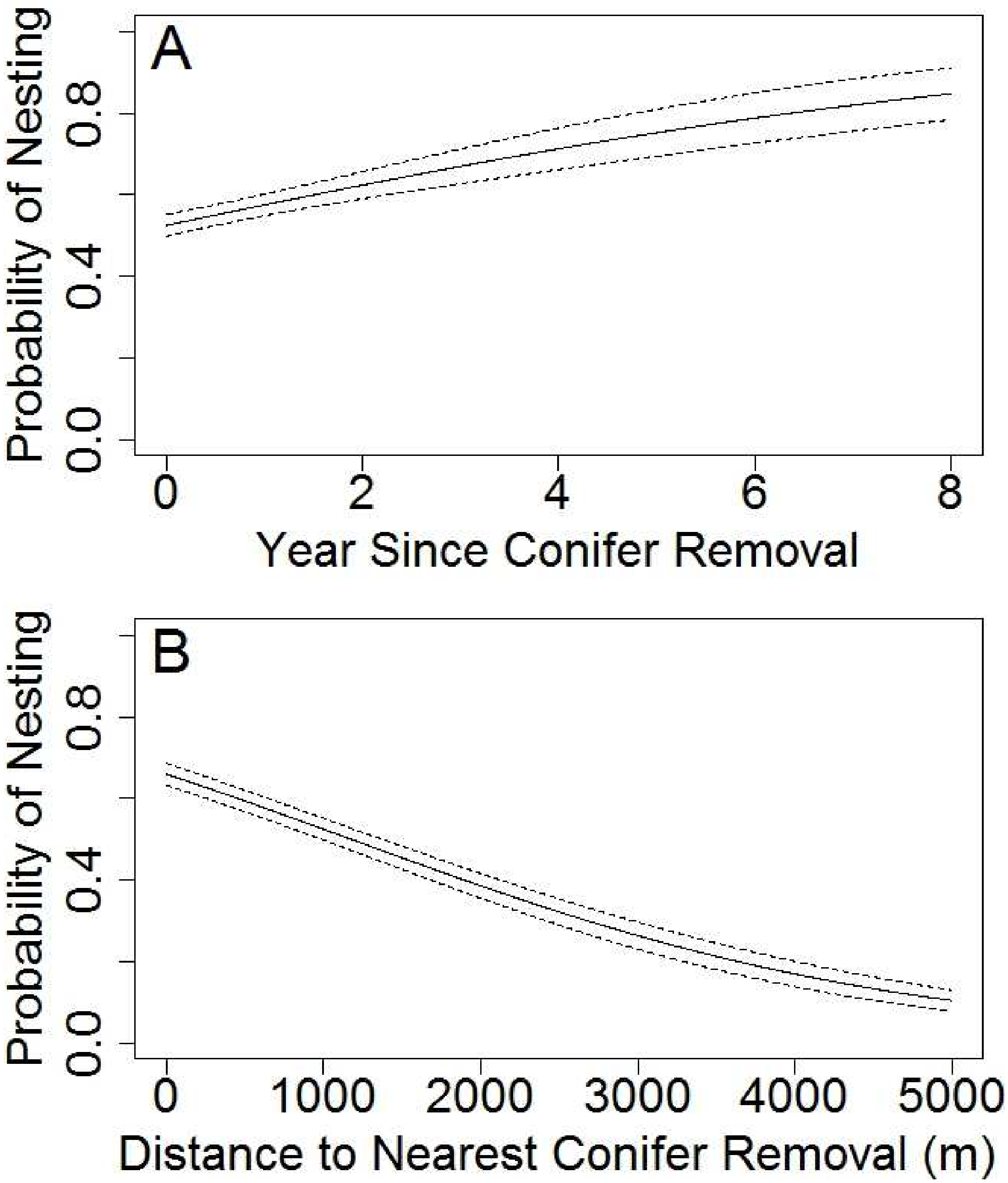

Figure 2.2. Response plots for probability of greater sage-grouse nesting relative to conifer removal areas in Oregon. Probability of nesting A) in a treated area as a function of time since cut and B) near a treated area as a function of distance to nearest removal area.

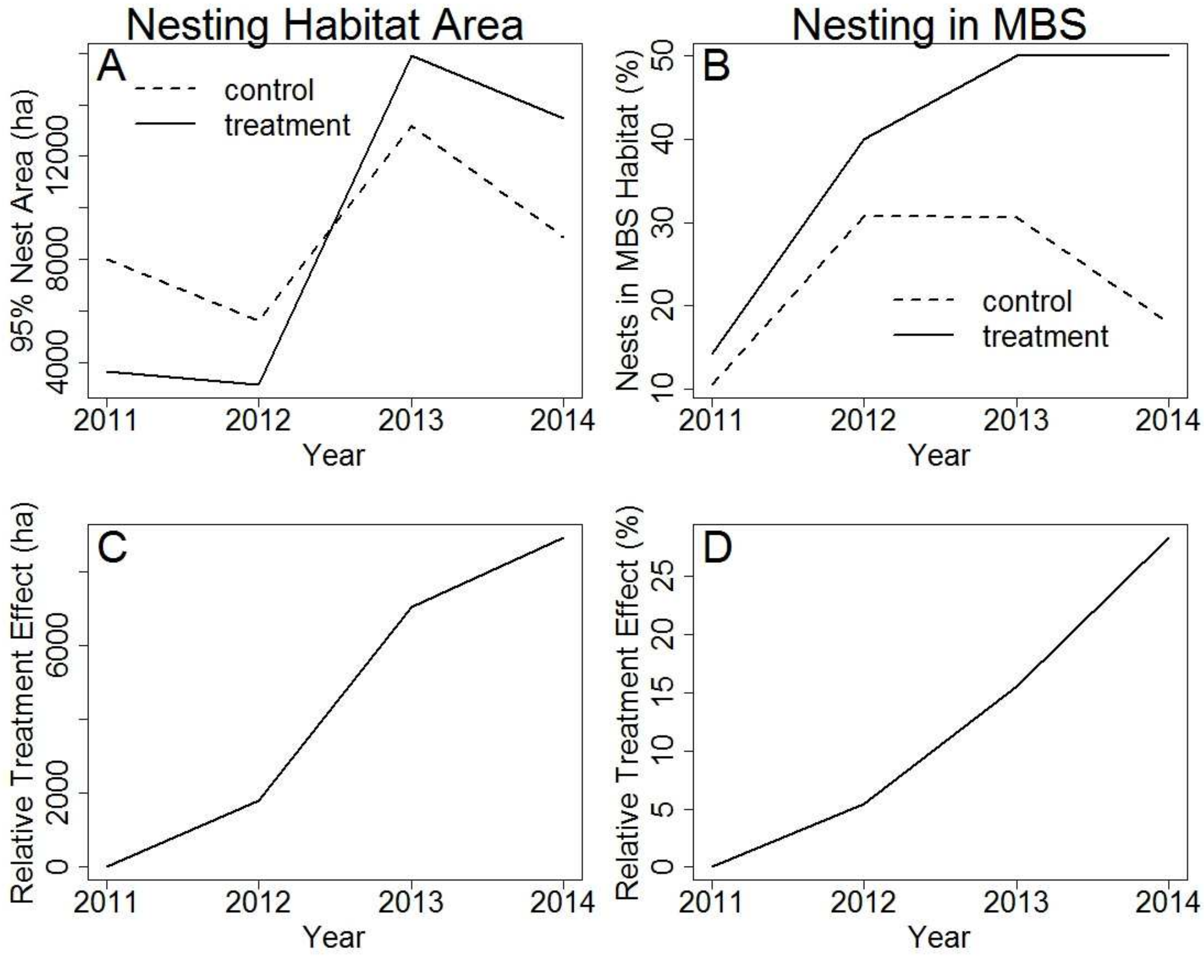

Figure 2.3. A) Interaction (p = 0.022) between time and study area with estimated greater sage-grouse nesting area calculated from 95% kernel density as the response. Treatments primarily started in 2012 and continued through 2014. B) Interaction (p = 0.015) between proportion sage-grouse nests in mountain 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.

CHAPTER 3

EFFECTS OF CONIFER ENCROACHMENT AND REMOVAL ON FEMALE GREATER SAGE-GROUSE SEASONAL HABITAT SELECTION IN THE NORTHERN GREAT BASIN

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) is an obligate sagebrush species that has decreased in abundance and distribution amidst the declining sagebrush biome. Conifer encroachment is thought to be an important threat to sage-grouse habitat. While conifer removal is often recommended for sage-grouse conservation, there is a paucity of information regarding the spatial and temporal effects of such action. I assessed effects of conifer encroachment and conifer management on female sage-grouse habitat selection at multiple scales using radio-telemetry locations in the northern Great Basin across all seasons. The most important scale was within 400 m of locations. I observed strong avoidance of conifers in every season, but avoidance was strongest during winter and weakest during summer. Conifer removal had the greatest positive effects during summer indicating that summer habitat had been limited by conifer encroachment. Increasing the availability of summer and brood-rearing habitat may help relieve an important limiting factor to the population. Cutting was more important than cutting with subsequent slash burning, and time since treatment also had positive effects on selection. These results will be crucial in understanding how sage-grouse response to conifer encroachment and how management can be focused to maximize benefits of conifer removal.

INTRODUCTION

The sagebrush (*Artemisia* spp.) biome in western North America has been experiencing numerous threats since the late 1800s including conversion to agriculture, energy development, catastrophic wildfires, overgrazing, and invasive species (Knick et al. 2003, Connelly et al. 2011, Knick and Connelly 2011) resulting in significant reduction and degradation of sagebrush habitat (Miller and Eddleman 2001). These losses result in reduced native wildlife populations, particularly sagebrush obligates (Knick et al. 2003, Welch 2005). For example, greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), was once widespread throughout western North America but, being an obligate sagebrush species, has declined commensurate with its required habitat (Knick and Connelly 2011). Sage-grouse range has contracted 44% since the late 1800s (Schroeder et al. 2004), and populations in remaining habitat are declining throughout much of their range (Garton et al. 2011). Conifer encroachment is thought to be an important threat to sage-grouse, but empirical field studies are limited (Connelly et al. 2011, United States Fish and Wildlife Service [USFWS] 2015).

Conifer encroachment is a major threat throughout the Great Basin and other sagebrush ecosystems (Davies et al. 2011, Miller et al. 2011). Species such as piñon pine (*Pinus* spp.) and juniper (*Juniperus* spp.) were historically restricted to sparsely vegetated areas that did not burn frequently such as rocky outcrops, but have increased 3–10 times in area and ~10 times in abundance in portions of the Great Basin to their current distribution of 18 million ha in the intermountain west (Miller and Tausch 2001, Miller et al. 2005, Miller at al. 2008). It has been suggested that these increases were caused by a combination of fire suppression, over-grazing, changing climate/weather patterns, and increases in atmospheric CO_2 (Miller and Rose 1995, 1999; Miller et al. 2005). Increased conifer abundance fragments and displaces sagebrush habitat, provides avian predator perches, and degrades range condition (Paton 1994; Wolff et al. 1999; Manzer and Hannon 2005; Miller et al. 2005, 2011).

Conifer removal has been recommended for sage-grouse conservation (Connelly et al. 2000, Baruch-Mordo et al. 2013), but little research has been completed relating sage-grouse behavior and abundance with conifer management. In general, conifer removal can prevent displacement and fragmentation of sagebrush systems, reduce available avian predator perches and nesting habitat, and improve range conditions (Young et al. 1985; Bates et al. 1998, 2000; Miller et al. 2005), but research is needed to confirm whether sage-grouse benefit from these treatments as well as the time frame of the response.

I observed female sage-grouse movements in Oregon, both before conifer treatments to evaluate the effects of encroachment, and after treatments to assess the effects of management on habitat selection. My objectives were to evaluate the effects of conifer encroachment at multiple scales and evaluate the effects of conifer cutting and slash removal on female sage-grouse seasonal habitat selection. I predicted year-round conifer avoidance that would be greatest during the winter due in part to generally more snow and colder temperatures in encroached areas, and avoidance would be least during summer when females and broods move to the cooler, moister areas with high productivity to avoid hot, dry areas with less food production. These selected areas tend to have increased conifer abundance (Miller and Eddleman 2001) which may result in a selection tradeoff. After conifer removal, I predicted that habitat use in and near cut and slash burned areas would increase with time since treatment. Additionally, if the seasonal variation in avoidance causes tradeoffs between aversion to conifers and attraction to productive areas, I predicted that conifer removal would have greater benefits during summer and would have minimal effects during winter.

METHODS

Study area

Data were collected in Lake County in south-central Oregon between the Warner Mountains and the Warner Valley and extended into Modoc County, California north of Cowhead Lake and into Washoe County, Nevada north of Mosquito Lake (Figure 3.1). The area was dominated by low sagebrush (*Artemisia arbuscula*) habitat, but other species included mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) at higher elevations, Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) at lower elevations, and other interspersed shrub species including antelope bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* spp.), saltbrush (*Atriplex* spp.), and mountain mahogany (*Cercocarpus* spp.). Western juniper (*Juniperus occidentalis*) tended to occur in a patchy distribution from mid to high elevation.

I used 2 study area boundaries for the 2 different portions of the analysis because of sage-grouse telemetry data and the location of the conifer removal treatments (Figure 3.1). From 2009 to 2011 I collected sage-grouse location data throughout a large study area (210,000 ha; Figure 3.1). When conifer removal started in 2012, I focused efforts in a smaller area around the treatments from 2012 to 2014 (34,000 ha; Figure 3.1). I delineated the exact boundaries based on grouse movement extent and geographic barriers such as lakes, forests, cliffs, and agriculture.

Conifer Management

The US Bureau of Land Management (BLM) removed juniper on federal land while the US Natural Resources Conservation Service (NRCS) in association with the Oregon Department of Fish and Wildlife (ODFW) assisted landowners with juniper removal on private land within and surrounding the treatment area (Figure 3.1). Treatments generally occurred from late fall to early spring. Most of the treated areas were Phase-I to Phase-II encroachment consisting of low to medium density and size trees (0–30% canopy cover) with generally intact understory herbaceous and shrub vegetation (Miller et al. 2005). The majority of treatments were conducted by hand-cutting with brush- and chainsaws, but some small areas were machine cut (e.g., feller-buncher) in fall 2013 to spring 2014. 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-and-leave generally occurred in areas with trees of low size and density. Cut-and-lop occurred with larger trees to remove branches which can serve as avian predator perches. Cut-and-burn included slash burning individual felled trees and occurred with larger, denser trees to expose the understory and encourage growth. Generally, cut trees were left to dry for ~1 year and then slash burned. Effort was made to burn only individual trees to limit shrub mortality and burn scars. Cut-pile-burn was used less often due to cost but was deemed necessary in some areas of much higher density of bigger trees to minimize burned areas.

Across all treatments, the objective was complete conifer removal, but an attempt was made to leave pre-settlement trees in locations that historically supported juniper, thus some areas still had standing trees after treatment (BLM 2011). BLM biologists identified pre-settlement 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, I grouped treatments into two categories to simplify the analysis and interpretation: 1) cutting without slash burning and 2) cutting with slash burning. I recorded month and year of cutting and slash burning for use in the analysis. Although some treatments occurred from 2007–2011 (<10%), a majority occurred from 2012–2014 and slash burning began in 2012

(Table 3.1). I therefore considered data collected prior to 2012 to be pretreatment data to assess effects of conifer encroachment. Within the study area, a total of 6488 ha of trees were cut and 2277 ha of trees were slash 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 3.1; Figure 3.1).

Seasonal and Random Locations

Female sage-grouse were captured during winter to spring 2009–2014 using spotlighting techniques (Geisen et al. 1982, Wakkinen et al. 1992) near leks and wintering habitat and were fitted with 22-g VHF radio-collars (Advanced Telemetry Systems, Isanti, MN, USA). I monitored females using radio telemetry ~2 times per week from February to July and ~1–4 times per month from August to January. Locations were obtained by approaching the female to within 30 m and recording the coordinates with a handheld global positioning system unit. Locations of females on nests were not used in this analysis. A number of random points equal to the number of sage-grouse locations for each season was populated within the large study area (pretreatment 2009–2011) and the small study area (pre- and posttreatment 2009–2014) using ArcMap 10.0 (ESRI 2011).

Seasons

I delineated 5 seasons based on sage-grouse biology, seasonal weather, and local knowledge of seasonal behavior. Winter was November, December, January and February based on previous research in Oregon (Hagen et al. 2011). Additionally, little to no herbaceous vegetation or invertebrates were available and the birds have reverted entirely to their winter diet of sagebrush by this time (Patterson 1952). Spring was March and April because the grouse move to their breeding grounds in March and move to nesting areas in

April. Early summer was May and June because this is the period when the eggs hatch and early brood locations are obtained. My median hatch date was ~15 May, and because nest locations were not included in the analysis, a majority of locations used during this period were females whose nests had terminated including those with broods. By the end of June, the estimated median brood age was ~45 days. Late summer was July and August because this period is hot and dry (National Oceanic and Atmospheric Administration [NOAA] 2015; Figure 3.2) and is an important brood rearing time (median brood age 107 days), thus grouse may use mesic habitats to meet dietary needs (Connelly et al. 2000). Fall was September and October which becomes wetter and cooler than summer (NOAA 2015; Figure 3.2). This period may represent late brood rearing or merely a transition from summer to winter habitat (Patterson 1952, Connelly et al. 2000). Chicks are ~2/3 full size in September and ~full size in November (Patterson 1952).

Geospatial Data

I acquired conifer data from the NRCS (Falkowski and Evans 2012, Poznanovic et al. 2014). The geospatial file consisted of a location and estimated crown diameter of individual conifer trees determined by spatial wavelet analysis to an accuracy of 1 m (Falkowski et al. 2006, 2008; Strand et al. 2006). I calculated percent canopy cover within multiple circular buffers including radii of 56 m (1 ha), 400 m (50 ha), and 800 m (201 ha) around sage-grouse locations and random points. The smallest buffer was chosen because I believed it was the smallest reasonable size given the resolution of the conifer layer. Each successive buffer was thought to provide biologically meaningful size increases for sage-grouse habitat selection and substantially increased the buffer area in an attempt to minimize spatial autocorrelation among buffers.

