

AN ABSTRACT OF THE DISSERTATION OF

Andrew Caleb Olsen for the degree of Doctor of Philosophy in Wildlife Science presented on March 15, 2019.

Title: Greater Sage-Grouse Demography, Habitat Selection, and Habitat Connectivity in Relation to Western Juniper and its Management.

Abstract approved: _____

Christian A. Hagen

The expansion of native, woody plants is a global phenomenon with characteristics and effects that are often indistinguishable from exotic invasions. These expansions have largely been driven by altered fire regimes and favorable climatic conditions. In the Great Basin of western North America, expansion of conifers such as western juniper (*Juniperus occidentalis*) is considered a primary threat to sagebrush (*Artemisia* spp.) ecosystems. The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a sagebrush obligate gallinaceous bird, utilizes sagebrush during every phase of its lifecycle. Sage-grouse have declined across their range and currently occupy approximately 56% of their pre-European settlement distribution. Management agencies are actively removing conifers that established after European settlement (~1870) in the Great Basin to restore sagebrush ecosystem function and benefit species such as sage-grouse that are inextricably tied to these landscapes. The literature on the response of sage-grouse to these broad-scale management actions is limited. My study utilized a “before-after-control-impact” study design to investigate the response of sage-grouse populations, habitat selection, and habitat connectivity to conifer removal. I was able to build upon a radio

telemetry data set that began in 2010 and with my work included a total sample of 417 females, their nests ($n = 378$), and broods ($n = 233$) for demographic and resource selection modeling.

In Chapter 2, I developed a hierarchical population model in a Bayesian framework that integrated telemetry data and lek (i.e., breeding arena) count data to estimate sage-grouse vital rates and population growth rates in a treatment area with conifer removal (Treatment) and a control area (Control). The model indicated that dynamics in population growth rates (λ) approximately tracked each other in the Treatment and Control. However, starting in 2013 (conifer removals initiated in 2012), λ in the Treatment steadily increased relative to the Control and was 11.2% higher by 2017. This trend was driven by increases in juvenile, adult, first nest, and yearling survival in the Treatment relative to the Control. These findings indicated that conifer removal is an effective technique for restoring sagebrush ecosystem function and increasing sage-grouse population growth rates.

In Chapter 3, I estimated resource selection functions for sage-grouse nest site and breeding season habitat selection. Conifer cover and conifer removal variables were among the most influential predictors of nest site and breeding season habitat selection. Sage-grouse selected nest sites in and near older conifer removal areas and were 16% less likely to nest in an area for every 1% increase in conifer cover within 400 m of the nest. During the breeding season, sage-grouse selected habitat closer to conifer removals and were 26% more likely to use a removal each year post-removal (1–5 years post-removal). By 2017, 75% of the treatment area was in the medium-high and high probability of use categories resulting from conifer removal, up from 49% in 2010. These findings demonstrated the efficacy of conifer removal for increasing usable space for sage-grouse in landscapes affected by conifer expansion.

In Chapter 4, I modeled the landscape connectivity in the Treatment with resistance

surfaces generated with a resource selection function. The change in resistance resulting from conifer removal was quantified within the habitat utilized by sage-grouse, which was modeled with Brownian bridge movement models and straight-line, movement pathways. Regardless of the habitat use metric used, there was a reduction in landscape resistance in the areas used by sage-grouse in the post-conifer removal period. When comparing areas used by females with broods and those without, breeding season home ranges of females without broods experienced greater increases ($\leq 81\%$ increase) in connectivity after conifer removal. These differences in landscape resistance held when comparing females with broods and those without in a given post-removal year. These findings indicated that conifer removal is an effective method of restoring landscape connectivity in landscapes affected by post-European settlement expansion of conifers. The difference in benefits for females with and without broods may have demographic implications and needs further investigation.

I sought to evaluate the response of sage-grouse to landscape-scale conifer removal. Collectively, I demonstrated increased population growth rates, usable space, and landscape connectivity resulting from conifer removal. While the extent of sagebrush ecosystems affected by conifer expansion in the Great Basin and the larger sage-grouse range is immense, these findings indicated that targeted conifer removal is an effective management technique to improve the ecosystem function of these landscapes and benefit sage-grouse and likely other sagebrush obligates.

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Greater Sage-Grouse Demography, Habitat Selection, and Habitat Connectivity in Relation to
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by
Andrew Caleb Olsen

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APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Andrew Caleb Olsen, Author