I acquired conifer removal data as geospatial polygons with month and year of cutting and slash removal from the BLM and NRCS. Treatment effects were potentially influenced by topographic features, thus I included terrain covariates to serve as nuisance variables and account for some confounding variation. A 10-m resolution digital elevation model (DEM) was used to assign elevation, slope, and aspect to each used and random point in ArcMap 10.0 (ESRI 2011). Additionally, I calculated terrain ruggedness and landform (terrain curvature) within the most important buffer size from the pretreatment analysis (400 m) using the Geomorphometry and Gradient Metrics Toolbox 2.0 (Evans et al. 2014) in ArcMap 10.0 (ESRI 2011). Ruggedness calculates the variability in elevation (Riley et al. 1999), while landform estimates the concavity (depression) or convexity (ridge; McNab 1989, Bolstad and Lillesand 1992). The ruggedness index units are arbitrary, but zero indicates flat terrain and increasing values indicate more rugged terrain. Landform units are also arbitrary, but zero is flat, while <0 is a depression and >0 is a ridge.

Pretreatment Encroachment Analysis

I compared linear and nonlinear models of conifer abundance (% cover) on habitat selection by buffer size and with and without seasonal effects and selected the model with the lowest Akaike's information criterion (AIC; Anderson 2008). I believed the conifer data would have a strong effect and were only concerned with conifer abundance and potential seasonal responses, thus I fit models with either a conifer only or a conifer × season interaction and always used individual bird as a random effect. I fit logistic generalized linear models (GLM) to evaluate linear responses and logistic generalized additive models (GAM; Wood 2006) to evaluate nonlinear responses. I fit GAMs with cubic regression splines with smoothing parameters fit using maximum likelihood and limited the maximum number of knots to 4 to improve interpretation and avoid overfitting. All models were fit with the gam function in the mgcv package (Wood 2006) in R 3.1.2 (R Core Team 2014).

Treatment Effect Analysis

I used the best model from the pretreatment analysis (nonlinear, 400-m scale, seasonal) as the base model for the treatment effects analysis. I assessed various measures of treatment area use in separate models to evaluate treatment effects. I used binary variables for whether a location was in a cut area or a cut and slash burned area and also used continuous variables for number of months since cutting or slash burning. I also calculated the proportional area of cut areas and slash burned areas as well as the age in months of the most abundant cut and slash burn within the most important buffer from the pretreatment analysis (400 m).

Because nonlinear models were best in the pretreatment analysis, I used GAMs to fit all treatment models and used a maximum of 4 knots for treatment covariates and 5 knots for nuisance covariates, and allowed the GAM to shrink the effect during each season to 0 (no effect) as an additional step toward parsimony (Wood 2006). I fit both individual female and year of the study as random effects to help control for autocorrelation within and variation among groups (i.e., females or years). Nuisance covariates included pretreatment conifer cover within 400 m to control for effects of conifer abundance as well as topographic characteristics including elevation, aspect, slope, landform, and ruggedness (see “Geospatial Data”). All smooths were fit with cubic regression splines with the exception that aspect was fit with the cyclic modification to match the ends of the circular distribution (Wood 2006). I compared the models containing treatment variables to a null model (which included nuisance variables only) using AIC to assess strength of treatment effect. I believed that each model with an AIC lower than the null model contributed information to our understanding of the treatment effects and therefore did not select a best model. I also reported the significance of the effect and my perception of the direction of the effect. Additionally, I produced selection response plots to interpret the effects.

RESULTS

Pretreatment Encroachment

I captured and monitored 198 female grouse from 2009–2011 for a total of 5302 locations (winter: 1797, spring: 1350, early summer: 951, late summer: 717, fall: 487). The 400-m scale had lower AIC values than the 56-m and 800-m scales for seasonal and non-seasonal as well as linear and nonlinear models by >80 AIC units in all cases (Table 3.2). The nonlinear seasonal model had lower AIC values than all other models for each scale by >30 AIC units and had 100% of the model weight (Table 3.2). Therefore, I selected the nonlinear seasonal model at the 400-m scale as the best model. Sage-grouse during winter, spring, fall, and early summer had monotonically decreasing responses to increasing conifer cover with the steepest decline in winter and less steep declines in the other seasons (Figure 3.3). Grouse during late summer had the weakest avoidance of conifer with a unimodal response peaking at ~1.8% conifer cover and decreasing abruptly with increasing conifer cover (Figure 3.3). The median and 95th percentile of used locations for each season and random locations were: winter: 0.005% and 1.3%, spring: 0.010% and 2.0%, early summer: 0.166% and 4.1%, late summer: 0.587% and 6.2%, fall: 0.128% and 2.7%, random: 0.791% and 12.1%.

Treatment Effect

I captured and monitored 169 females in the treatment area from 2009–2014 for a total of 3402 locations (winter: 560, spring: 792, early summer: 1177, late summer: 682, fall: 191).

All models with treatment variables had lower AIC's than the null model by 4.5–37.6 units (Table 3.3), thus I interpreted all treatment variables. Whether a location was in a cut area or not had a positive logistic coefficient (0.45 ±0.12 SE), while points in slash burned areas also had a positive coefficient (0.12 ±0.26 SE) with confidence intervals overlapping zero. The largest positive effects for each variable assessed occurred during early and late summer (Table 3.3). Spring and fall had some positive effects and some non-effects while winter had a combination of negative and non-effects (Table 3.3; Figure 3.4). For each pair of variables (cut versus slash burn), cutting had lower AIC values than slash burning by >20 AIC units (Table 3.3). The most important variable was the age of the most abundant cut within 400 m, which had the greatest positive effects in early and late summer, slight positive effect in spring, no effect in fall, and slight negative effect in winter (Table 3.3; Figure 3.4C). Overall, the treatments generally had positive effects with the greatest positive effects during summer, neutral to slightly positive effects during spring and fall, and neutral to slightly negative effects during winter (Table 3.3; Figure 3.4).

DISCUSSION

My study provides some of the first insights to scale-dependent negative effects of conifer encroachment on female sage-grouse seasonal habitat selection. Specifically, sage-grouse selected habitats further from conifer in winter and more proximate during summer. Several studies have documented sage-grouse avoidance of trees during individual seasons (Gregg 1992; Freese 2009; Doherty et al. 2008, 2010; Atamian et al. 2010; Casazza et al. 2011). However, my work is the first to document seasonal variation in avoidance of a population throughout its life history. The seasonal variation in avoidance has implications for addressing specific limiting factors during each life cycle stage. Productive areas at high elevation are both encroached by conifers (Miller and Eddleman 2001) and desirable summer and brood rearing habitat (Coates et al. in revision), I hypothesized that treatment effects would be greatest during summer, which I verified for each measure of treatments I assessed.

Similar to other work, I found sage-grouse selection occurring at a 400-m scale. Doherty et al. (2010) observed avoidance of conifers within 100 m of nesting sites, which is consistent with my results. At the population level, Baruch-Mordo et al. (2013) found that 1000 m was an important scale for breeding ground occupancy. Because sage-grouse are mobile, they may be more tolerant of conifers in their daily movements, and not as tolerant of conifers on the landscape near their permanent breeding grounds. Because a 400-m radius was important, it may be that to maintain or restore habitat connectivity, an 800-m wide habitat corridor is needed to maximize movement potential. This information, along with the response curves will be crucial for conservation planners in order to better understand connectivity and landscape resistance.

I did not assess thresholds, but my results can help inform specific management actions. Baruch-Mordo et al. (2013) suggested 4% conifer cover as a critical threshold within 1000 m of breeding grounds to affect occupancy. Similarly, Freese (2009) suggested 5% cover as a threshold limiting wintering habitat. My results indicate that at 4–5% conifer cover, female sage-grouse habitat selection during spring and winter was greatly diminished, but selection declined rapidly at any cover greater than 0%. While I observed the greatest avoidance of conifers during the winter, this is due in large part to sage-grouse selecting lower elevations and low sagebrush habitat to avoid deep snow (Hagen et al. 2011), which is why I predicted that treatments would have minimal impact during winter habitat selection. I found less avoidance and some selection for conifers at <1.8% cover during the summer, but the increased use of treated areas indicated that conifer encroachment had limited preferred summer habitat, rather than being preferred itself. If sage-grouse had preferred conifers during summer, use of treated areas would be expected to decline, which I failed to observe. Because brood success is a critical demographic parameter for sage-grouse (Taylor et al. 2012), increasing the availability of high quality summer habitat could help reduce an important limiting factor. More research is needed to assess the effects of treatments on brood success, however.

My study is the first to document large scale sage-grouse habitat selection responding to conifer treatments. The treatments had varying effects on selection during different times of year with the greatest positive effects in the summer. The early and late summer seasons that I assessed correspond with early and late brood-rearing seasons, and although not all females that were monitored had broods, I believe this is strong evidence for the benefits of conifer removal to brood-rearing habitat. In my study area and throughout much of the Great Basin, conifer generally encroaches in high elevation mountain big sagebrush communities that are cooler and moister in the summer (Miller and Eddleman 2001), which produce herbaceous vegetation (Davies and Bates 2010) that can provide cover and food (see Chapter 4) as well as invertebrate food species.

Various factors affected sage-grouse selection of treated areas. Sage-grouse selected habitat in cut areas, but the response to cutting with slash burning areas was unclear. However, time since cut and time since slash burn both had important positive effects during summer, fall, and spring. Additionally, proportion of area cut and proportion of area slash burned both had positive effects in all seasons except winter. Cutting was more important than cutting with slash burning, but that may be due partially to less area in the latter category than the former and less time available during the study after slash burning than after cutting because burning occurred >1 year after cutting. Further research is needed to assess longer term effects of slash burning downed trees.

MANAGEMENT IMPLICATIONS

Understanding factors limiting sage-grouse populations in specific areas is important to management. Low percent cover of conifer can be limiting for sage-grouse throughout the year, but in my study area, appeared to have the greatest negative effects in summer (i.e., brood) habitat due to a tradeoff between productive habitat and conifer invasion. Conifer removal was effective at increasing available summer habitat, but managers should strive for removal of conifer in blocks >50 ha (400-m radius) to maximize seasonal habitat for sage-grouse. If brood habitat is limiting, management efforts should focus on potential brood habitat, such as mountain big sagebrush and mountain shrub communities or riparian areas. Furthermore, to maximize movements, treeless corridors of >800 m wide may be necessary for connectivity between habitats.

Slash burning after cutting was much less important than just cutting; therefore, if funds are limited, cutting and leaving the downed trees in a large area may be more beneficial than cutting and slash burning the downed trees in a smaller area, but specific circumstances and local knowledge should be considered. Because time appears to be one of the most important factors in sage-grouse use of treated areas, grouse use should not be expected immediately, but might take several years to become evident.

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Table 3.1. Area of cut and slash burned conifer in the treatment study area each year in southern Oregon used to assess female greater sage-grouse response to conifer removal. The greater treatment area included the treatment area as well as the immediate surrounding area (see Figure 3.1).

Year	Treatment Area		Greater Treatment Area		Average Size (ha)
	Cut (ha)	Slash Burn (ha)	Cut (ha)	Slash Burn (ha)	
2007	143	–	143	–	72
2010	17	–	57	–	29
2011	432	–	781	–	71
2012	2073	95	2709	97	68
2013	1331	991	2288	1989	76
2014	2492	1191	3465	1454	144
Total	6488	2277	9443	3540	87

Table 3.2. Delta AIC values of models of female greater sage-grouse habitat selection relative to conifer canopy cover in southern Oregon comparing linear (GLM) and nonlinear (GAM) models at 3 different scales, both with and without seasons.

Model	ΔAIC	k	Weight	Deviance
GAM-400m-Seasonal	0.0	15	1	12811.7
GLM-400m-Seasonal	37.9	6	0	12867.4
GAM-800m-Seasonal	128.8	16	0	12938.6
GLM-800m-Seasonal	256.5	6	0	13086.1
GAM-400m-Non-Seasonal	305.4	4	0	13139.0
GLM-400m-Non-Seasonal	351.0	2	0	13188.6
GAM-800m-Non-Seasonal	390.9	4	0	13224.5
GLM-800m-Non-Seasonal	452.9	2	0	13290.5
GAM-56m-Seasonal	500.1	15	0	13311.5
GLM-56m-Seasonal	558.4	6	0	13388.0
GAM-56m-Non-Seasonal	745.3	4	0	13578.8
GLM-56m-Non-Seasonal	858.2	2	0	13695.8

Table 3.3. Comparison of and direction of effect for different measures of treatment effects on female greater sage-grouse by season. “+” is positive effect. “-“ is negative effect. “0” is no effect. Double symbol (“+ +” or “– –“) is a marginally significant effect (0.05 < p < 0.10). Triple symbol (“+ + +” or “– – –“ is a significant effect (p < 0.05).

Treatment Variable	ΔAIC	Winter	Spring	Early Summer	Late Summer	Fall
In Cut + Age	5.3	– – –	0	+	+	0
In Burn + Age	30.3	0	0	+	+ +	+
Age of Abundant Cut	0.0	–	+	+ + +	+ + +	0
Age of Abundant Burn	33.1	–	+ +	+	+	+
% Area Cut – 400 m	9.2	0	+	+ + +	+ +	0
% Area Burn – 400 m	29.4	0	0	+ + +	+ + +	+
Null	37.6	NA	NA	NA	NA	NA

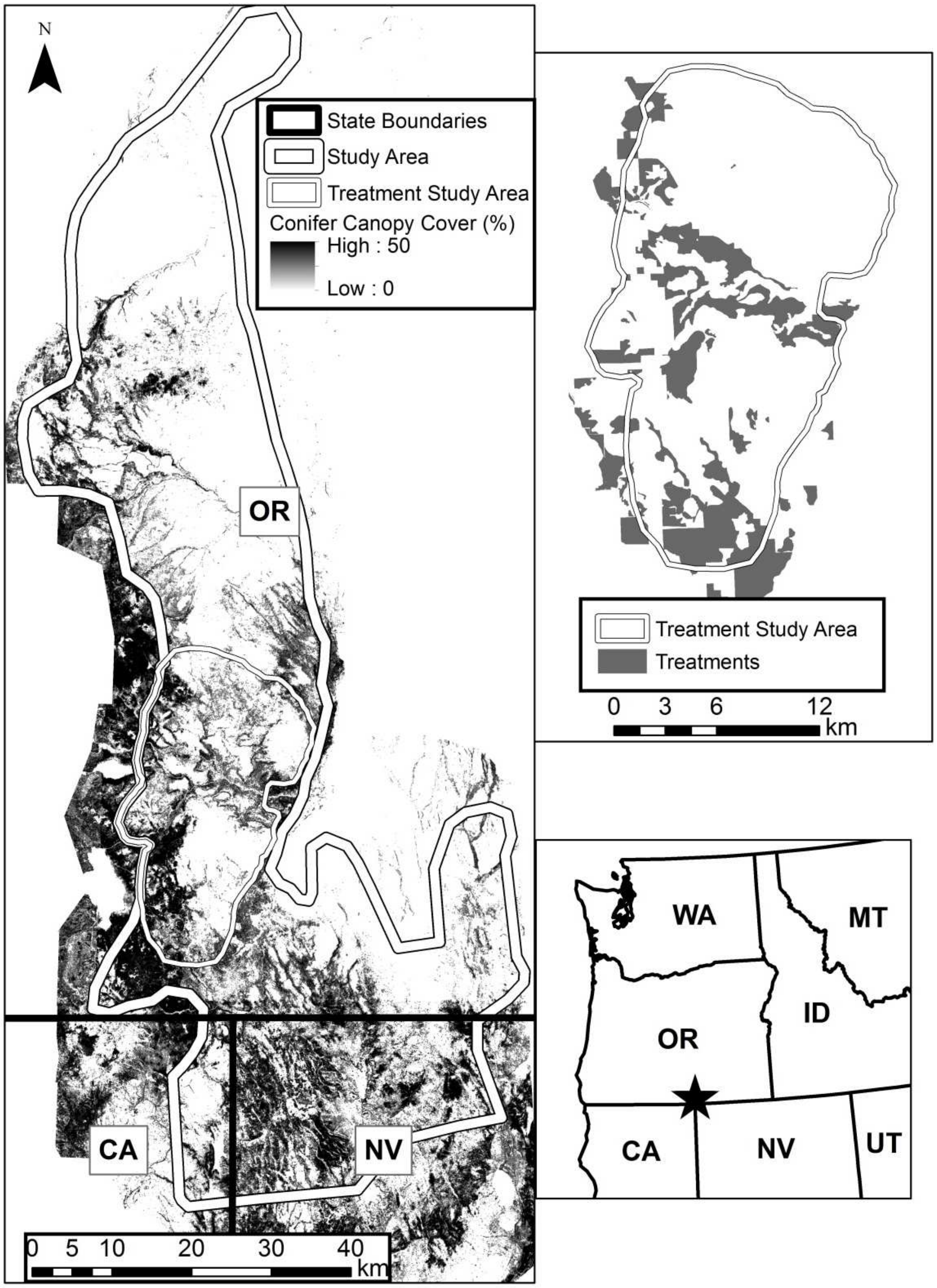

Figure 3.1. Bottom Right: Northwestern United States showing state boundaries and study area as a star. Left: Study area boundary used to assess female greater sage-grouse seasonal habitat selection response to conifer encroachment. Background map is conifer canopy cover. Smaller boundary was used to assess treatment effects (See top right). Top Right: Treatment area boundary used to assess effects of conifer treatments on sage-grouse habitat selection. Treatments shown as gray polygons.

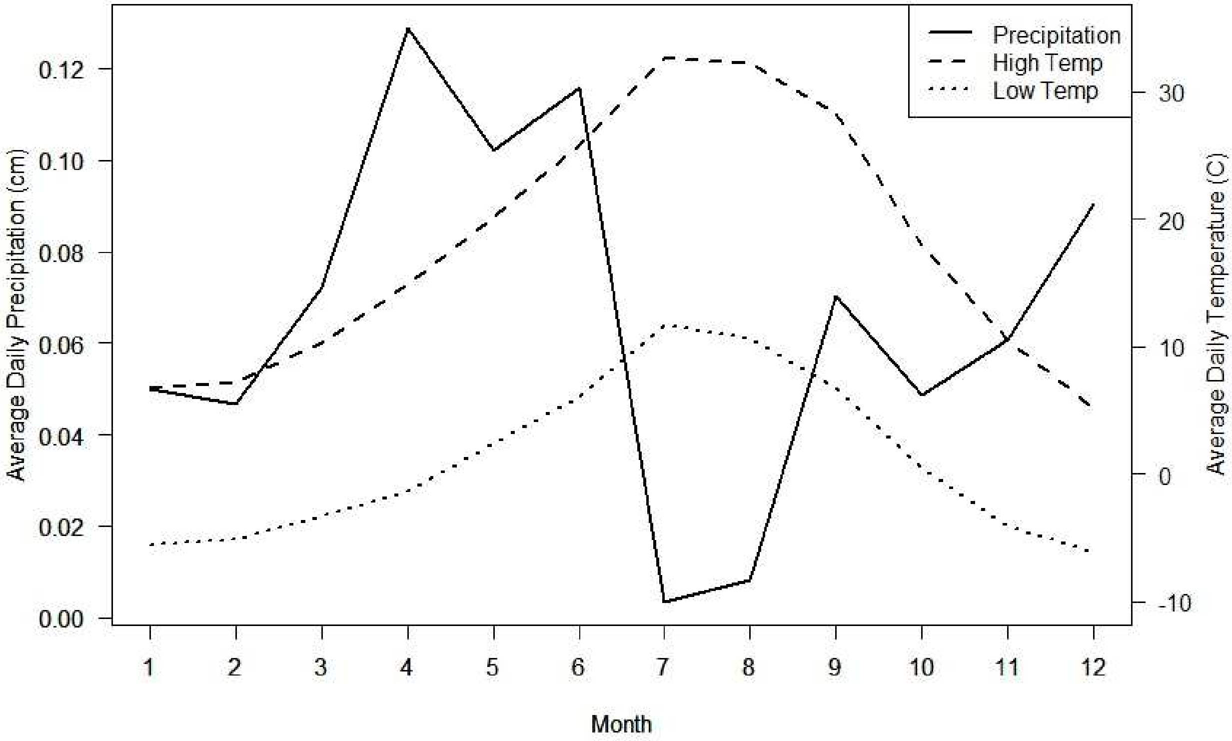

Figure 3.2. Average daily precipitation and high and low temperature by month for Adel, Oregon from 2009 to 2014. Months are 1 = January to 12 = December.

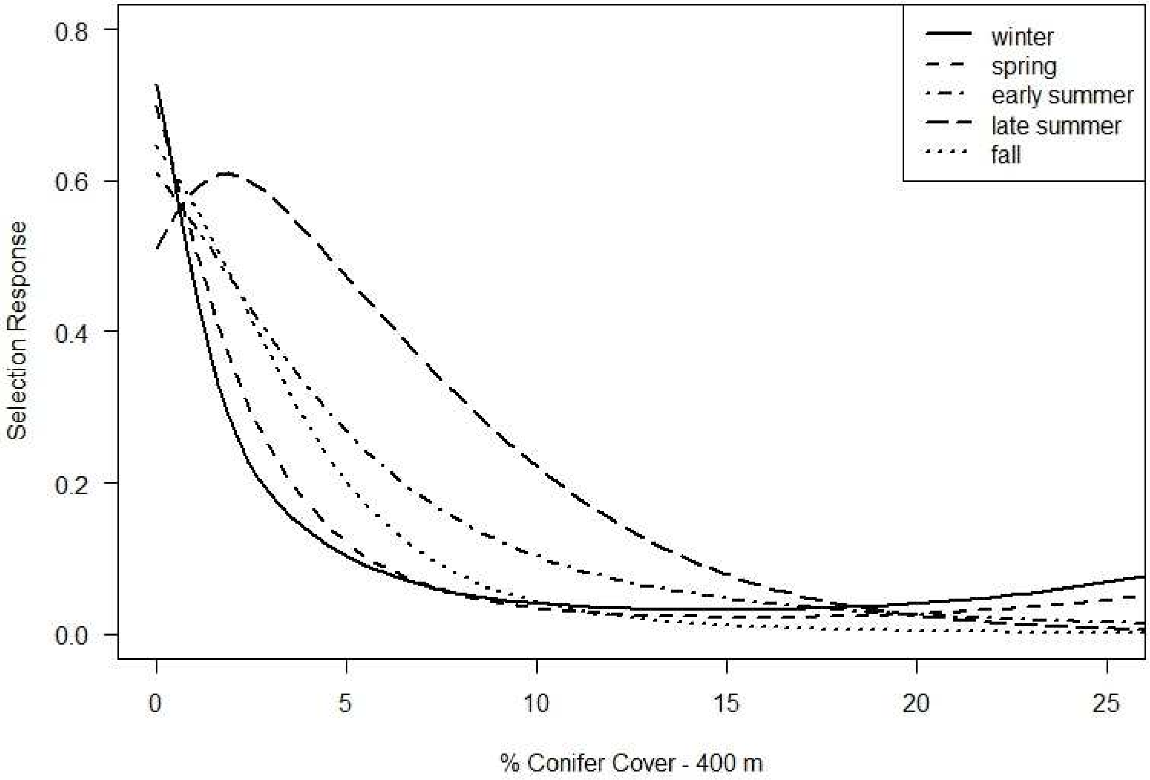

Figure 3.3. Seasonal habitat selection response of female greater sage-grouse to percent conifer cover in southern Oregon.

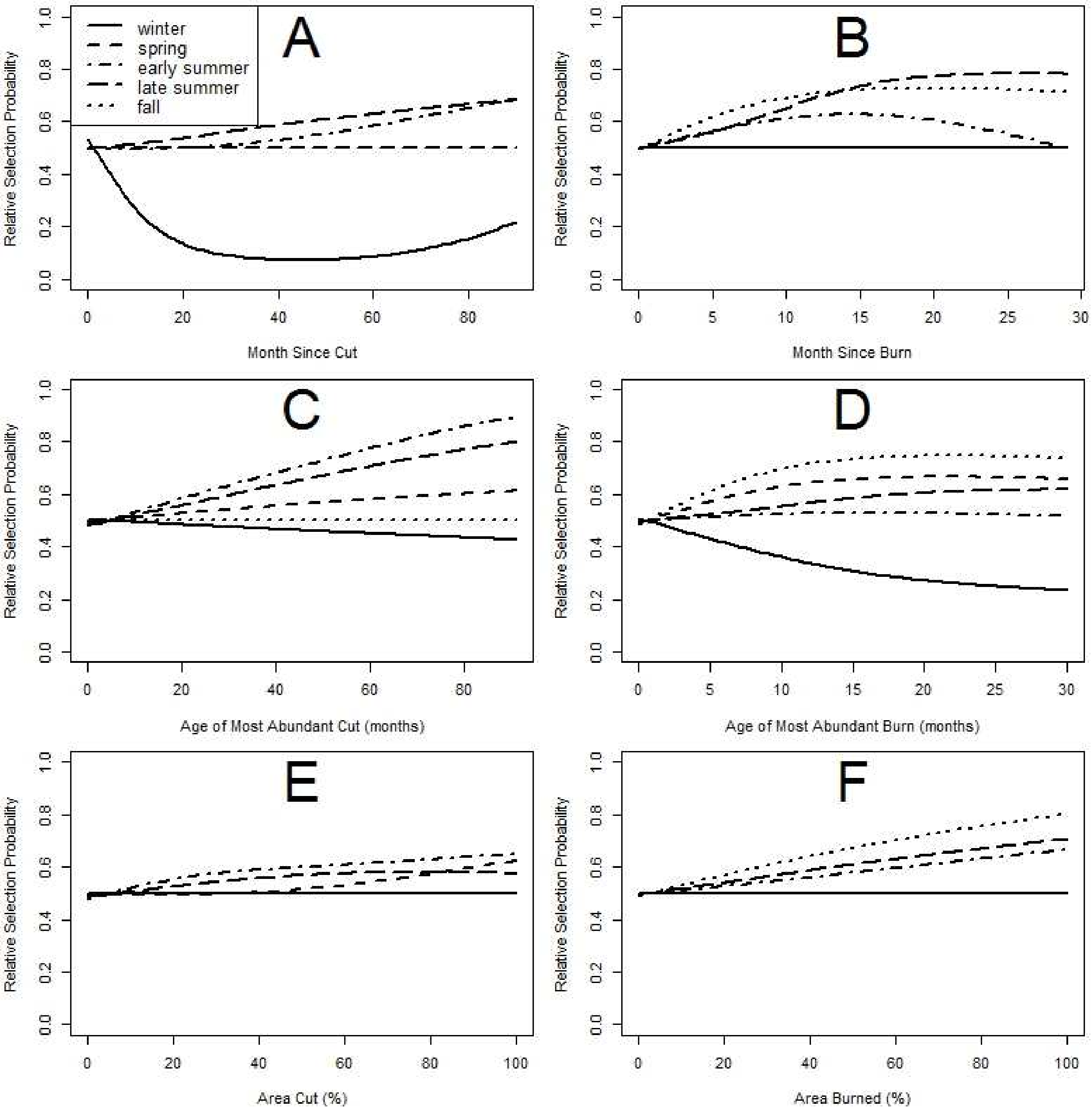

Figure 3.4. Female greater sage-grouse selection response to 6 different measures of conifer removal. Seasons with no effect are 0-slope lines at 0.5 selection probability and occasionally overlap, obstructing other lines. See Table 3.3 for seasons with no effect. A and B were measured at each location. C through F were measured within 400 m of each location.

CHAPTER 4

CONIFER ENCROACHMENT AND REMOVAL RELATIVE TO GREATER SAGE-GROUSE NESTING HABITAT

ABSTRACT

Conifer woodlands have expanded into sagebrush (*Artemisia* spp.) ecosystems causing numerous negative impacts including habitat degradation for sagebrush obligate species including the imperiled greater sage-grouse (*Centrocercus urophasianus*). Conifer management is increasing despite a lack of empirical evidence to assess outcomes to grouse and their habitat. Although assessments of vegetation recovery after conifer removal are common, comparisons of successional trends with habitat guidelines or actual data on habitat used by sage-grouse is lacking. I assessed impacts of conifer encroachment on vegetation characteristics known to be important for sage-grouse nesting. Using a controlled repeated measures design, I then evaluated vegetation changes for 3 years after conifer removal. I compared these results to data from 356 local sage-grouse nests as well as to published habitat guidelines. I observed negative effects of conifer cover on many characteristics important for sage-grouse nesting habitat including percent cover of forbs, grasses, and shrubs, and richness of forbs. Following conifer removal, I observed increases in herbaceous vegetation, primarily grasses. I did not observe an increase in shrubs due to the short (3-yr) study period relative to response time required for woody species. In untreated habitat, herbaceous vegetation values were slightly below those at local nest sites, while shrub and sagebrush values were well below local nest data. Based on habitat guidelines, my measured habitat values were below

suitable levels, but the encroachment and treatment analyses further indicated that posttreatment habitat was progressing toward or expected to progress toward suitable habitat.

INTRODUCTION

Growing concern for greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), a sagebrush (*Artemisia* spp.) obligate 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 upon which they depend (United States Fish and Wildlife Service [USFWS] 2015). A combination of land management policy revisions and proactive restoration efforts have been undertaken to address a variety of threats ranging 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).

Conifer woodlands have been expanding into sagebrush 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; Davies et al. 2011; Miller et al. 2005, 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 the sagebrush steppe (Miller et al. 2011, USFWS 2015). Conifer expansion and infill reduces grass and forb abundance and diversity due to limitation of nutrients, water, sunlight, and space, thereby increasing surface water runoff and erosion (Buckhouse and Gaither 1982, Gaither and Buckhouse 1983, Miller et al. 2011). With increased runoff, interception of rainfall, and increased transpiration, conifers can lower the water table, thus reducing spring and stream-flows (Baker 1984, Wilcox 2002).

Conifer removal in sage-grouse habitat has been recommended (Connelly et al. 2000), and subsequently, conifer management has been increasing for sage-grouse conservation (Baruch-Mordo et al. 2013). From 2010–2014 in Oregon alone, the amount of conifer-encroached lands treated by partners through the Sage Grouse Initiative (SGI) grew 1411%, addressing roughly two-thirds of the early phase encroachment on priority private lands (Natural Resources Conservation Service [NRCS] 2015). However, little effort has been expended on assessing the spatial and temporal effects of conifer management on sage-grouse habitat (USFWS 2015).

Monitoring and evaluating ecological restoration projects is crucial to success and to informing future management (Michener 1997). One way to assess the potential effects of restoration on a wildlife species is to track short-term changes in habitat, assuming that these will lead to long-term population changes. Effects of conifer removal on sagebrush vegetation have been mixed depending on site conditions, conifer abundance, pretreatment vegetation, time since removal, and management technique (Bates et al. 2000, 2005, 2007; Roundy et al. 2014). In general, herbaceous vegetation, often including invasive annual grasses, tends to increase, while shrubs tend to remain stable or, in the case of fire treatment, decrease over the short term (Bates et al. 2005, Miller et al. 2014, Roundy et al. 2014). While some conifer removal studies have considered sage-grouse habitat characteristics (Miller et al. 2014), no studies have directly compared the post-removal vegetation successional trajectories to habitat used by local sage-grouse.

Using a controlled repeated measures design, I evaluated the effects of conifer encroachment and removal on vegetation characteristics at two spatial scales in potential sage-grouse nesting habitat in southeastern Oregon using both treatment and control areas. My objectives were to determine effects of conifer abundance on understory vegetation characteristics important to sage-grouse nesting and whether nesting habitat improved after conifer removal. I then compared these data to published sage-grouse nest habitat guidelines as well as data from 356 nests found locally to assess whether the areas were suitable or progressing toward suitable habitat. As my monitoring data were collected concurrently with a sage-grouse radio-tracking project in the same area, my study was uniquely suited to this comparison. I predicted negative effects of conifer abundance on nesting habitat characteristics including herbaceous and shrub cover and richness and that herbaceous vegetation would begin recovering within 2 years of conifer removal but shrub recovery would be negligible over this short period.

METHODS

Study area

I collected vegetation data within the South Warner Juniper Removal Project Area (Bureau of Land Management [BLM] 2011) in southern Lake County in south-central Oregon between the Warner Mountains and the Warner Valley (Figure 4.1). I collected sage-grouse nest habitat data here as well as north to Abert Rim and south of Warner Valley extending into Modoc County, California and into Washoe County, Nevada (Figure 4.1). The entire area ranged in elevation from 1360 m to 2180 m with an average of 1700 m above sea level and was dominated by low sagebrush (*Artemisia arbuscula*), but other habitat types included mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) at higher elevations, Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) at lower elevations, and many other interspersed shrub species including antelope bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* spp.), saltbrush (*Atriplex* spp.), and mountain mahogany (*Cercocarpus* spp.). Western juniper tended to occur in a patchy distribution from mid to high elevation. Characteristic forb taxa are listed under "Vegetation Monitoring" below. Characteristic perennial grasses included Sandberg's bluegrass (*Poa secunda*), bottlebrush squirreltail (*Elymus elymoides*), bluebunch wheatgrass (*Psuedoroegeneria spicata*), and Thurber's needlegrass (*Achnatherum thurberianum*). The dominant annual grass was cheatgrass (*Bromus tectorum*).

Conifer Management

Conifer invasion transitions through 3 successional phases (Miller et al. 2005): In Phase-I, conifers are present with shrubs and herbaceous plants still dominant; in Phase-II, conifers co-dominate the vegetation community; and in Phase-III, the landscape is dominated by conifers with decreased understory. Most of the treated areas in my study were Phase-I to Phase-II encroachment (Miller et al. 2005, 2008) with generally intact understory herbaceous and shrub vegetation. Treatments generally occurred from late fall to early spring and were designed to maximize sagebrush retention. Grazing was generally deferred during the years before and after treatment. All conifer removal treatments were conducted by hand-cutting with brush- and chainsaws. Additional slash treatment of cut conifers was conducted where necessary to reduce woody fuels and vertical structure. Treatments consisted of either cut-and-leave or cut-and-burn. Cut-and-leave involved cutting trees without additional slash treatment and primarily occurred in areas with trees of small size and low density. Cut-and-burn occurred with larger, denser trees to expose the understory and encourage growth. In general, cut trees were left to dry for ~1 year and then burned individually during the winter to minimize the impact. Effort was made to burn only individual trees to reduce shrub mortality and burn scar area. Across all treatments, pre-settlement trees were left in locations that historically supported juniper, thus some areas still had standing trees after treatment (BLM 2011). I consolidated all treatments into cut or not cut. I defined the year of the cut as the year of the first growing season following treatment. I only surveyed treatments designated as cut-2012, cut-2013, or not-cut during the study.

Treatment Monitoring Locations

I established 12 random vegetation monitoring locations in each of 4 strata using the conifer removal management plan (BLM 2011). The strata included cut in 2012 (no pretreatment, 3 years posttreatment), cut in 2013 (1 year pretreatment, 2 years posttreatment), an on-site control in close proximity to treated areas but not cut, and an off-site control in an adjacent study area to the southeast; Figure 4.1). All areas had >16% conifer cover estimated in the plan. I buffered the areas 50 m inward to avoid potential edge effects and randomized the 12 points in each strata while restricting points to >200 m apart to reduce correlated vegetation. Because the plan limited the available strata locations, the treatments were not randomized and the monitoring locations potentially suffered from autocorrelation; I therefore used spatial and temporal controls to minimize these effects. I monitored vegetation at each of these locations annually from 2012 to 2014.