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1 – INTRODUCTION

The expansion of native, woody plants is a global phenomenon with characteristics and effects that are often indistinguishable from exotic invasions (Nackley et al. 2017). Trees have rapidly expanded into shrub and grassland ecosystems driven largely by changes in fires regimes, land use patterns, climate, and CO₂ concentrations (Miller and Wigand 1994; Van Auken 2009; Staver et al. 2011). In the northwestern Great Basin of western North America, a coniferous tree, western juniper (*Juniperus occidentalis*), has expanded its range 10-fold since European settlement and at an unprecedented rate during the Holocene (Miller and Wigand 1994; Miller et al. 1999). Tree ring data and evidence from pollen in lake sediment cores indicate a rapid increase in western juniper establishment since the 1870s (Mehring 1987; Wigand 1987; Miller et al. 2005). It is estimated that western juniper woodlands (with $\geq 10\%$ canopy cover) in eastern Oregon increased from 185,000 ha in 1936 to 890,000 ha by 1988 (Cowlin et al. 1942, Gedney et al. 1999). Western juniper currently occupies approximately 3.6 mil ha (Azuma et al. 2005; Miller et al. 2005) and most (90%) of the expansion since European settlement has occurred in sagebrush (*Artemisia* spp.) ecosystems (Davies et al. 2011; Miller et al. 2011).

The Greater Sage-Grouse (*Centrocercus urophasianus*; sage-grouse) is widespread in the Great Basin and a “sagebrush obligate” utilizing sagebrush during every phase of its lifecycle (Connelly et al. 2011). Additionally, sage-grouse often occupy distinct seasonal ranges that cover a range of sagebrush communities (Connelly et al. 2011). These characteristics of sage-grouse ecology make the species an indicator of sagebrush ecosystem health. The sage-grouse only occupies 56% of its pre-European settlement distribution (Schroeder et al. 2004). Range-wide counts of sage-grouse males indicate annual declines of 0.83% since 1965 and similar trends were observed in 8 of the 11 states where sage-grouse occur for the same period (Western

Association of Fish and Wildlife Agencies 2015). Model forecasts of long-term population trajectories indicate that at least 3 of the 24 sage-grouse breeding populations will decline below effective population sizes of 50 within 30 years if current conditions and population trends continue (Garton et al. 2011).

Conifer expansion likely impacts sage-grouse through a variety of mechanisms. Sage-grouse exhibit avoidance of conifers at low levels of conifer cover. Baruch-Mordo et al. (2013) modelled lek (i.e., breeding arena) activity in Oregon ($n = 152$) as a function of conifer-related and other biotic and abiotic covariates. Probability of lek activity decreased significantly when conifer canopy cover within 1,000 m of the lek exceeded 4% (Baruch-Mordo et al. 2013). Similar thresholds ($\leq 4\%$) to probability of use have also been documented in recent studies using marked sage-grouse including one study that documented a threshold as low as 1.5% (Severson 2016; Coates et al. 2017; Severson et al. 2017). The sagebrush and herbaceous understory is predominantly intact at these levels of conifer cover (Miller et al. 2000; Miller et al. 2005), which suggests other mechanisms as drivers of sage-grouse habitat use in areas with limited conifer cover. Expanding conifers may provide more perch sites and increase the presence and success of sage-grouse nest predators (e.g., common raven [*Corvus corax*]) and predators of adult sage-grouse (e.g., golden eagle [*Aquila chryseatos*]; Wolff et al. 1999; Anderson et al. 2009). These occurrences may contribute to demographic consequences, particularly when moving through conifers (Prochazka et al. 2017). Movement between seasonal ranges is an important aspect of sage-grouse behavior and ecology for many populations and post-European settlement conifer expansion may reduce landscape connectivity (Reinhardt et al. 2017).

Using a long-term telemetry data set (2010-2017) from a treatment area with conifer removal (Treatment) and a control area without conifer removal (Control), I sought to build on previous demographic and habitat use analyses in the project area that assessed the short-term (1–3 years post-removal; 2012–2014) response of sage-grouse to conifer removal (Severson 2016; Severson et al. 2017a-d). Specifically, I investigated the response of sage-grouse demography, resource selection, and habitat connectivity to landscape-scale removal of conifers.

2 – POPULATION RESPONSE OF GREATER SAGE-GROUSE TO WESTERN JUNIPER MANAGEMENT

Abstract

The sagebrush (*Artemisia* spp.) biome is considered one of the most imperiled ecosystems in the United States. A key threat to sagebrush communities that dominate the Great Basin and those species that depend on it is the expansion of pinyon-juniper (*Pinus* spp.-*Juniperus* spp.) woodlands. The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a “sagebrush obligate” species, is widespread in the Great Basin and it utilizes sagebrush during every phase of its lifecycle. Sage-grouse, which have experienced widespread population declines and range contraction, may serve as indicators of sagebrush ecosystem health. Using a long-term (2010–2017) telemetry data ($n = 417$ females) set and lek counts ($n = 260$), an integrated population model was developed in the Bayesian framework in a “before-after-control-impact” design to assess the population response of sage-grouse to conifer removal. Population growth rates (λ) in a treatment area (Treatment) with conifer removal and a control area (Control) without conifer removal generally tracked each other through time. However, the difference in λ between study areas indicated a steady increase in the Treatment relative to the Control starting in 2013 (removals initiated in 2012), with differences of 0.122 and 0.112 in 2016 and 2017, respectively. Retrospective sensitivity analysis suggested that the dynamics in λ were driven by increases in juvenile, adult, first nest, and yearling survival in the Treatment relative to the Control. These findings indicated that conifer removal is an effective management technique to restore sagebrush ecosystem function for sagebrush obligates and increase sage-grouse populations in landscapes affected by conifer expansion.

Introduction

The Great Basin is considered one of the most imperiled ecoregions in the United States (Center for Science, Economics and Environment 2002; Noss et al. 1995; Chambers and Wisdom 2009). Threats to the sagebrush (*Artemisia* spp.) communities that dominate the Great Basin and species that depend on them include human development, altered fire regimes, invasion of exotic plants such as cheatgrass (*Bromus tectorum*), and expansion of pinyon-juniper (*Pinus* spp.-*Juniperus* spp.) woodlands (Chambers and Wisdom 2009; Wisdom et al. 2005). The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) is widespread in the Great Basin and a “sagebrush obligate,” utilizing sagebrush during every phase of its lifecycle (Connelly et al. 2011). Additionally, sage-grouse often occupy distinct seasonal ranges that cover a range of sagebrush communities (Connelly et al. 2011). These characteristics of sage-grouse ecology make it an indicator of sagebrush ecosystem health and their range contraction and population declines highlight the jeopardy of sagebrush ecosystems in the Great Basin and across the sage-grouse range. The sage-grouse occupies 56% of its pre-European settlement distribution (Schroeder et al. 2004). Counts of sage-grouse males indicate estimated declines of 0.83% per year range-wide since 1965 and that 8 of the 11 states where sage-grouse occur had negative population trends from 1965 to 2015 (Western Association of Fish and Wildlife Agencies 2015). Model forecasts of long-term population trajectories indicate that at least 3 of the 24 sage-grouse breeding populations will decline below effective population sizes of 50 within 30 years if current conditions and population trends continue (Garton et al. 2011).

Western juniper (*J. occidentalis*; juniper) is a common, coniferous tree native to California, Idaho, Nevada, Oregon, and Washington that occupies approximately 3.6 mil ha (Azuma et al. 2005, Miller et al. 2005). The range of juniper changed significantly from prior to European settlement of the Intermountain West during the late Pleistocene and into the Holocene

(Miller et al. 2005). These changes are largely attributed to long-term variability in temperature, precipitation, and fire on the landscape (Davis 1982, Van Devender et al. 1987, Miller et al. 2005, Wigand et al. 1995). Range expansion of post-European settlement juniper woodlands has been occurring at rates higher than at any other time during the Holocene (Miller and Wigand 1994, Miller and Tausch 2001). Tree ring data and evidence from pollen in lake sediment cores indicate a rapid increase in juniper establishment since the 1870s (Mehring 1987, Miller et al. 2005). It is estimated that juniper woodlands with $\geq 10\%$ canopy cover in eastern Oregon increased from 185,000 ha in 1936 to 890,000 ha in 1988 (Cowlin et al. 1942, Gedney et al. 1999). As much as 90% of conifer expansion is occurring in sagebrush ecosystems upon which sage-grouse depend (Davies et al. 2011, Miller et al. 2011).

Although the understory vegetation components that are important to sage-grouse can degrade at higher levels of juniper canopy density (Burkhardt and Tisdale 1969, Bates et al. 2000, Miller et al. 2000, Roberts and Jones 2000, Miller et al. 2005), impacts to sage-grouse have been detected at low levels of conifer cover. Baruch-Mordo et al. (2013) modelled lek activity in Oregon leks ($n = 152$) as a function of conifer-related and other biotic and abiotic covariates. Probability of lek activity decreased significantly when conifer canopy cover within 1,000 m of the lek exceeded 4% (Baruch-Mordo et al. 2013). Similar thresholds ($\leq 4\%$) to probability of use have also been documented in recent studies using marked sage-grouse (Severson 2016; Coates et al. 2017; Severson et al. 2017). At these levels of conifer cover, the sagebrush understory is predominantly intact (Miller et al. 2000; Miller et al. 2005) suggesting mechanisms other than changes in understory vegetation as the drivers of changes in sage-grouse habitat use in areas with limited conifer cover. Encroaching juniper may provide more perch sites and increase the presence and success of sage-grouse nest predators such as the common

raven (*Corvus corax*) and predators of adult sage-grouse such as the golden eagle (*Aquila chryseatos*; Wolff et al. 1999; Anderson et al. 2009). Sage-grouse population growth rates (λ) are sensitive to adult female survival, nest success, and chick survival (Taylor et al. 2012; Dahlgren et al. 2016), and management actions that affect these vital rates may have population-level effects.