Vegetation Monitoring

I collected vegetation data at nests and random treatment monitoring points over a small extent (10 × 10-m area) typical of sage-grouse nest habitat studies that I called patch. I also collected data at the treatment monitoring points at over a larger extent (60 × 120-m area; modified from Davies et al. 2006) I called stand to capture another scale potentially important to nest-site selection. Patch-scale vegetation at nests and random points was surveyed between late May and early July each year from 2012 to 2014. An array of two 10-m orthogonal transects was oriented in a random direction centered on the established monitoring point or the nest bowl. I used the line intercept method (Canfield 1941) to estimate the percent cover for each shrub species. I also recorded the cover of each shrub species between 40 and 80 cm tall (determined by the uppermost portion of the canopy; Connelly et al. 2000), which I called medium height. Cover data on juniper was collected with the shrub data to estimate conifer abundance but kept separate from the other shrubs for the analysis. I removed data within 1 m of the center of the crossed transects from the shrub cover estimate to reduce bias induced by centering on shrubs at nests (Musil 2011). I summarized the data into total shrub richness (number of species), shrub cover, total sagebrush cover, medium shrub cover, and medium sagebrush cover.

I estimated patch-scale grass and forb cover at monitoring points and nests using ten 20 × 50-cm frames placed at 1, 3, 5, 7, and 9 m along each transect (Daubenmire 1959). Forb data included total forb cover, key forb cover, key forb richness (number of species), and tall forb cover (>18 cm; Connelly et al. 2000). Key forbs consisted of 16 taxa that were found to be important for nesting females and broods in nearby study areas including desert parsley (*Lomatium* spp.), hawksbeard (*Crepis* spp.), false dandelion (*Agoseris* spp.), milkvetch (*Astragalus* spp.), broomrape (*Orbanche* spp.), clover (*Trifolium* spp.), slender phlox (*Phlox gracilis*), fleabane daisy (*Erigeron* spp.), common dandelion (*Taraxacum officinale*), goatsbeard (*Tragopogon dubius*), yarrow (*Achillea millefolium*), aster (*Aster* spp.), moneyflower (*Mimulus* spp.), groundsmoke (*Gayophytum* spp.), pussytoes (*Antennaria* spp.), and eyelashweed (*Blepharipappus* spp.; Barnett and Crawford 1994, Drut et al. 1994, Gregg 2006). Grass cover was divided into total cover and tall cover (>18 cm) similar to forbs. I also recorded total and tall perennial grass cover and total annual grass cover. I combined forbs and perennial grasses to derive total and tall herbaceous cover.

Due to time constraints, I conducted stand-scale surveys at vegetation monitoring points only. I randomly oriented and centered on the survey point an array of four parallel 60-m transects, each 40 m apart (modified from Davies et al. 2006). I collected stand-scale vegetation data from early July to early August, and therefore did not collect data on forbs because of senescence induced by lack of moisture. I identified shrub species and measured line intercept (Canfield 1941) and height. Thirteen 20 × 50-cm frames (Daubenmire 1959) were placed every 5 m from 0 to 60 m along each transect and grass cover was estimated in the following categories: tall perennial (>18 cm), total perennial, total annual, tall grass cover (>18 cm), and total grass cover.

Encroachment Analysis

I assessed effects of conifer encroachment on vegetation characteristics with data from the cut-2013, on-site control, and off-site control strata collected during 2012 because this provided the greatest not-cut sample. I analyzed relationships at both the patch and the stand scales for the treatment monitoring plots between vegetation response variables and conifer canopy cover explanatory variable using generalized linear models in the R environment (R Core Team 2014) with a Poisson distribution and log link for key forb and shrub richness and a Gaussian distribution and identity link for all other response variables. I assessed each model individually using p-values from the χ^2 test for the Poisson regression and the F test for the Gaussian regression. I interpreted the slope as the effect of conifers on the vegetation variables and the y-intercepts as estimates of the variable in the absence of conifers.

Treatment Analysis

I assessed effects of conifer removal on the vegetation characteristics using data from all strata and years. In the R environment, I used generalized linear mixed effects models with Poisson distribution and log link for the key forb and shrub richness response variables and linear mixed effects models for all others. I modeled the time × strata interaction as the fixed effect and time within individual monitoring points as random effects to account for autocorrelation of repeated measures thereby utilizing spatial and temporal controls to optimize information in the data. Because of the non-random sampling, the main effects were unimportant in my design, and I therefore assessed the models using p-values of the interaction between time and strata. For significant interactions, I estimated the effect size and significance of each stratum relative to the on-site control as a reference condition.

The models and data had complex structures; hence the estimated relative effects not only aided in interpretation, but also allowed logical checks on the integrity of the controls and of the analysis in general. Contrary to the encroachment analysis, I assessed effects of treatment on conifer cover. The interaction of conifer cover should be significant in the cut-2013 stratum only (cut-2012 was treated before monitoring started). Additionally, because I did not expect shrubs and sagebrush to recover during this study, these time × strata interactions were not expected to be significant.

Sage-grouse Nest Habitat Data

To provide local habitat data for comparison, I captured sage-grouse females during winter to spring 2009–2014 in the treatment area and 2010–2014 in the control area using spotlighting techniques (Geisen et al. 1982, Wakkinen et al. 1992) near leks and wintering habitat and fitted them with radio-collars (22-g VHF radio-collars, Advanced Telemetry Systems, Isanti, MN, USA). I monitored radio-marked females twice per week during the potential nesting seasons from 2010–2014. When a grouse 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. I then surveyed nest habitat with the same methods as previously described for patch-scale vegetation.

I compared the means, standard errors, and y-intercepts of vegetation characteristics affected by conifer encroachment and removal from the aforementioned analyses with nest data. I then compared the monitoring data and nest data to the rangewide nesting habitat guidelines described below.

Sage-grouse Nest Habitat Guidelines

I compared 2 sources of nesting habitat information to the vegetation survey data. The recommendations of Connelly et al. (2000) are the most used and cited sage-grouse habitat guidelines. Stiver et al. (2015) modified and expanded those guidelines for more general use, especially values for marginal habitat. Hagen et al. (2007) conducted a meta-analysis on nesting habitat using multiple published studies. I therefore compared my vegetation monitoring data to the Stiver et al. (2015) guidelines and the results of the Hagen et al. (2007) meta-analysis.

RESULTS

I surveyed each of the 48 monitoring points for patch- and stand-scale vegetation from each year from 2012 to 2014. One point in the on-site control was influenced by a natural gas pipeline and was removed from the analysis resulting in a sample of 47 points surveyed once in each of 3 years.

Encroachment Effects

In the encroachment analysis, all slopes were negative indicating reduced abundance and richness with increasing conifer cover. However, only 6 of the 15 patch-scale variables were statistically different from zero (key forb richness: $\chi^2_{(1,33)} = 5.95$, $p = 0.015$; total forb cover: $F_{(1,33)} = 5.40$, $p = 0.027$; total herbaceous cover: $F_{(1,33)} = 4.91$, $p = 0.034$; medium shrub cover: $F_{(1,33)} = 5.40$, $p = 0.026$; total shrub cover: $F_{(1,33)} = 11.07$, $p = 0.002$; shrub richness: $\chi^2_{(1,33)} = 4.34$, $p = 0.037$) and 2 of the patch-scale variables were marginally significant (perennial grass cover: $F_{(1,33)} = 3.98$, $p = 0.054$; total sagebrush cover: $F_{(1,33)} = 3.20$, $p = 0.083$; Table 4.1; Figure 4.2). None of the slopes for the tall herbaceous variables or annual grass cover were statistically different from zero. In the stand analysis, slopes of 4 of the 8 variables were different from zero (perennial grass cover: $F_{(1,33)} = 4.866$, $p = 0.035$; total grass cover: $F_{(1,33)} = 6.886$, $p = 0.013$; total shrub cover: $F_{(1,33)} = 11.340$, $p = 0.002$; and total sagebrush cover: $F_{(1,33)} = 6.744$, $p = 0.014$; Table 4.1; Figure 4.2). At both scales, shrub cover had the most deviance explained by conifer cover with 25.1% and 25.6% at the patch and stand scales, respectively (Table 4.1). Shrub cover decreased by 0.47 and 0.68 percentage points per percentage point increase in conifer cover at these 2 scales (Table 4.1; Figure 4.2).

Treatment Effects

In the treatment analysis, the time × strata interaction was statistically different from zero for 3 of the patch-scale herbaceous variables including perennial grass cover ($F_{(3,92)} = 3.10$, $p = 0.032$), total grass cover ($F_{(3,92)} = 4.70$, $p = 0.004$), and total herbaceous cover ($F_{(3,92)} = 5.20$, $p = 0.002$), and was marginally significant for 2 of the stand-scale herbaceous variables including tall perennial grass cover ($F_{(3,92)} = 2.50$, p = 0.062) and tall grass cover ($F_{(3,92)} = 2.40$, p = 0.073; Table 4.1; Figure 4.3; Appendix B). For each of these variables, the effect in the cut-2012 stratum relative to the on-site control was different from zero (perennial grass: β = 1.49 ± 1.20 CI; total grass: β = 1.86 ± 1.39 CI; total herbaceous: β = 1.90 ± 1.53 CI; tall perennial grass: β = 0.29 ± 0.22 CI; tall grass: β = 0.32 ± 0.25 CI) while the effects in the cut-2013 stratum was not different from zero (Figure 4.3). Overall, the cut-2012 stratum benefited from conifer removal, while the cut-2013 stratum had not.

As anticipated, the time × strata interaction for conifer cover was different from zero at both scales (patch: $F_{(3,92)} = 3.11$, p = 0.030; stand: $F_{(3,92)} = 4.40$, p = 0.006) and the cut-2013 stratum had a significant negative effect relative to the on-site control (patch: β = -3.62 ± 3.12 CI; stand: β = -3.21 ± 2.53 CI; Table 4.1; Figure 4.3; Appendix B). However, unexpectedly, there was a marginally significant conifer cover decrease at the stand scale in the off-site control relative to the on-site control (β = -2.26 ± 2.53 CI; Figure 4.3). Additionally, shrub cover at the stand scale had a marginally significant negative effect in both cut strata (cut-2012: β = -2.03 ± 2.14 CI; cut-2013: β = -2.12 ± 2.14 CI; Figure 4.3). Because the controls generally did not differ from each other, they appeared to be adequate controls for the analysis. The number of significant variables in cut areas and nonsignificant variables in control areas provide further confirmation.

Sage-grouse Nesting Habitat Comparison

I found and surveyed 356 nests from 2010 to 2014. My cut monitoring points had lower total shrub (20.8%) and total sagebrush (12.6%) cover than the uncut points, but both had lower cover than the nests (33.3% and 24.1%; Table 4.2). These estimates were lower than those reported by Hagen et al. (2007; 25.1% and 21.5%) and fell into the marginal class of Stiver et al. (2015; Figure 4.4). However, the y-intercept from the regression of sagebrush on conifer cover, at 15.8% (Figure 4.2, 4.3), was within the suitable habitat range indicating that conifer removal could improve conditions for nesting sage-grouse.

Forb and grass cover was greater in areas with less conifer cover, and grass cover also increased after conifer removal (Table 4.1), suggesting lower conifer cover provides higher quality sage-grouse nesting habitat in terms of herbaceous vegetation. While below the suitable habitat category, the perennial grass cover averages at nests (6.0%) and cut areas (5.3%) were within the marginal range, and both perennial grass and forb cover were close to the meta-analysis values and the nest averages (Figure 4.4). Tall (>18) grass and forb cover, recommended as important for nesting cover, was not affected by conifer cover but showed marginally significant increases after treatment at the stand scale (Table 4.1). Values for key forb richness were not given by Stiver et al. (2015), but they noted that increased forb diversity was beneficial. Although conifer removal did not increase forb richness, conifer cover negatively impacted forb richness (Table 4.1; Figure 4.2).

DISCUSSION

My study is the first to combine information on the effects of conifer encroachment and removal on vegetation with nest habitat data from locally monitored sage grouse and established nest habitat guidelines. I observed negative effects of conifer encroachment on vegetation characteristics important to sage-grouse nesting and positive benefits of conifer removal in <3 years. Average monthly precipitation from January to June in 2012 to 2014 was 1.42, 0.99., and 0.98 cm which were all below the 15-yr average of 1.74 cm (median: 1.91 cm; interquartile range: 1.04–2.17 cm). Only one year (2001: 0.77 cm January to June monthly average) was drier than 2013 and 2014 over the last 15 years. I would expect even greater herbaceous response after treatments in years with increased precipitation.

Negative effects of conifer encroachment on sagebrush vegetation are well documented (Miller et al. 2005, 2011; Coultrap et al. 2008; Roundy et al. 2014). Coultrap et al. (2008) observed negative trends on various richness and cover estimates with increasing conifer cover similar to my observations. In general, as conifer abundance increases, other vegetation decreases (Miller et al. 2011, Roundy et al. 2014), possibly contributing to the avoidance of sage-grouse to trees during every life history stage (Gregg 1992; Doherty et al. 2008, 2010; Freese 2009; Atamian et al. 2010; Casazza et al. 2011). Vegetation provides necessary benefits to sage-grouse including structure for nesting cover (Gregg et al. 1994, Delong et al. 1995, Doherty et al. 2014), forbs for food during nesting and brood-rearing (Barnett and Crawford 1994, Drut et al. 1994, Gregg et al. 2008), and sagebrush for food during winter (Patterson 1952). My nesting habitat assessment demonstrated negative effects of conifer encroachment and benefits of conifer removal on cover and food required by nesting grouse.

Although several vegetation characteristics did not respond to conifer treatments, I observed increases in multiple measures of herbaceous vegetation, which is consistent with other studies (Bates et al. 2005, 2007; Dodson et al. 2008; Miller et al. 2014; Roundy et al. 2014). Understory vegetation recovery depends on several factors including site conditions, conifer abundance, pretreatment vegetation, time since removal, and management technique (Bates et al. 2000, 2005, 2007; Dodson et al. 2008; Roundy et al. 2014). Many studies have not observed recovery of shrub communities (Miller et al. 2014, Roundy et al. 2014) due to the short monitoring time, while recovery of herbaceous vegetation is common, but may take several years (Bates et al. 2000). Bates et al. (2005) reported maximum herbaceous recovery at 5–6 years. I observed herbaceous recovery in the sites cut in 2012 but not at those treated in 2013. Because of my inability to completely randomize the treatments, this may have been due to site effects I could not control. More monitoring is needed to evaluate longer time periods and assess site factors.

An unexpected result was the marginal decrease in shrub cover at the stand scale in the treated areas. Although I could not control for it in my dataset, this may have been caused by either the decrease in precipitation among the study years or the burning of individual trees during winter to eliminate woody debris. An effort was made to minimize the impact of the slash burning, but some nearby shrubs likely were killed. The effect size was a decrease of ~4 percentage points over the course of the study in the treated areas which can be considered minimal. Burning individual fallen trees during the winter to eliminate slash and minimize impact can provide other benefits to posttreatment succession such as increased growth of perennial grass (Bates and Svejcar 2009), but managers should consider potential tradeoffs with the approach and make every effort to minimize negative impacts.

Overall, the encroachment and treatment analyses indicated that the herbaceous vegetation in this portion of the species range is capable of recovering toward suitable nesting habitat for sage-grouse after conifer removal. My vegetation monitoring points generally had low herbaceous cover which increased posttreatment. Additionally, because the habitat used by local nesting sage-grouse had lower herbaceous cover than the guidelines consider suitable, recovery to suitable levels may not be possible or even necessary at this site. Furthermore, the herbaceous vegetation results in the meta-analysis (Hagen et al. 2007) are similar to my local nest data and to the monitoring points.

The short-term nature of my study was inadequate to observe treatment effects on shrubs. Sagebrush cover at the monitoring points was marginal for nesting and well below both the meta-analysis results (Hagen et al. 2007) and the local nest data, but because conifer cover negatively impacted shrub cover, I anticipate that given sufficient time, the shrubs will recover.

MANAGEMENT IMPLICATIONS

Conifer encroachment has negative impacts on sagebrush vegetation including those characteristics necessary for sage-grouse nesting, but conifer removal can improve nesting conditions given enough time. For sage-grouse nesting habitat improvement, managers should focus on areas that have the greatest potential for nesting. Because I observed relatively quick herbaceous recovery, focusing on treating areas with intact understory communities (Phase-I and Phase-II) may provide the most immediate benefits. Knowledge of local sage-grouse habitat is beneficial, in addition to established guidelines, to help develop recovery goals and expectations. Herbaceous vegetation will recover quickly, while the shrub communities will recover more slowly, but more research is needed to evaluate the specific effects of site conditions and the time frame necessary for recovery. While cheatgrass did not increase after my treatments, managers should consider all possible threats from invasive species prior to treatments.

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Table 4.1. Effects of conifer canopy cover (%) on understory vegetation response variables during summer 2012 and conifer removal treatment effect from 2012–2014 in southern Oregon. Units are percent cover except richness (number of species) and height (cm).