My study built upon Severson et al. (2017) who assessed the response of female annual survival (April–March) and nest survival (37 days) to juniper removals in a treatment area (Treatment) relative to a control area (area without juniper removal; Control) 2010–2014 with treatments initiated in 2012. The best supported model of female annual survival indicated a 6.6% (85% CI: -1.6–14.7) increase in annual survival in the Treatment relative to the Control 3 years after removals were initiated (Severson et al. 2017). Nest survival increased more dramatically with an 18.8% increase (85% CI: 6.4–31.2) in the Treatment relative to the Control by 2014 (Severson et al. 2017). Severson et al. (2017) incorporated adult and nest survival estimates from best supported models and range-wide vital rates from Taylor et al. (2012) in matrix projection models to estimate λ in the Treatment and Control. This analysis indicated a mean λ of 0.85 (85% CI 0.49–0.62) for the Control and 1.10 (85% CI: 0.89–1.39) for the Treatment. Other studies have also estimated the response of individual vital rates to conifers and conifer removal (Coates et al. 2017; Sanford et al. 2017), but a robust analysis of population-level effects of conifer removal is currently lacking. Given the ongoing, wide-spread conifer removal across the Great Basin which is often implemented with the goal of increasing or conserving sage-grouse populations, a rigorous analysis of population-level response of sage-grouse to these habitat management actions is needed.

The overall objectives of my study were to continue to estimate demographic rates of sage-grouse in the Treatment relative to the Control, model population dynamics, and assess contributions of individual vital rates to observed changes in population dynamics as a result of juniper removal. First, I estimated annual demographic rates in the Treatment and Control, then I estimated annual abundance and λ , and finally I assessed contributions of demographic rates to observed dynamics in λ . Given the sensitivity of sage-grouse population dynamics to adult, nest, and chick survival, I predicted that λ in the Treatment would increase relative to the Control because of increases in these vital rates after juniper removal.

Study Area

The majority of the study area was in Lake County, Oregon within the Lakeview BLM Resource Area (Figure 2.1). The Treatment encompassed ~40,000 ha and extended ~15 km north and south of Oregon Route 140. North of Route 140 the area was bounded by County Highway 3-13 to the west and Lynch's Rim to the east. South of Oregon Route 140 the area was bounded by Big Valley Road to the west and South Warner Rim to the east. The Control was separated from the Treatment by the Warner Valley, stretched south ~10 km into Nevada, and encompassed ~33,000 ha. It was bounded by Greaser Reservoir to the north, Barrel Springs road to the south, Twelvemile and Twentymile Creeks to the west, and the Coleman Valley to the east.

Elevation in the project area ranged from ~1,200 to ~2,200 m with an average of ~1,700 m. The majority of the study area lay above 1,600 m. Total annual precipitation ranged from 28 to 53 cm with most precipitation falling as snow. Temperatures were extremely variable with summer temperatures as high as 38 degrees C and winter lows below -18 degrees C. Dominant vegetation types in the project area were low sagebrush-bunchgrass and mountain big sagebrush

(*A. tridentatata* subsp. *vaseyana*)-bunchgrass. The most common grasses were Sandberg's bluegrass (*Poa secunda*), bottlebrush squirreltail (*Elymus elymoides*), Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Thurber's needlegrass (*Achnatherum thurberianum*).

The ecosystem resilience and resistance framework is useful for describing potential ecosystem response to disturbance including juniper expansion and management (Chambers et al. 2014a, 2014b). Chambers et al. (2014a) define resilience as the capacity of an ecosystem to regain its fundamental structure, processes, and functioning when altered by stresses. Resistance is the capacity of an ecosystem to retain its fundamental structure, processes, and functioning despite stresses, disturbances, or invasive species (Chambers et al. 2014a). Resilience and resistance are measured in terms of soil temperature and moisture regimes (Chambers et al. 2014a, 2014b). Sites with warm (mesic) soil temperatures and dry (aridic) soil moisture regimes tend to be less resilient and resistant to disturbance than those with cooler (frigid to cryic) soil temperatures and moist (xeric to ustic) soil moisture regimes (Chambers et al. 2014a, 2014b). Global Information System (GIS) data layers from the Landscape Conservation Management and Analysis Portal indicated that the majority of the Treatment and Control had moderate to high potential resilience and resistance rating. Approximately 10,000 ha of the study area in northwest Nevada and northeast California had a low potential resilience and resistance rating.

Juniper woodlands covered approximately 43% (17,000 ha) of the Treatment prior to removals with 14,000 ha considered encroaching into bitterbrush (*Purshia tridentata*) and sagebrush-steppe habitats, low sagebrush (*A. arbuscula*) habitats, and aspen (*Populus tremuloides*) stands (Bureau of Land Management 2011). Miller et al. (2005) described 3 transitional phases of juniper woodland succession: 1) phase I- trees are present but shrubs and

herbs are the dominant vegetation that influence ecological processes; 2) phase II- trees are codominant with shrubs and herbs and all 3 vegetation layers influence ecological processes; 3) phase III- trees are the dominant vegetation and the primary plant layer influencing ecological processes. Of the 17,000 ha of juniper in the project area, 3,000 ha were considered phase I, 12,000 ha were considered phase II, and 2,000 ha were considered phase III (Bureau of Land Management 2011). The BLM initiated removal of ~9,983 ha of juniper in the Treatment in 2012 consisting of 1,566 ha of phase I, 7,864 ha of phase II, and 553 ha of phase III juniper. Additionally, the Natural Resource Conservation Service (NRCS) completed 3,683 ha of removals on private lands within the study area. Hand cutting was the primary removal technique employed (Bureau of Land Management 2011). When trees were sparse, cut trees were left where they fell or branches were lopped to < 1.2 m to minimize their utility as perch sites for avian predators after felling (Bureau of Land Management 2011). When trees were dense, felled individual trees were burned or slash was piled and burned. Cut trees were dried for ~1 year prior to burning and most burning took place during winter months when impacts from fire to non-target habitat were minimized (Bureau of Land Management 2011). The majority of removals (81%; 11,177 ha) were completed by the end of 2014 and all remaining removals were completed by 2017.

Methods

Experimental Design

I used a “Before-After-Control-Impact” (BACI) experimental design to assess the impact of juniper management on sage-grouse. This study design is commonly used for impact assessments and is considered a “quasi-experiment” because it lacks replication and random allocation of treatments (Stewart-Oaten et al. 1992, Block et al. 2001). Although the inference of

quasi-experiments is limited, true experiments at large scales are difficult and often logistically and financially unfeasible (Michener 1997). The BACI design of this study followed the description of Block et al. (2001). There was a Control where no juniper removals occurred and a Treatment where juniper was removed. Geographic features separate the 2 study areas such that there is a minimal chance that sage-grouse will move between areas. Movement between the 2 areas in a given year was rare (mean = 2.25 movements per year, $n = 18$) and only 2 permanent movements from one area to the other were documented 2010–2017. The 2 areas were similar to each other in habitat characteristics prior to juniper removal and subsamples were collected at both areas before and after juniper removal. I considered the sage-grouse populations at the 2 areas collectively as the population of inference.

Count Data

Counts of males at leks (i.e., breeding sites) were conducted following established protocols (Connelly et al. 2003; Hagen 2011a) collaboratively by Bureau of Land Management, Oregon Department of Fish and Wildlife, University of Idaho, and Oregon State University within the study area boundaries. Counts were completed 2–3 times at each lek at 7–10-day intervals between March 15 and April 30. Individual counts occurred within the first 2 hours after sunrise under calm, mostly clear conditions.

Vital Rate Data

Female sage-grouse were captured using spotlighting techniques (Giesen et al. 1983; Wakkinen et al. 1992) in winter habitat from 2009–2017 and fitted with radio collars (22-g VHF, Advanced Telemetry Systems, Isanti, MN, USA) or rump-mounted GPS backpacks (22-g PTT-100 solar Argos/GPS PTT, Microwave Telemetry, Inc., Columbia, MD, USA; 22-g solar GPS PTT with 3.5-g Holohil PD-2 VHF transmitter attached, GeoTrak, Inc., Apex, NC, USA) with

the goal of marking 40 females in both the Treatment and Control prior to the start of the breeding season (April 1). Marking with GPS transmitters began in 2015 and by the breeding season of 2017, all females were marked with GPS transmitters. Females marked with VHF transmitters were located twice per week March–July and approximately once per month using aerial telemetry August–February. Locations were collected from females marked with GPS transmitters 4–5 times per day year round.

Nests of females marked with VHF transmitters were identified by 2 consecutive locations in the same spot and then visual confirmation of the female on a nest at <30m without flushing. Nests of females marked with GPS transmitters were identified by ≥ 3 consecutive points at a same location and subsequent visual confirmation as above. Nests of females marked with VHF transmitters were monitored biweekly until nest fate was determined [successful (≥ 1 egg hatched), failed (depredated or abandoned)]. Clutch size was determined by inspection of egg shells after hatch of successful nests. Data from depredated nests was not used for clutch size analysis due to difficulty in counting shells and missing shells.

Prior to 2015, brood flush counts were conducted for hens with successful nests at 28 and 50 days post-hatch. Marked females were located using radio telemetry near sunrise and chicks were counted by gridding the area within ~30 m of the female's location and flushing all chicks present (Gregg and Crawford 2009). If no chicks were counted, another count was conducted within ~2 days to confirm brood fate. Additional repeat counts were occasionally employed when the hen exhibited "broody" behavior (i.e. clucking, reluctance to flush) but no chicks were detected. During 2015–2017, flush counts were conducted at 14, 24, 34, 44, and 54 days post-hatch. I truncated the chick survival data set to 34 days due to the reduced detection of older chicks and because the majority of sage-grouse chick mortality occurs prior to 34 days

(Johnson and Boyce 1990). The VHF transmitters had 8-hr mortality switches and the fate of mortalities was typically determined within ~5 days during the breeding season. Mortalities of individuals marked with GPS transmitters were determined by remote inspection of GPS locations indicating >18 hours (~3 locations) without movement and subsequent recovery and identification of fate within ~5 days.