						Treatment Effect Time × Strata Interaction	
	Conifer Encroachment Effect						
Response Variable	β_0 (SE)	β_1 (SE)	Dev (%)	$F_{(1,33)}$	p[7]	$F_{(3,92)}$	p[7]
Patch[1]							
Key Forb Richness	0.82[5] (0.14)	-0.02 (0.01)	14.7	5.95[6]	0.015**	0.43[6]	0.732
Key Forb	1.37 (0.29)	-0.02 (0.01)	7.4	2.64	0.114	1.20	0.314
Tall[3] Forb	0.29 (0.09)	0.00 (0.00)	0.2	0.06	0.806	0.88	0.453
Total Forb	3.04 (0.36)	-0.04 (0.02)	14.1	5.40	0.027**	0.70	0.566
Tall[3] Perennial Grass	0.98 (0.31)	-0.02 (0.01)	5.6	1.95	0.172	1.75	0.162
Perennial Grass	5.54 (0.69)	-0.06 (0.03)	10.8	3.98	0.054*	3.10	0.032**
Annual Grass	1.48 (0.87)	-0.02 (0.04)	1.1	0.35	0.557	0.89	0.447
Total Grass	7.02 (1.17)	-0.08 (0.05)	7.3	2.60	0.116	4.70	0.004**
Tall[3] Herbaceous	1.26 (0.33)	-0.02 (0.01)	5.3	1.86	0.182	1.98	0.122
Total Herbaceous	8.58 (0.8)	-0.09 (0.03)	18.6	7.52	0.010**	5.20	0.002**
Medium Shrub	7.89 (1.62)	-0.16 (0.07)	14.1	5.40	0.026**	1.75	0.162
Total Shrub	30.19 (3.36)	-0.47 (0.14)	25.1	11.07	0.002**	0.20	0.904
Shrub Richness	0.88[5] (0.14)	-0.02 (0.01)	18.9	4.34[6]	0.037**	0.15[6]	0.929
Medium[4] Sagebrush	0.96 (0.35)	-0.02 (0.02)	5.7	2.00	0.167	1.75	0.162
Total Sagebrush	15.8 (2.34)	-0.18 (0.10)	8.8	3.20	0.083*	1.30	0.277
Conifer Cover	—	—	—	—	—	3.11	0.030**
Stand[2]							
Tall[3] Perennial Grass	0.82 (0.22)	-0.01 (0.01)	1.0	0.34	0.563	2.50	0.062*
Perennial Grass	6.09 (0.75)	-0.10 (0.04)	12.9	4.87	0.035**	0.90	0.446
Annual Grass	0.63 (0.20)	-0.02 (0.01)	5.8	2.04	0.162	1.00	0.397
Tall[3] Grass	1.04 (0.27)	-0.02 (0.02)	2.8	0.96	0.335	2.40	0.073*
Total Grass	6.72 (0.73)	-0.11 (0.04)	17.3	6.89	0.013**	0.50	0.671
Total Shrub	33.99 (3.41)	-0.68 (0.20)	25.6	11.34	0.002**	2.20	0.092*
Total Sagebrush	19.18 (1.94)	-0.30 (0.12)	17.0	6.74	0.014**	0.40	0.722
Sagebrush Height (cm)	39.54 (4.71)	-0.14 (0.28)	0.7	0.24	0.631	1.00	0.334
Conifer Cover	—	—	—	—	—	4.40	0.006**

[1] measured on two 10-m transects.

[2] measured on four 60-m transects.

[3] >18 cm in height.

[4] 40 to 80 cm in height.

[5] Poisson regression. Intercepts back-transformed to response scale: Key Forb Richness = 2.27, Shrub Richness = 2.40.

[6] Poisson regression. Test statistic was chi-square.

[7] ** = significant ($p \leq 0.05$). * = marginally significant ($0.05 < p \leq 0.10$).

Table 4.2. Vegetation cover (%) at conifer removal monitoring points and sage-grouse nests in southern Oregon from 2010–2014.

		Nests (SE)	Cut (SE)	Not Cut (SE)	Intercept[2] (SE)
	Sample Size	356	60	81	–
Herbaceous	Key Forb Rich[1]	2.8 (0.1)	2.3 (0.2)	2.1 (0.2)	2.3 (0.3)
	All Forb	3.6 (0.2)	2.7 (0.3)	2.3 (0.2)	3.0 (0.4)
	Per. Grass	6.0 (0.2)	5.3 (0.5)	4.5 (0.4)	5.5 (0.7)
	All Grass	6.7 (0.2)	6.1 (0.6)	5.1 (0.5)	7.0 (1.2)
	All Herb	10.3 (0.3)	8.1 (0.6)	6.8 (0.4)	8.6 (0.8)
Sagebrush	40–80 cm	3.8 (0.3)	2.6 (0.7)	0.7 (0.2)	1.0 (0.4)
	Total	24.1 (0.6)	12.6 (1.5)	13.3 (1.2)	15.8 (2.3)
All Shrubs	40–80 cm	7.3 (0.5)	8.8 (1.4)	5.4 (0.8)	7.9 (1.6)
	Total	33.3 (0.8)	20.8 (2.3)	22.9 (1.8)	30.2 (3.4)

[1] Number of key forb species observed at each site.

[2] Intercept is estimated value at 0% conifer cover from regression on habitat variables.

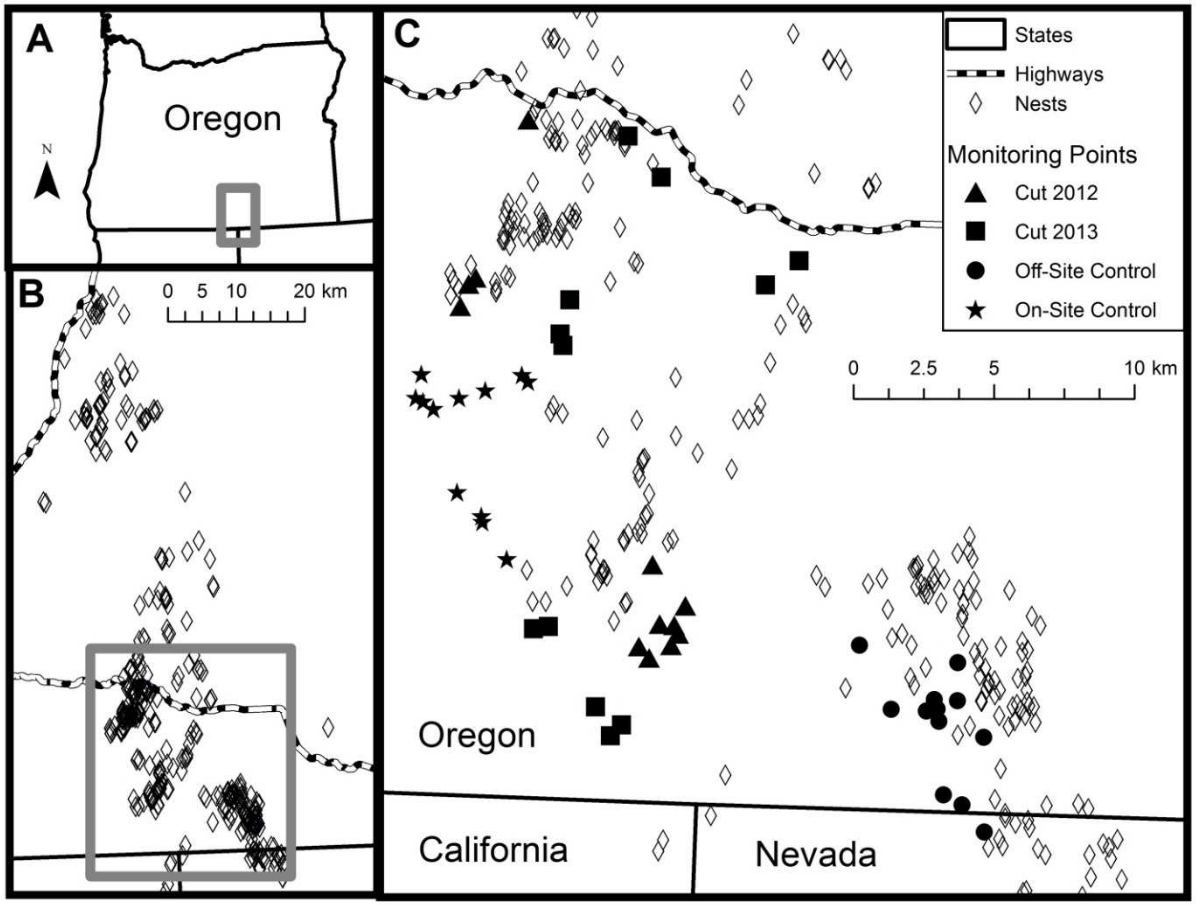

Figure 4.1. A) Gray box shows study area location within Oregon. B) Study area of sage-grouse nesting study from 2010–2014. C) Vegetation monitoring points for conifer removal study from 2012–2014.

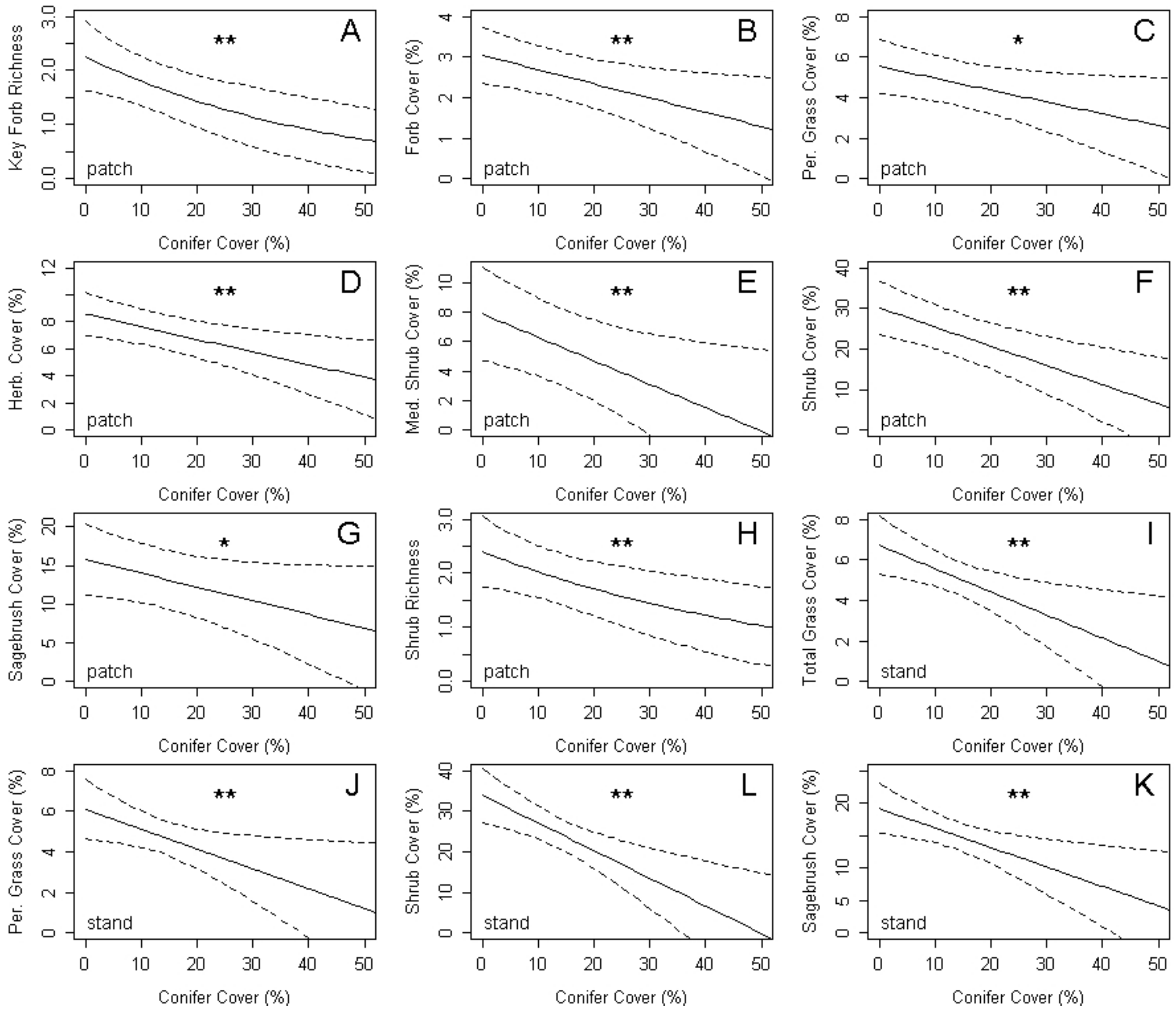

Figure 4.2. Effects of conifer cover on vegetation characteristics in southern Oregon during 2012 at 2 scales. Patch was two 10-m transects (A–H). Stand was four 60-m transects (I–K). ** = significant ($p < 0.05$). * = marginally significant ($0.05 < p < 0.10$).

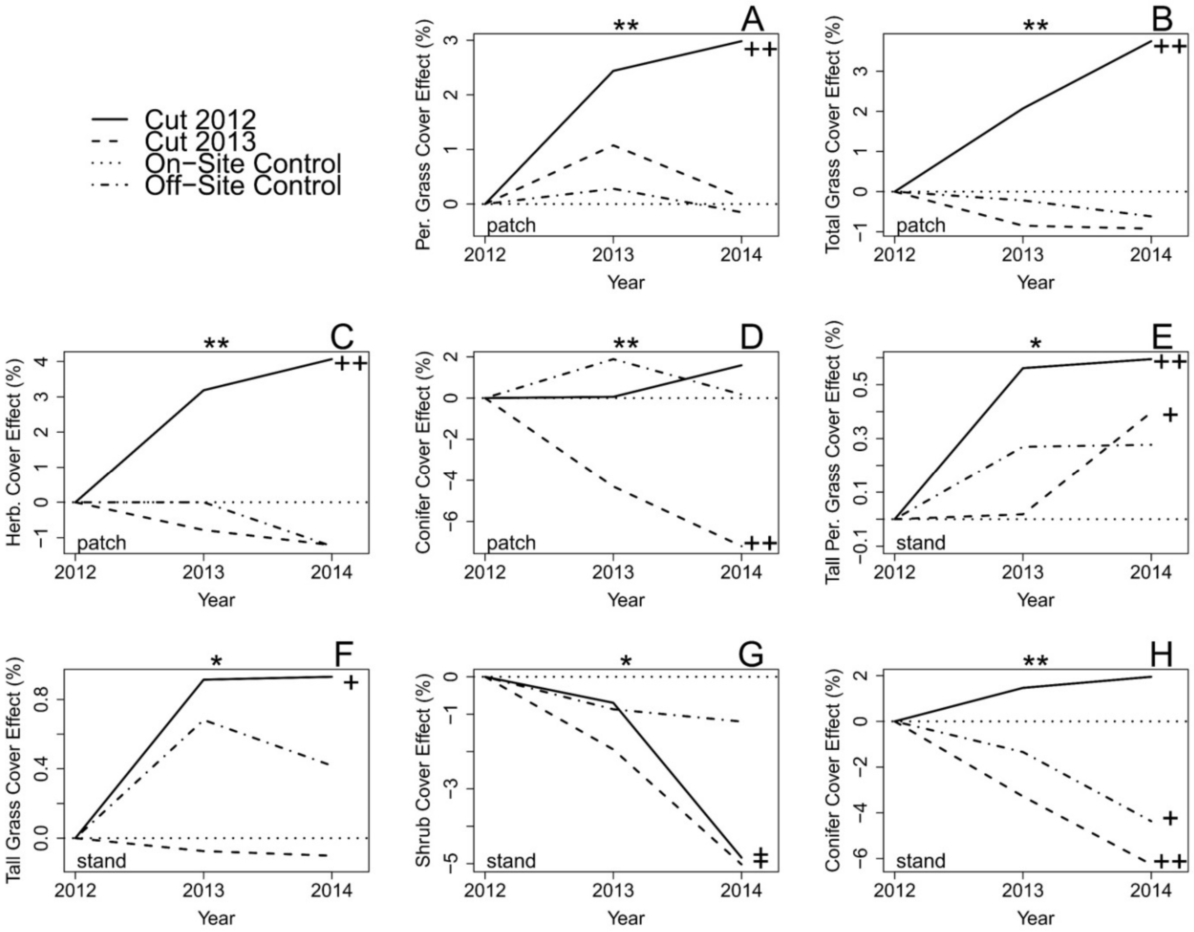

Figure 4.3. Effects (relative to on-site control) of time × strata interaction on vegetation characteristics in southern Oregon during 2012–2014 at 2 scales. Lines are standardized difference between means of strata and on-site control. Strata included an on-site and off-site control and areas cut in 2012 and 2013. Patch was two 10-m transects (A–D). Stand was four 60-m transects (E–H). Interaction main effect (above plot): ** = significant ($p < 0.05$), * = marginally significant ($0.05 < p < 0.10$). Group effect relative to on-site control (symbol at right end of associated group line): ++ = significant ($p < 0.05$), + = marginally significant ($0.05 < p < 0.10$).

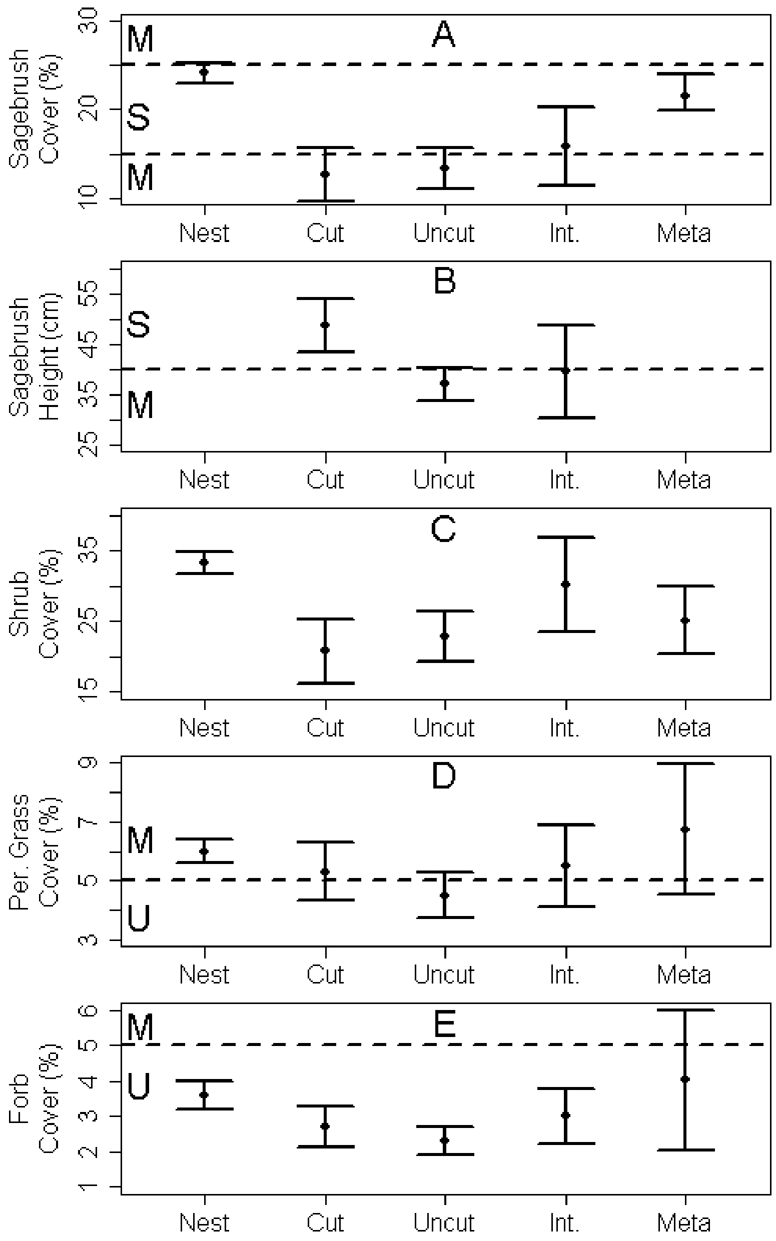

Figure 4.4. Comparison of important sage-grouse nesting habitat characteristics in conifer removal areas (cut) and conifer encroached areas (uncut) in southern Oregon with local nest data, GLM y-intercept (estimate at 0% conifer cover), and rangewide meta-analysis values (Hagen et al. 2007). Horizontal dashed lines are boundaries between suitable (S), marginal (M), and unsuitable (U) nesting habitat (Stiver et al. 2015). Missing values or suitability classes were unavailable. Error bars represent 95% confidence intervals.