N-Mixture Model

I modeled lek data using open N -mixture models prior to inclusion in the integrated population model (IPM, see *Integrated Population Model*) to account for imperfect detection and provide improved estimates of male population size (Kéry et al. 2009; McCaffery et al. 2016). The N -mixture model is comprised of a state and observation process (i.e. state-space model). In this case, the state process was the true, unobserved male abundance and the observation process was the observed count data. I modeled abundance at a given lek in a given year (N_{ik}) with a Poisson distribution with Poisson intensity λ_{ik} :

$$N_{ik} \sim \text{Poisson}(\lambda_{ik})$$

I adapted the log transformed Poisson intensity from Kéry et al. (2009) and McCaffery et al. (2016) and included a random effect of year (α_k) and a random effect of lek (ε_i):

$$\log(\lambda_{ik}) = \alpha_k + \varepsilon_i$$

$$\alpha_k \sim \text{Normal}(0, 0.001)$$

$$\varepsilon_i \sim \text{Normal}(\mu_{lek}, \sigma_{lek}^2)$$

$$\mu_{lek} \sim \text{Normal}(0, 0.001)$$

$$\sigma_{lek}^2 \sim \text{Uniform}(0, 100)$$

Given the above state process, I modeled repeated counts at leks (y_{ijk}) with a binomial distribution where N_{ik} is the number of males on a lek in a given year during a given survey and p_{ijk} is the probability of detecting an individual male during that survey:

$$(y_{ijk} | N_{ik}) \sim \text{Binomial}(N_{ik}, p_{ijk})$$

I described logit-transformed detection probability at lek i during survey j with an intercept (β_0), effect of day of the year (β_{date}), and quadratic effect of day of the year (β_{date^2}):

$$\text{logit}(p_{ij}) = \beta_0 + \beta_{\text{date}} \times x_{\text{date},ij} + \beta_{\text{date}^2} \times x_{\text{date},ij}^2$$

The quadratic effect of day of year in the observation process accounted for the rise, peak, and decline in male attendance at leks over the course of the breeding season. Given the limited sample size of leks in the project area, there was significant uncertainty around estimates of detection probability which subsequently greatly reduced the certainty around abundance estimates. To remedy this, I used the larger statewide lek data set for the detection portion of the N -mixture model.

I analyzed the open N -mixture model in the Bayesian framework and I implemented it using JAGS (Plummer 2012) in R version 3.2.2 (R Core Team 2015). I ran 2 parallel chains for 10,000 iterations, and the first 5,000 iterations were discarded. I determined convergence by $\hat{R} < 1.1$ (Gelman et al. 2004) and visual inspection of history plots (Link and Barker 2010).

Integrated Population Model

I used an IPM to estimate vital rates and λ . These models draw information from multiple data sources for more precise demographic parameter estimates and can be used to estimate parameters for which no data was collected under some circumstances (Besbeas et al. 2002; Schaub and Abadi 2011; Kéry and Schaub 2012). Additionally, IPMs are robust to violations of the assumption of independence between datasets and the improvement of the

precision and accuracy of parameter estimates provided by these models is often more pronounced at small sample sizes (Besbeas et al. 2003; Abadi et al. 2010). In this case, I combined count data from lek surveys and data from marked females to estimate mean annual vital rates, annual abundance, and λ for the Treatment and Control.

I modeled the likelihood of population count data (i.e. output of N -mixture models) with a state-space model (see *Count Data and N-mixture Model*; Besbeas et al. 2002). The state process can be described using a pre-breeding matrix projection model (Caswell 2001) as

$$\begin{bmatrix} N_{1,h(t+1)} \\ N_{2+,h(t+1)} \end{bmatrix} = \begin{bmatrix} f_{1,h(t)}\phi_{juv,h(t)}0.5 & f_{2+,area,t}\phi_{juv,h(t)}0.5 \\ \phi_{1,h(t)} & \phi_{2+,h(t)} \end{bmatrix} \begin{bmatrix} N_{1,h(t)} \\ N_{2+,h(t)} \end{bmatrix}$$

where N_1 is the number of yearlings, N_{2+} is the number of adults, f_1 is yearling fecundity, f_{2+} is adult fecundity, ϕ_{juv} is juvenile survival from hatch to first breeding, ϕ_1 is yearling annual survival, and ϕ_{2+} is adult annual survival. Subscript h denotes Treatment or Control and 0.5 is the proportion of female offspring assuming equal sex ratios at hatch (Atamian and Sedinger 2010). I modeled the state process for yearling (N_1) and adult females (N_{2+}) as

$$N_{1,h(t+1)} \sim \text{Poisson} \left[\left((N_{1(t)}f_{1,h(t)} + (N_{2+(t)}f_{2+,h(t)})) \phi_{juv,h(t)}0.5 \right) \right]$$

$$N_{2+,h(t+1)} \sim \text{Bin}(N_{1,h(t)}\phi_{1h(t)}) + \text{Bin}(N_{2+,h(t)}\phi_{2+,h(t)})$$

where symbols and subscripts follow the matrix model above.