CHAPTER 5

DEMOGRAPHIC RESPONSE OF FEMALE SAGE-GROUSE TO LANDSCAPE-SCALE CONIFER REMOVAL

ABSTRACT

Sagebrush (*Artemisia* spp.) obligate wildlife species such as the imperiled greater sage-grouse (*Centrocercus urophasianus*) face numerous threats including conifer expansion. Conifer removal is accelerating despite a lack of empirical evidence on grouse population response. Using a before-after-control-impact design at the landscape scale, I evaluated effects of conifer removal on two important demographic parameters, female and nest survival, by monitoring 219 female sage-grouse and 225 nests in the northern Great Basin from 2010 to 2014. Treatment effects garnered little support, but model averaged estimates showed an increase of 1.8% annual female survival and 5.2% nest survival relative to the control area, while the best treatment interaction model showed an increase of 11.2% female survival and 22.0% nest survival relative to the control area. Additionally, nest survival in mountain big sagebrush (MBS), which is most susceptible to conifer encroachment, was 13% higher than in low sagebrush and 19% higher than in Wyoming big sagebrush, indicating potentially large negative impacts when MBS becomes encroached and unavailable for nesting as well as potential opportunities for restoration. However, distance of nests to nearest conifer removal area showed negative effects on nest survival closer to treatments potentially indicating an ecological trap in certain areas. My results showed potential landscape-scale population benefits of conifer removal, but also increased risk for some individuals. This

information will be crucial in fine-tuning conifer removal plans for maximum population level benefits.

INTRODUCTION

The sagebrush (*Artemisia* spp.) biome in western North America has experienced numerous threats since the late 1800s including conversion to agriculture, energy development, altered fire regimes, overgrazing, and invasive species (Knick et al. 2003, Connelly et al. 2011, Knick and Connelly 2011) resulting in significant reduction and degradation of sagebrush habitat (Miller and Eddleman 2001). These losses reduce native wildlife populations, particularly sagebrush obligates (Knick et al. 2003, Welch 2005).

Conifer encroachment is a major threat throughout the Great Basin and other sagebrush ecosystems (Davies et al. 2011, Miller et al. 2011). Although native, species such as piñon pine (*Pinus* spp.) and juniper species (*Juniperus* spp.) were historically restricted to low fuel areas that did not burn frequently, such as rocky outcrops, but have increased 3–10 times in distribution and ~10 times in abundance in portions of the Great Basin (Miller et al. 2005, Miller at al. 2008) and currently occupy 18 million ha in the intermountain west (Miller and Tausch 2001). Factors thought to have contributed to conifer expansion include fire suppression, fire fuel reduction via over-grazing, changing climate/weather patterns, and increases in atmospheric CO_2 (Miller and Rose 1995, 1999; Miller et al. 2005). Increased conifer abundance fragments and displaces sagebrush habitat, provides avian predator perches, and degrades range condition (Paton 1994; Wolff et al. 1999; Manzer and Hannon 2005; Miller et al. 2005, 2011).

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) was once widespread throughout western North America but, being an obligate sagebrush species, has declined along with its required habitat (Knick and Connelly 2011). Sage-grouse distribution has contracted 44% since the late 1800s (Schroeder et al. 2004), and populations continue to decline in the remaining habitat (Garton et al. 2011). Conifer encroachment is thought to be an important threat to sage-grouse, but empirical field studies are limited (Connelly et al. 2011, United States Fish and Wildlife Service [USFWS] 2015).

Conifer removal has been recommended for sage-grouse conservation (Connelly et al. 2000, Baruch-Mordo et al. 2013), but little research has been completed relating sage-grouse behavior and abundance with conifer management. Monitoring is a key step in ecological restoration (Hobbs and Norton 1996, Suding 2011), and evaluating restoration experiments is important to understanding their efficacy (Mirchener 1997). Evaluating a wildlife species' demographics is crucial in linking a conservation action with a population response (Block et al. 2001). Reduced sage-grouse breeding ground occupancy and survival with increasing conifer abundance have been documented and used to infer benefits of management (Baruch-Mordo et al. 2013, Coates et al. in revision), but no studies have directly linked conifer removal with sage-grouse population parameters. In general, conifer removal can prevent displacement and fragmentation of sagebrush systems, reduce available avian predator perches and nesting habitat, and improve range conditions (Young et al. 1985; Bates et al. 1998, 2000; Miller et al. 2005), but research is needed to confirm whether sage-grouse benefit from these treatments and determine the time frame of the response. Two of the most important vital rates affecting sage-grouse population growth are annual female survival and nest survival, and managing these parameters should be a focus of sage-grouse conservation (Taylor et al. 2012).

Using a before-after-control-impact (BACI) framework, I compared female sage-grouse survival and nest survival before and after conifer removal in both a treatment area and a control area from 2010 to 2014. Because conifer removal may increase high quality habitat availability and limit avian predator distribution and abundance, I predicted increased female survival after conifer removal with the greatest improvement during nesting and early summer/brood rearing seasons when females are in closer proximity to conifers and more susceptible to predation (see Chapter 3; Coates et al. in revision). For the same reasons, I also predicted increased nest survival after treatments. To gain further insight into treatments, I examined habitat covariates at individual nests including habitat type and treatment covariates. I predicted that mountain big sagebrush (MBS; *Artemisia tridentata* ssp. *vaseyana*) would have the greatest nest survival and that nests in and near treatments would have greater nest survival than those outside.

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 (Figure 5.1). I delineated discrete boundaries for treatment and control study areas guided by natural barriers (e.g., canyons, cliffs, and forest) as well as observed sage-grouse movements (Figure 5.1). The treatment area encompassed 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 encompassed 40,000 ha and ranged in elevation from 1360 m to 2180 m with an average of 1680 m above sea level. Both areas were dominated by low sagebrush (*A. arbuscula*) habitat, but other dominant species included MBS at higher elevations, 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.). 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 Natural Resources Conservation Service in association with the Oregon Department of Fish and Wildlife assisted landowners with juniper removal on private land within and surrounding the treatment area (Figure 5.1). 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 brush- 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 vertical structure. 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 year 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 pre-settlement trees in locations that historically supported juniper, thus some areas still had standing trees after treatment (BLM 2011). BLM biologists identified pre-settlement trees using criteria including size, leader growth, crown form, bark, and habitat (Miller et al. 2005). For my analysis I grouped all treatments together.

Although some treatments occurred from 2007–2011 (<10%), most occurred from 2012–2014 and slash burning also began in 2012. I therefore used spring of 2012 as the break between before and after treatment. Within the treatment area, 6488 ha of trees were cut and 2277 ha of trees were slash 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 5.1; Figure 5.1).

Telemetry and Nest Data

Sage-grouse females were captured during winter and spring from 2009–2014 in the treatment area and 2010–2014 in the control area using spotlighting techniques (Geisen et al. 1982, Wakkinen et al. 1992) near leks and wintering habitat with a goal of ~40 radio-collared (22-g VHF radio-collars, model #A4060, Advanced Telemetry Systems, Isanti, MN, USA) females at start of nesting (~1 April) in each of the two areas. While transmitters were equipped with 8-hr mortality switches, encounters generally consisted of telemetry locations acquired by approaching to within 30 m of the birds without flushing. For the survival analysis, I tried to encounter each bird 1–2 times per week during February–July and 1–4 times per month during August–January. For the nest survival analysis, I monitored radio-marked females twice per week during the potential nesting seasons from 2011–2014. 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). All nests were included as independent replicates for the analyses even though some females nested in multiple years (n = 33) or re-nested after failure during the same year (n = 19). Although autocorrelation in these instances likely exists, I believe including all data was more beneficial than disregarding these potential pseudo-replicates.

Female Survival BACI Analysis

I estimated female sage-grouse survival with the nest survival model in MARK (White and Burham 1999, Dinsmore et al. 2002) using the RMark package (Laake 2013) as an interface within R 3.1.2 (R Core Team 2014). Because the control area data collection started in the fall of 2010, I used treatment area data also beginning at this time. As treatments generally concluded at the start of the sage-grouse nesting season (March or April), I defined years biologically as April to March. Survival histories were relatively complete from April to July (1–2 encounters per week), but were sparse during the rest of the year (1–2 encounters per month). While I used weekly encounter histories to take full advantage of the data, and therefore estimated weekly survival, I held longer intervals constant with the smallest constant interval being 1 month to minimize the number of estimated parameters.

I initially compared monthly, seasonal, and annual survival models with corrected Akaike’s information criterion (AICc; Anderson 2008) to select a structure to control for nuisance variation in the subsequent conifer removal analysis (Table 5.2). I assessed 3 seasonal models including 1) nest/summer where the intervals were April–May (nesting), June–July (early summer/brood rearing), and August–March, 2) breeding where April–July was separated from the rest of the year, and 3) seasonal where 3 intervals were used: April–July, August–November, and December–March.

In an environmental impact analysis, the important parameter is the impact × area (e.g., control or treatment) interaction (Stewart-Oaten et al. 1986). The impact can be represented as before-after impact, continuous through time, or as a gradient of impact (Weins and Parker 1995). Because conifer removal accumulated over time, in my analysis I assessed 4 different measures of impact including interactions between study area and 1) before-after impact using April 2012 as the split, 2) continuous time by month, 3) continuous time by year, and 4) cumulative area of conifer removal accumulated by month (Table 5.2). I compared each of the 4 interaction models with each of the 4 models without the interaction using AICc and model weights.

To assess the magnitude of treatment effect on survival, I model averaged (Anderson 2008) the parameters in all 8 models and evaluated the change in weekly survival through time graphically. I also calculated the annual survival and the standardized difference between the control and treatment areas to assess potential impacts of conifer removal on this important vital rate (Taylor et al. 2012). Because the 2014 data ended in August, I incorporated September to December estimates from 2013 with the 2014 estimates to form a complete year (i.e., September 2013 to August 2014) to allow comparison to previous years. Additionally, to explore a best case scenario, I estimated weekly and annual survival for the AICc best interaction model.

Nest Survival BACI Analysis

I estimated daily nest survival with the nest survival model in MARK (White and Burham 1999, Dinsmore et al. 2002) using the RMark package (Laake 2013) as an interface within R 3.1.2 (R Core Team 2014). For the BACI analysis, I used only nests from 2011 onward because this was the first nest season of data collection.

I initially compared weekly, biweekly, and monthly nest survival models along with female age, continuous time trend within year, and nest type (first or renest) with AICc (Anderson 2008) to select a structure to use as a nuisance parameter in the subsequent conifer removal analysis (Table 5.3). Similar to the female survival treatment effect models, I assessed interactions between study area and 1) before-after impact using 2012 as the split, 2) continuous time by year, and 3) cumulative area of conifer removal at the beginning of April for each year (Table 5.3). I compared each of the 3 interaction models with each of the 3 models without the interaction using AICc and model weights.

To assess the magnitude of treatment effect on survival, I model averaged (Anderson 2008) the parameters in all 6 models and evaluated the change in daily nest survival through time graphically. I also calculated the total nest survival (using a 27-day incubation period; Schroeder et al. 1999) and the standardized difference between the control and treatment areas to assess potential impacts of conifer removal on this important vital rate (Taylor et al. 2012). Additionally, to explore a best case scenario, I estimated daily and total nest survival for the AICc best interaction model.

Nest Survival Covariate Analysis

To further explore effects of treatments on nest survival, I also assessed covariates for individual nests rather than by study area. I calculated nest survival by habitat type determined by dominant sagebrush species for all nests from 2010 to 2014. I also assessed 3 covariates related to treatments (from Chapter 2) including 1) whether a nest was in a conifer removal area or not for all treatment area nests, 2) years since treatment for all nests in a conifer removal area, and 3) distance to nearest conifer removal area using only nests within 800 m of a removal area (determined from previous multiscale nest-site selection analysis; see Chapter 1). Because sample size varied for each covariate assessed, the likelihood scales were not comparable and AIC could not be used to compare all covariates. I therefore compared all 4 of these variables to a null model with AICc and model weights to determine strength of influence. I then plotted the covariate estimates with 85% confidence intervals (Arnold 2010) to inspect the effects graphically.

RESULTS

Female Survival BACI

I captured 108 and 116 female sage-grouse from 2010–2014 in the control and treatment areas, respectively. Five birds were removed from the analysis because they left the study area or were not encountered after capture resulting in a sample of 107 and 112 in the control and treatment areas, respectively. Of the 219 birds, 141 died during the study and 78 were censored because the transmitter failed or the study concluded in August 2014.

The breeding season model (April–July, August–March) was the best temporal structure to estimate survival with a weight of 0.52 (Table 5.2A) and was used as the base structure in the subsequent conifer removal analysis. All 4 treatment interaction models had less support than their additive counterparts by 1.32–1.90 ΔAICc (model weights: 0.28–0.34). The best interaction model included study area × month trend interaction which had a 0.34 weight compared to without the interaction and 0.10 overall model weight (Table 5.2). The model averaged survival estimates showed a potential interaction with a positive trend through time of the difference between the treatment and control (Figure 5.2). The standard errors were large relative to the effect, but the estimated treatment effect in annual survival was a 1.8% increase in the treatment area relative to the control area over the course of the study (Table 5.4). The best interaction model (study area × month trend) show a steeper positive trend with a greater effect during the breeding period than the nonbreeding period (Figure 5.2), resulting in an estimated treatment effect in annual survival of 11.2% increase in the treatment area over the course of the study. Because the breeding period had lower survival (Figure 5.2) than the rest of the year and may be more important to population growth, I separated out April–July (Table 5.4). The estimated treatment effect for the model averaged estimates was a 1.3% increase in the treatment area during the breeding period.

Nest Survival BACI

I located 109 and 123 nests from 2011–2014 in the control and treatment areas, respectively. Seven nests were removed because they were abandoned and I suspected observer influence. Of the remaining, 116 nests were successful and 109 were unsuccessful.

The null model was the best survival structure with a weight of 0.39 (Table 5.3A) and was used as the base structure in the conifer removal analysis. All 3 interaction models had less support than their additive counterparts and the study area × area cut interaction was uninformative (ΔAICc = 2.00). Year and before-after interactions had ΔAICc = 0.68 and 1.49 relative to their additive counterparts, respectively, with model weights of 0.42 and 0.32. The best interaction model was study area × year trend interaction which had 0.13 overall model weight (Table 5.3B). The model averaged survival estimates showed a potential interaction with a positive trend through time of the difference between the treatment and control areas

(Figure 5.3). The standard errors were large relative to the effect, but the estimated treatment effect over the 27-day exposure period was a 5.2% total nest survival increase in the treatment area relative to the control area over the course of the study (Table 5.4). The best interaction model (study area × year trend) show a steeper positive trend (Figure 5.3), resulting in an estimated treatment effect of 22.0% increase in the treatment area over the course of the study.

Nest Survival Covariates

The nest survival models of habitat type by dominant sagebrush species used 246 nests found in both the control and treatment areas from 2010 to 2014 and had a slightly lower AICc than the null model (Table 5.5A) with a model weight of 0.51. The mountain big sagebrush habitat had the highest nest survival (daily nest survival [DNS] = 0.978 ± 0.007 CI, 27-day = 0.543 ± 0.107 CI, n = 84) followed by low sagebrush (DNS = 0.968 ± 0.007 CI, 27-day = 0.415 ± 0.082 CI, n = 147) and Wyoming big sagebrush (DNS = 0.962 ± 0.026 CI, 27-day = 0.355 ± 0.255 CI, n = 15; Figure 5.4A).

There were 139 nests located in the treatment area from 2010–2014, 30 of which were in conifer removal areas. Whether a nest was in a conifer removal area was largely uninformative (ΔAICc = 1.82, weight = 0.29; Table 5.5B; Figure 5.4B). Years since the conifer treatment had a slightly higher AICc than the null model (ΔAICc = 0.30) with a model weight of 0.46 (Table 5.5C) and a negative trend (Figure 5.4C). There were 67 nests found within 800 m of a conifer removal area from 2010–2014. Distance to nearest conifer removal area was 1.50 AICc units lower than the null model with a 0.68 model weight (Table 5.5D) and had positive trend (Figure 5.4D).

DISCUSSION

My study is the first to link sage-grouse demographic rates with conifer removal treatments. At the landscape scale, I observed support for potentially increased female survival and nest survival, which are two of the most important demographic parameters affecting population growth (Taylor et al. 2012). Using the sensitivity estimates of Taylor et al. (2012; i.e., nest survival = 0.9 and female survival = 1.7), my estimated increase of 5.2% and 1.8% for nest survival and female survival would increase λ by 4.7% and 3.1%, respectively, for a total increase in the population growth rate of 7.7%. While further monitoring is needed, my results indicate possible positive effects on sage-grouse population growth which is the overall goal of wildlife habitat restoration (Block et al. 2001). Baruch-Mordo et al. (2013) found conifer encroachment decreased lek occupancy, which is a proxy for population size, and recommended conifer removal near leks, while Coates et al. (in revision) suggested that decreases in populations are in part due to decreased female survival caused by increased conifer abundance. However, I provide the first empirical evidence that conifer removal may be successful at increasing sage-grouse population size.

I suggest the mechanisms effecting survival in my study include reduced avian predator populations and hunting efficiency as well as increased availability of high quality habitat (see Chapter 2). Avian predators are important sources of mortality for sage-grouse adults and eggs throughout their range (Hagen 2011) with corvids focusing on eggs (Coates and Delehanty 2010) and raptors largely preying on adults (Blomberg et al. 2013). Avian predator distribution and abundance are limited by nesting and perching sites (Coates et al. 2014, Howe et al. 2014), and reducing these sites may be beneficial in reducing depredation rates. Additionally, changes in available habitat as a result of conifer removal may also impact survival. Because sage-grouse select seasonal habitats and nest sites in areas susceptible to conifer encroachment (see Chapters 1 and 3; Coates et al. in revision), conifer removal in those areas increases the availability of potentially better habitat. I found the greatest nest survival in mountain big sagebrush habitats, which are also more susceptible to conifer encroachment than low sagebrush or Wyoming big sagebrush habitats (Miller and Edelman 2001) which indicates large reductions in nest survival as encroachment continues, but also potential for effective restoration.

Contrary to the landscape-scale analysis, the nest-specific treatment covariates indicated negative effects of conifer removal. It may be possible that large conifer removal treatments increase survival at the population level (e.g., decreased overall predator efficiency), but the increased available habitat in and around treatments could be detrimental to some individual nests. I warned of potential ecological traps in Chapters 1 and 3, where I observed some selection for areas with low conifer cover, and in Chapters 2 and 3, I observed increased selection in and near treated areas. Coates et al. (in revision) observed selection for, but reduced survival in, highly productive areas with low conifer cover and recommended that treatments in these areas should remove all conifers to minimize the potential of an ecological trap. It has long been known that many wildlife species are attracted to edges (Leopold 1933), but more recent studies have documented decreased nest success near edges (Gates and Gysel 1978, Paton 1994, Batary and Baldi 2004). Because my individual removal areas were relatively small at a landscape scale (87 ha average), there were often old-growth conifers remaining in close proximity potentially increasing availability of high quality habitat near conifer stands which serve as avian predator perches. It may be the case that the soft, ecotone edge provided by successively smaller size and abundance of encroaching trees away from stands of larger trees (Strand et al. 2007) acts as a buffer which restricts sage-grouse to greater distances from the larger trees used by avian predators. My treatments focused on early to mid-successional trees, thereby removing the buffer and producing a hard edge between available habitat and mature conifer stands which placed some grouse at greater risk. Similarly, reduced nest success has been observed in hard compared to soft edges in other studies (Ratti and Reese 1988, Suarez et al. 1997).

The overall increases in survival at the landscape scale shows potential population level benefits, while the treatment covariates show potential increases in risk to some individual birds and nests. While more research is needed, my results indicate the potential increased risk in some areas is small relative to the landscape-scale benefits as indicated by the area-wide increases in survival. This information is crucial in designing conifer removal projects to minimize risk to these individuals thereby producing maximum population-level benefits.

Although management of tree invasions has long been suggested for conserving prairie and sage-grouse (Connelly et al. 2000, Grange 1948, Hagen et al. 2004, Hamerstrom et al. 1952), few studies have actually assessed those effects (Hagen et al. 2004, USFWS 2015). Many studies have documented negative effects of woody encroachment on prairie grouse habitat selection (Cassaza et al. 2011, Freese 2009, Lautenbach 2015, McNew et al. 2012), but my study represents a major step forward in evaluating the effects of a landscape-scale habitat restoration on landscape-scale demographics resulting in population growth. While my results generally indicate positive outcomes of conifer removal on sage-grouse, much remains to be learned. Further monitoring at this site, as well as other sites throughout the sage-grouse range, will be necessary to understand the effects of conifer removal on survival at both the landscape scale and to the individual birds. Future analyses should include other demographic parameters (e.g., brood survival) and long-term population trends from lek counts.

MANAGEMENT IMPLICATIONS

In general, conifer removal benefits female sage-grouse and nest survival, potentially resulting in population growth. However, risk can increase for individual birds in some areas near treatments and remaining conifer stands. To minimize these risks, I recommend maximizing the contiguous area of conifer removal and existing treeless habitat; small patches of removal adjacent to standing conifers may produce ecological traps. Woodland edges adjacent to potential habitat should be minimized with the understanding that total risk reduction over the entire area may be unattainable. While maintaining these principles, it may also be beneficial to focus efforts in productive habitat such as the mountain big sagebrush habitat in my area where nest survival was greater. Additionally, because lek count data are widely available throughout the sage-grouse distribution, managers should, at a minimum, assess lek trends for restoration success. However, due to the small changes in survival that I observed at a landscape scale, the inherent noise in lek data, and potential time lags, managers should not expect to see an immediate population response.

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Table 5.1. Area of cut and slash burned conifer in the treatment study area each year in southern Oregon used to assess greater sage-grouse response to conifer removal. The greater treatment area included the treatment area as well as the immediate surrounding area (see Figure 5.1).

	Treatment Area		Greater Treatment Area		Average Size
Year	Cut (ha)	Slash Burn (ha)	Cut (ha)	Slash Burn (ha)	(ha)
2007	143	—	143	—	72
2010	17	—	57	—	29
2011	432	—	781	—	71
2012	2073	95	2709	97	68
2013	1331	991	2288	1989	76
2014	2492	1191	3465	1454	144
Total	6488	2277	9443	3540	87

Table 5.2. Survival models assessed for female sage-grouse in southern Oregon from 2011 to 2014. A) Overall temporal structure of survival assessed for use in conifer removal experiment assessment in B. B) Set of models used in model averaging comparing with and without treatment effect (interaction) for 4 different treatment variables.

	Model[1]	k	AICc	ΔAICc	Weight	Deviance
A)	S(~Breeding)	2	1189.10	0.00	0.52	1185.10
	S(~Season3)	3	1190.56	1.46	0.25	1184.56
	S(~NestSummer)	3	1190.97	1.87	0.20	1184.96
	S(~FYear + Breeding)	6	1195.40	6.30	0.02	1183.39
	S(~1)	1	1199.67	10.57	0.00	1197.67
	S(~FYear)	5	1203.31	14.21	0.00	1193.30
	S(~FMonth)	12	1204.32	15.22	0.00	1180.29
	S(~FMonth + Breeding)	13	1206.33	17.23	0.00	1180.29
	S(~FMonth + FYear)	16	1210.92	21.82	0.00	1178.86
	S(~FYear + FMonth + Breeding)	17	1212.93	23.83	0.00	1178.86
B)	S(~Breeding + TreatCont + AreaCut)	4	1192.24	0.00	0.19	1184.23
	S(~Breeding + TreatCont + TimeMonth)	4	1192.25	0.02	0.19	1184.25
	S(~Breeding + TreatCont + Year)	4	1192.43	0.19	0.17	1184.42
	S(~Breeding + TreatCont + BA)	4	1192.75	0.52	0.15	1184.75
	S(~Breeding + TreatCont × TimeMonth)	5	1193.58	1.34	0.10	1183.57
	S(~Breeding + TreatCont × AreaCut)	5	1194.01	1.78	0.08	1184.01
	S(~Breeding + TreatCont × Year)	5	1194.13	1.89	0.07	1184.12
	S(~Breeding + TreatCont × BA)	5	1194.65	2.41	0.06	1184.64

[1] Breeding = 2 seasons: April–July and August–March. Season3 = 3 seasons: April–July, August–November, and December–March. NestSummer = 3 seasons: April–May, June–July, and August–March. FYear = categorical year. FMonth =categorical month. TreatCont = Treatment (conifer removal) area or control area. AreaCut = cumulative area of cut conifers. TimeMonth = continuous month trend. Year = continuous year trend. BA = categorical before and after treatments began.

Table 5.3. Nest survival models assessed for sage-grouse in southern Oregon from 2011 to 2014. A) Overall survival structures assessed for use in conifer removal experiment assessment in B. B) Set of models used in model averaging comparing with and without treatment effect (interaction) for 3 different treatment variables.

	Model	k	AICc	ΔAICc	Weight	Deviance
A)	S(~1)	1	665.52	0.00	0.39	663.52
	S(~NestType)	2	667.07	1.55	0.18	663.07
	S(~TimeTrend)	2	667.37	1.85	0.16	663.36
	S(~HenAge)	2	667.47	1.96	0.15	663.47
	S(~FMonth)	3	668.94	3.43	0.07	662.94
	S(~FBiweek)	7	669.80	4.28	0.05	655.77
	S(~FWeek)	13	678.21	12.69	0.00	652.11
B)	S(~TreatCont + BA)	3	662.44	0.00	0.45	656.43
	S(~TreatCont × BA)	4	663.92	1.49	0.21	655.91
	S(~TreatCont + Year)	3	664.19	1.75	0.19	658.18
	S(~TreatCont × Year)	4	664.87	2.43	0.13	656.86
	S(~TreatCont + AreaCut)	3	669.15	6.71	0.02	663.15
	S(~TreatCont + AreaCut)	4	671.16	8.72	0.01	663.15

[1] NestType = 1st nest or renest. TimeTrend = trend within nesting period. HenAge = adult or juvenile. FMonth = categorical month within nesting period. FBiweek = categorical biweekly intervals within nesting period. FWeek = categorical weekly intervals within nesting period. TreatCont = Treatment (conifer removal) area or control area. AreaCut = cumulative area of cut conifers. Year = continuous year trend. BA = categorical before and after treatments began.

Table 5.4. Annual, breeding period, and nest survival (based on 27-day incubation) estimates of female sage-grouse in southern Oregon during 2011–2014 in a conifer removal area (treatment) and control area derived from model averaged parameter estimates.

	Year	Control (SE)	Treatment (SE)	Standardized Difference[1] (SE)
Annual Survival	2011	0.464 (0.058)	0.485 (0.057)	0.000 (0.082)
	2012	0.479 (0.044)	0.510 (0.043)	0.010 (0.062)
	2013	0.489 (0.046)	0.526 (0.045)	0.016 (0.065)
	2014	0.491 (0.050)	0.530 (0.049)	0.018 (0.071)
April–July Survival	2011	0.691 (0.048)	0.706 (0.046)	0.000 (0.067)
	2012	0.700 (0.035)	0.722 (0.034)	0.007 (0.050)
	2013	0.707 (0.034)	0.731 (0.032)	0.009 (0.048)
	2014	0.701 (0.040)	0.729 (0.037)	0.013 (0.056)
Nest Survival	2011	0.286 (0.092)	0.286 (0.086)	0.000 (0.128)
	2012	0.444 (0.064)	0.476 (0.070)	0.033 (0.095)
	2013	0.463 (0.054)	0.507 (0.049)	0.044 (0.073)
	2014	0.480 (0.058)	0.532 (0.058)	0.052 (0.082)

[1] Estimated treatment effect. The difference between control area and treatment area and standardized with pretreatment (2011) set to zero.

Table 5.5. Comparison of 4 habitat covariates to null models for sage-grouse nest survival in southern Oregon from 2011 to 2014. A) Dominant sagebrush species. B) Nest in conifer removal area or not. C) For nests in removal areas, years since treatment occurred. D) Distance to nearest conifer removal area.

	Nests	Model	k	AICc	ΔAICc	Weight	Deviance
A)	246	S(~DomSp)	3	742.26	0.00	0.51	736.25
		S(~1)	1	742.30	0.04	0.49	740.30
B)	139	S(~1)	1	444.35	0.00	0.71	442.35
		S(~Treated)	2	446.18	1.82	0.29	442.17
C)	30	S(~1)	1	105.92	0.00	0.54	103.91
		S(~TreatmentAge)	2	106.21	0.30	0.46	102.19
D)	67	S(~DistNearest)	2	205.97	0.00	0.68	201.96
		S(~1)	1	207.47	1.50	0.32	205.47

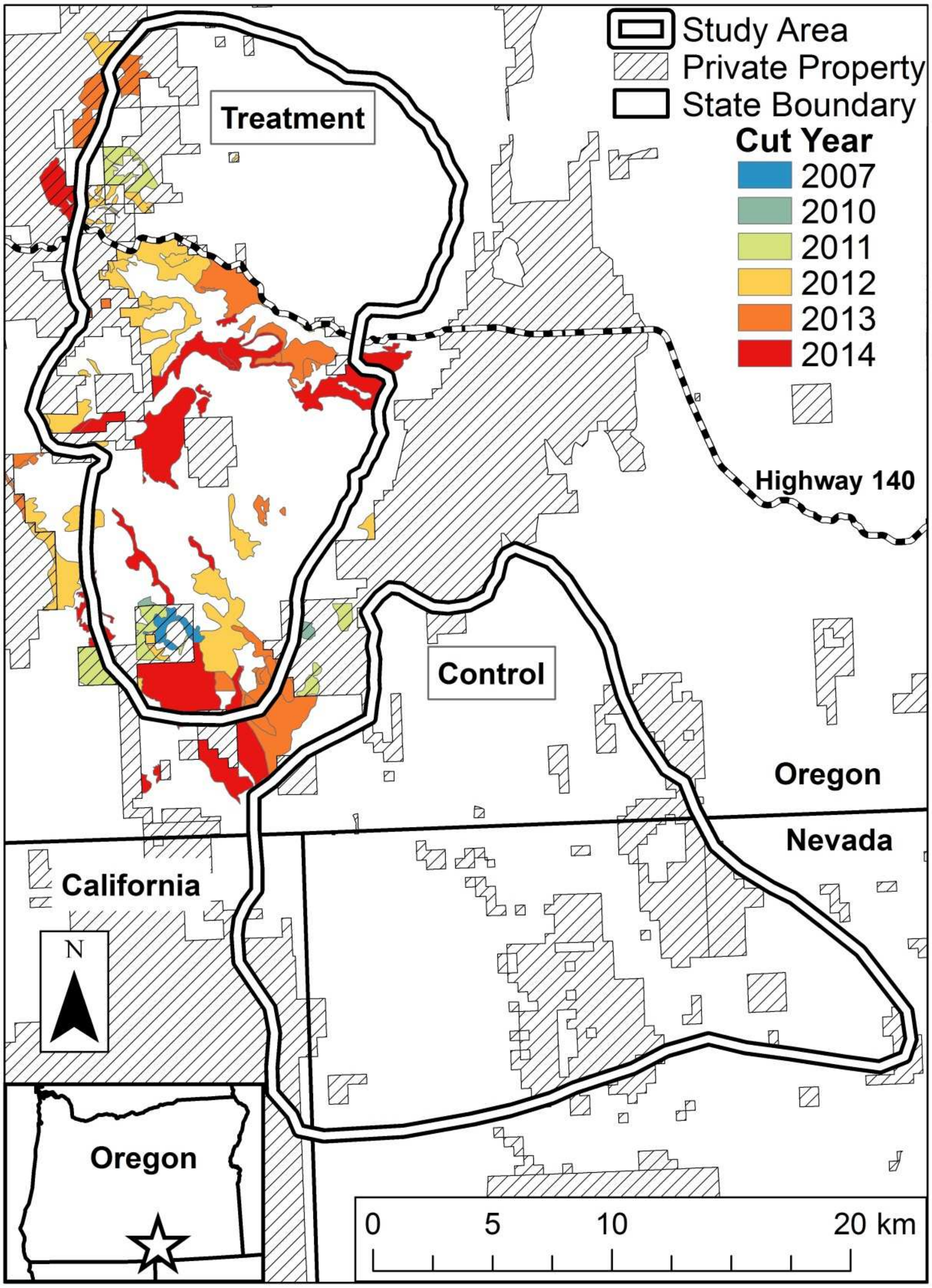

Figure 5.1. Study area boundaries for female sage-grouse survival analysis from 2011 to 2014. Conifer removal areas and years shown as colored polygons.

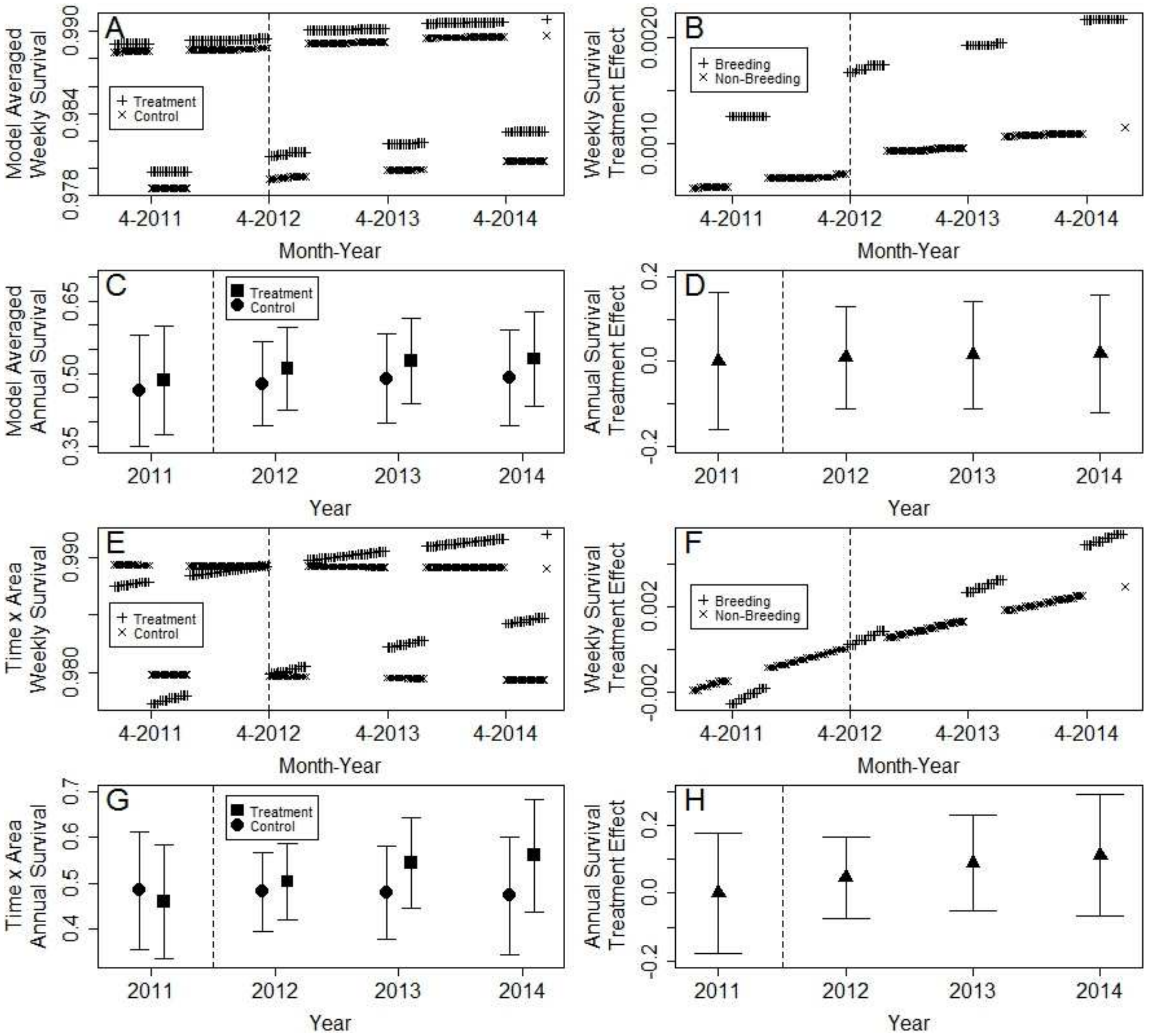

Figure 5.2. Female sage-grouse survival in southern Oregon from 2011 to 2014 for model averaged estimates (A–D) and the best interaction model (Time × Area; E–H). Vertical dashed line indicates approximate start of conifer removal. A) and E) Weekly survival estimates in the control and treatment (conifer removal) areas. B) and F) Difference in weekly estimates between control and treatment area survival for breeding (April–July) and nonbreeding periods. C) and G) Estimated annual survival in the control and treatment areas. D) and H) Difference in annual estimates between control and treatment areas. A positive slope in B, D, F, and H indicates potential treatment effect. Error bars are 95% confidence intervals.