Fecundity (f) was comprised of first nest propensity (NP_1), reneest propensity (NP_2), first nest survival (ϕ_{nest1}), reneest survival (ϕ_{nest2}), first nest clutch size (CS_1), reneest clutch size (CS_2), egg hatchability (ϕ_{egg}), and chick survival (ϕ_{chick}) such that

$$f_{hi(t)} = (NP_{1,i(t)}\phi_{nest1,h(t)}CS_{1,(t)}\phi_{egg,h(t)}\phi_{chick,h(t)}0.5)$$

$$+ \left((1 - \phi_{nest,h(t)})NP_{2,i(t)}\phi_{nest2,h(t)}CS_{2,(t)}\phi_{egg,h(t)}\phi_{chick,h(t)}0.5 \right)$$

where the first and second terms of the equation represent the component fecundities from first and renests, respectively, and $(1 - \phi_{nest,h(t)})$ represents the conditional probability of a first nest failing (depredated or abandoned). Subscript h denotes Treatment or Control and i denotes yearling or adult.

I modeled yearling and adult first ($NP_{1,i(t)}$) and reneest propensities ($NP_{2,i(t)}$) using binomial distributions with the following general format

$$y_{np,i(t)} \sim \text{Binomial}(n_{np,i(t)}, p_{np,i(t)})$$

$$\text{logit}(p_{np,i(t)}) = \beta_{0,np,i} + \alpha_t$$

$$\text{logit}(\alpha_t) \sim \text{Normal}(0, \sigma_\alpha^2)$$

where y is the number of hens of a given age attempting a given nest (first or second) in a given year, n is the number of hens followed through the nesting season in the case of first nest propensity and number of hens with failed first nests in the case of reneest propensity, and p is the probability of attempting a nest. The probability of nesting (p_{np}) on the logit scale is a linear function of overall mean nest propensity across years (β_0) by age for a given nest attempt and the random effect of year (α_t). Informative prior distributions for overall mean nest propensity varied by age and nesting attempt and came from Taylor et al. (2012):

$$\text{logit}(\beta_{0,np1,yearling}) \sim \text{Beta}(2.88, 0.36)$$

$$\text{logit}(\beta_{0,np2,yearling}) \sim \text{Beta}(0.65, 2.96)$$

$$\text{logit}(\beta_{0,np1,adult}) \sim \text{Beta}(2.61, 0.11)$$

$$\text{logit}(\beta_{0,np2,adult}) \sim \text{Beta}(1.73, 2.29)$$

I modeled nest survival to 37 days (combined laying and incubation periods) with a Bernoulli distribution as follows:

$$y_{ij} \sim \text{Bernoulli}(y_{ij-1}\phi_{ij})$$

$$\text{logit}(\phi_{ij}) = \beta_{0,\phi_{ij}} + \beta_{treatment(t)} \times x_{treatment,i} + \beta_{renew(t)} \times x_{renew,i} + \alpha_{(t)}$$

$$\text{logit}(\beta_{0,\phi_{ij}}) \sim \text{Uniform}(0, 1)$$

$$\text{logit}(\beta_{treatment(t)}) \sim \text{Normal}(\mu_{treatment}, \sigma_{treatment}^2)$$

$$\mu_{treatment} \sim \text{Normal}(0, 0.001)$$

$$\text{logit}(\beta_{renew(t)}) \sim \text{Normal}(\mu_{renew}, \sigma_{renew}^2)$$

$$\mu_{renew} \sim \text{Normal}(0, 0.001)$$

$$\text{logit}(\alpha_{(t)}) \sim \text{Normal}(0, \sigma_{\alpha}^2)$$

The nest data consisted of a 37 day encounter histories where y_{ij} is the nest state (1 for alive, 0 for dead, NA for not checked) for a given individual on a given day. Daily nest state arises from a Bernoulli distribution of the product of the previous nest state (y_{ij-1}) and the probability of surviving that interval (ϕ_{ij}). The probability of surviving an interval is a linear function of overall mean survival over a given interval ($\beta_{0,\phi_{ij}}$), the time varying effects of being in the Treatment ($\beta_{treatment(t)}$; Treatment coded as 1) and renews ($\beta_{renew(t)}$; renew coded as 1), and the random effect of year ($\alpha_{(t)}$). I derived annual estimates of first and renew survival by area by raising the logit of the linear function with the appropriate variable values to the power of 37.

I modeled first and renew clutch sizes by year ($CS_{nest(t)}$) with Poisson distributions with the general format

$$y_{nest(t)} \sim \text{Poisson}(CS_{nest(t)})$$

$$\log(CS_{nest(t)}) = \beta_{0,CS_{nest}} + \alpha_{nest(t)}$$

$$\log(\beta_{0,CS_1}) \sim \text{Poisson}(7.88)$$

$$\log(\beta_{0,CS_2}) \sim \text{Poisson}(6.38)$$

$$\log(\alpha_{(t)}) \sim \text{Normal}(0, \sigma_{\alpha, nest}^2)$$

where the natural log of $CS_{nest(t)}$ is a linear function of an overall mean clutch size for first (β_{0,CS_1}) or renests (β_{0,CS_2}) and a first or second clutch random year effect ($\alpha_{nest(t)}$). Informative priors for overall mean clutch size are averaged across both age classes reported in Taylor et al. (2012).