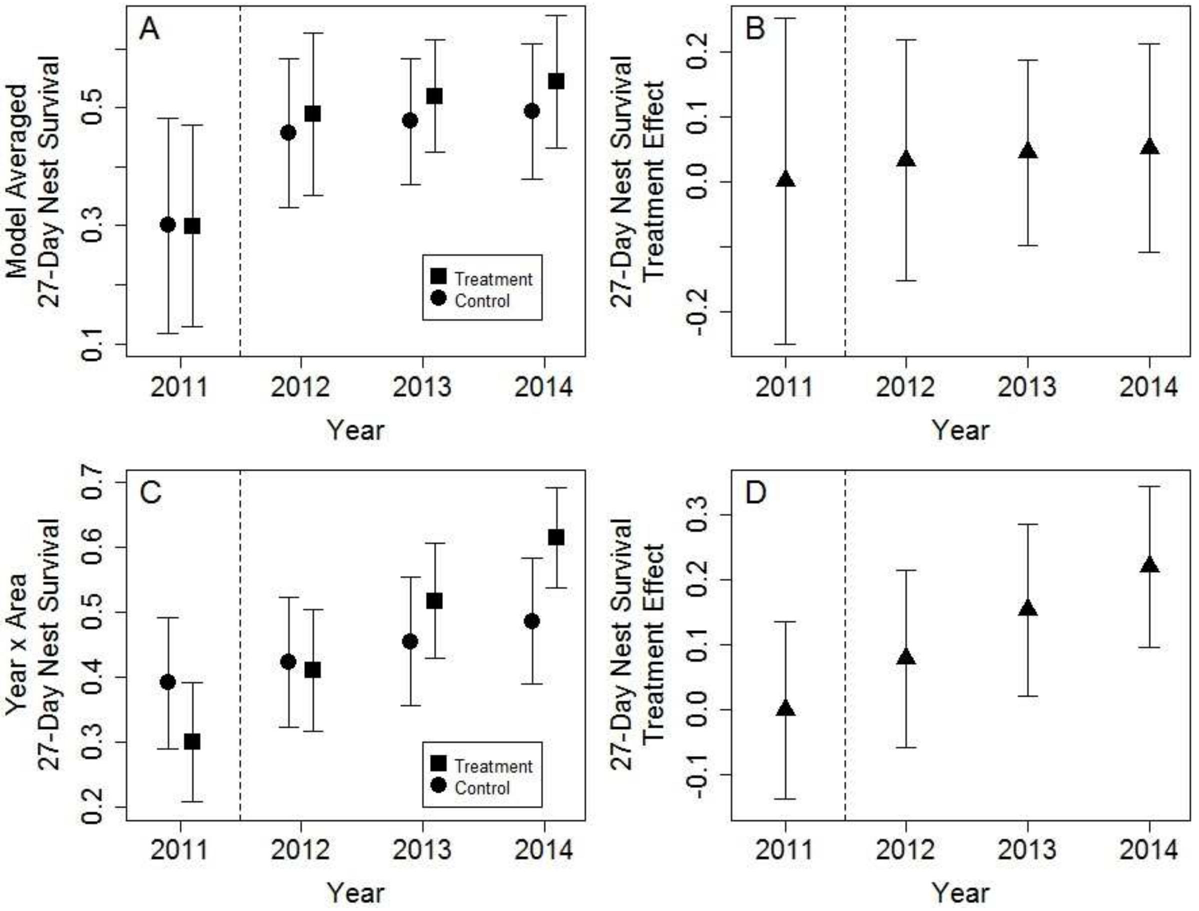

Figure 5.3. Sage-grouse nest survival in southern Oregon from 2011 to 2014 for model averaged estimates (A–B) and the best interaction model (Year × Area; C–D). Vertical dashed line indicates approximate start of conifer removal. A) and C) 27-day nest survival estimates in the control and treatment (conifer removal) areas. B) and D) Difference in daily nest survival estimates between control and treatment area. A positive slope in B and D indicates potential treatment effect. Error bars are 95% confidence intervals.

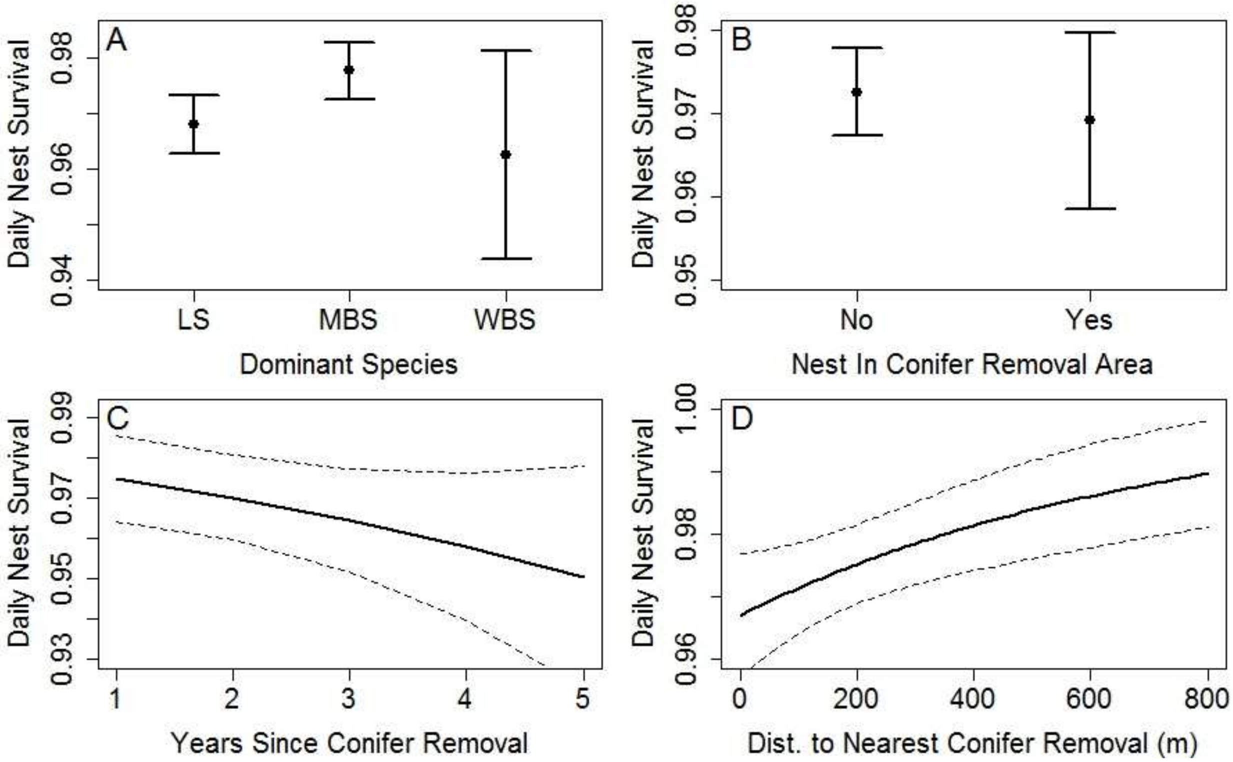

Figure 5.4. Estimated sage-grouse nest survival in southern Oregon from 2010 to 2014 for A) nests in 3 different habitat types (LS = low sagebrush, MBS = mountain big sagebrush, WBS = Wyoming big sagebrush), B) nests in conifer removal areas or not, C) years since removal for nests in treated areas, and D) distance to nearest conifer removal area.

APPENDIX A

Optimization of Weighting Parameter in Generalized Models

We optimized the weighting parameter prior to 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 over-weight 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 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; GLM) and extremely flexible (GAM; 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 subsequently used in the 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).

REFERENCES

Venables, W. N., and Ripley, B. D., 1999. Modern Applied Statistics with S-Plus, third edition. Springer, New York City, NY, USA.

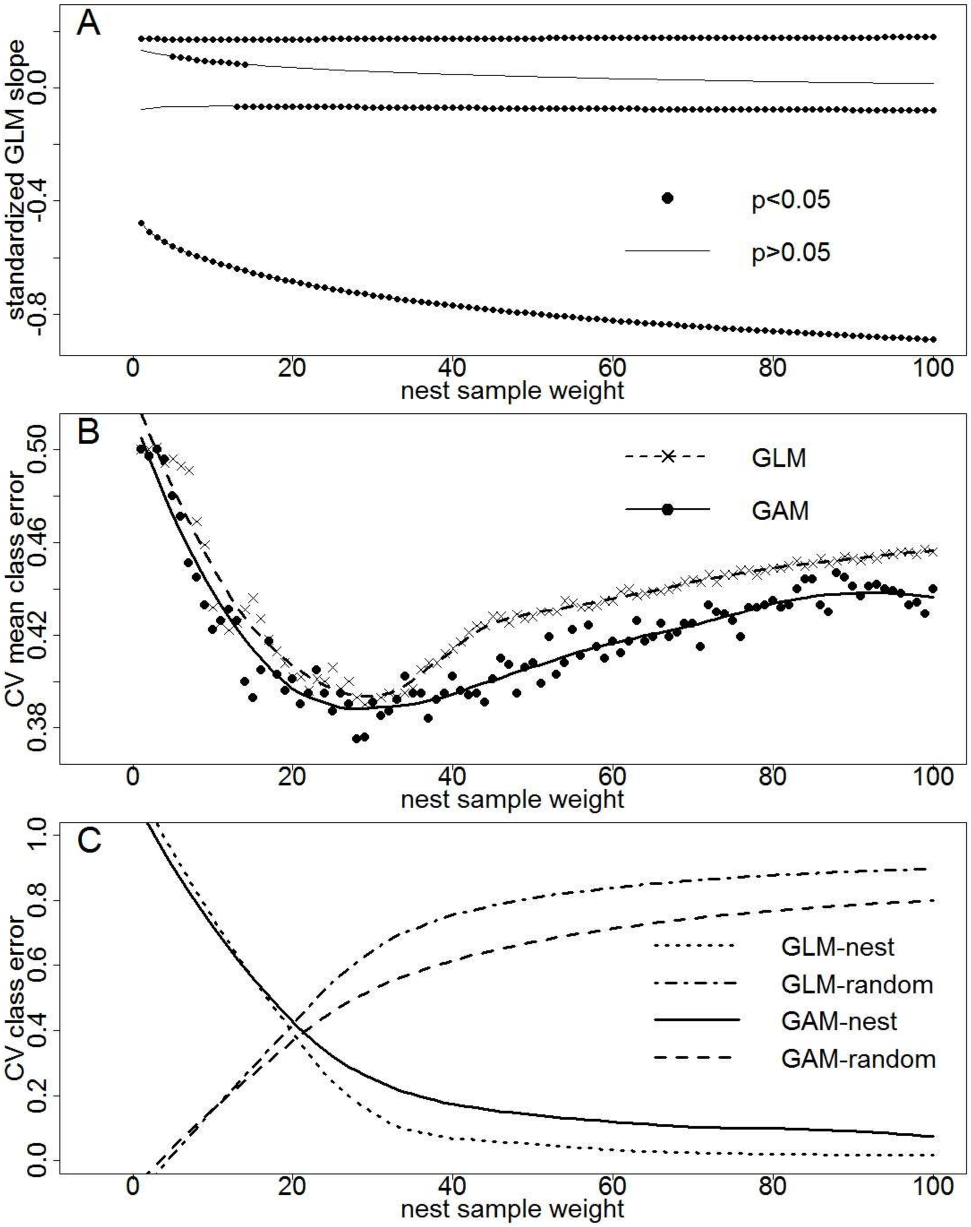

Figure A.1. Effects of class weight specification on regression outcomes in greater sage-grouse nest-site selection in Oregon. There were 20 times as many random samples as nests. X-axis represents nest:random weights as x:1. A) Change in generalized linear model (GLM) regression slope and significance for the 4 variables in Table 2.2. B) Cross-validated (CV) mean class error rate for GLMs and generalized additive models (GAM). C) CV class error for GLMs and GAMs.

APPENDIX B

Treatment Interaction of Non-standardized Vegetation Characteristics

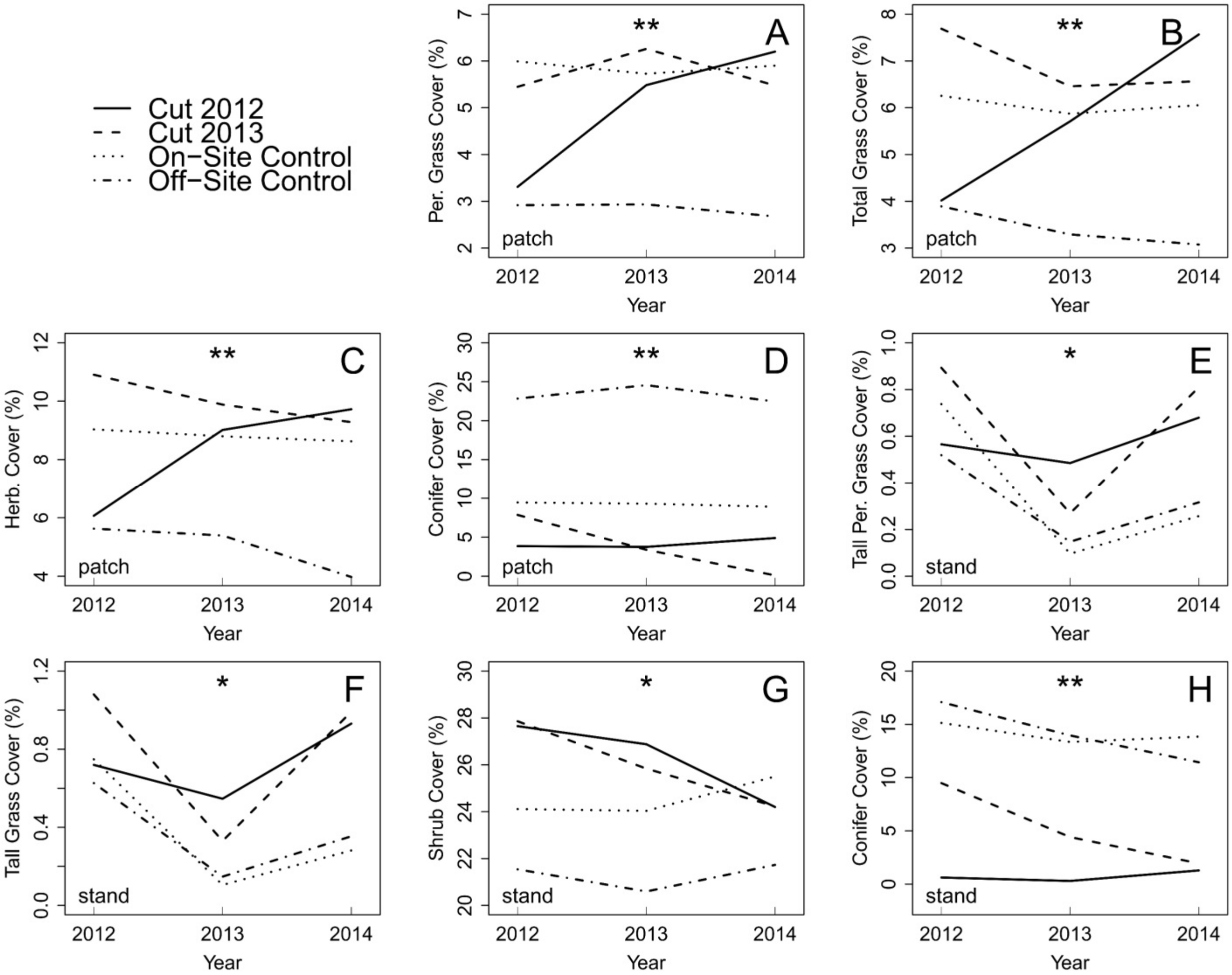

Figure B.1. Effects of time × strata interaction on vegetation characteristics in southern Oregon during 2012–2014 at 2 scales. Lines are strata means. Strata included an on-site and off-site control and areas cut in 2012 and 2013. Patch was two 10-m transects (A–D). Stand was four 60-m transects (E–H). ** = significant ($p < 0.05$). * = marginally significant ($0.05 < p < 0.10$).