I modeled egg hatchability by area and year ($\phi_{egg,h(t)}$) with a binomial distribution as follows:

$$y_{ij} \sim \text{Binomial}(n_{ij}, \phi_{egg,h(t)})$$

$$\text{logit}(\phi_{egg,h(t)}) = \beta_{0,\phi_{egg}} + \beta_{treatment(t)} \times x_{treatment,i} + \alpha_{(t)}$$

$$\text{logit}(\beta_{0,\phi_{egg}}) \sim \text{Uniform}(0, 1)$$

$$\text{logit}(\beta_{treatment(t)}) \sim \text{Normal}(\mu_{treatment}, \sigma_{treatment}^2)$$

$$\mu_{treatment} \sim \text{Normal}(0, 0.001)$$

$$\alpha_{(t)} \sim \text{Normal}(0, \sigma_{\alpha}^2)$$

The egg data consisted of number eggs in a given clutch from a successful nest (n_{ij}) and number of eggs that hatched (y_{ij}). The logit of the probability of an egg hatching in a successful nest is a linear function of overall mean egg hatchability ($\beta_{0,\phi_{egg}}$), the time varying effect of being in the Treatment ($\beta_{treatment(t)}$; Treatment coded as 1), and the random effect of year ($\alpha_{(t)}$). Similar to nest survival, I derived annual egg hatchability by computing the logit of the linear function using the appropriate variables.

The data for chick survival consisted of number of hatched eggs in successful nests (n_{ij}) and number chicks counted at 34 days post-hatch (y_{ij}). The model for chick survival by area and year ($\phi_{chick,h(t)}$) and the derived annual estimates followed the same structure as the egg hatchability model above.

$$y_{ij} \sim \text{Binomial}(n_{i,j}, \phi_{chick,h(t)})$$

$$\text{logit}(\phi_{chick,h(t)}) = \beta_{0,\phi_{chick}} + \beta_{treatment(t)} \times x_{treatment,i} + \alpha_{(t)}$$

$$\text{logit}(\beta_{0,\phi_{chick}}) \sim \text{Uniform}(0, 1)$$

$$\text{logit}(\beta_{treatment(t)}) \sim \text{Normal}(\mu_{treatment}, \sigma_{treatment}^2)$$

$$\mu_{treatment} \sim \text{Normal}(0, 0.001)$$

$$\alpha_{(t)} \sim \text{Normal}(0, \sigma_{\alpha}^2)$$

Adult and yearling annual survival had similar model structure to the nest survival model:

$$y_{ij} \sim \text{Bernoulli}(y_{ij-1}\phi_{ij})$$

$$\text{logit}(\phi_{i,j}) = \beta_{0,\phi_{i,j}} + \beta_{treatment,t} \times x_{treatment,i} + \beta_{yearling,t} \times x_{yearling,i} + \alpha_t$$

$$\text{logit}(\beta_{0,\phi_{i,j}}) \sim \text{Uniform}(0, 1)$$

$$\text{logit}(\beta_{treatment,t}) \sim \text{Normal}(\mu_{treatment}, \sigma_{treatment}^2)$$

$$\mu_{treatment} \sim \text{Normal}(0, 0.001)$$

$$\text{logit}(\beta_{yearling,t}) \sim \text{Normal}(\mu_{yearling}, \sigma_{yearling}^2)$$

$$\mu_{yearling} \sim \text{Normal}(0, 0.001)$$

$$\text{logit}(\alpha_t) \sim \text{Normal}(0, \sigma_{\alpha}^2)$$

The survival data consisted of a 12 month encounter histories where $y_{i,j}$ is state of the marked female (1 for alive, 0 for dead, NA for not checked) for a given individual during a given month. Monthly survival state arises from a Bernoulli distribution of the product of the state in the previous month (y_{ij-1}) and the probability of surviving that interval ($\phi_{i,j}$). The probability of surviving an interval is a linear function of overall mean survival over a given interval ($\beta_{0,\phi_{i,j}}$), the time varying effects of being in the Treatment ($\beta_{treatment(t)}$; Treatment coded as 1) and being a yearling ($\beta_{yearling(t)}$; yearling coded as 1), and the random effect of year ($\alpha_{(t)}$). I defined years as April–March to coincide with the reproductive cycle of sage-grouse (Severson et al. 2017). I

derived annual estimates of adult ($\phi_{2+,h(t)}$) and yearling survival by area ($\phi_{1,h(t)}$) by raising the logit of the linear function with the appropriate variable values to the power of 12.

No data was collected on juvenile survival (ϕ_{juv}) from 34 days post-hatch to first breeding (~April). However, I assumed a relationship between juvenile and adult survival and derived it annually as follows:

$$\phi_{juv,h(t)} = \phi_{2+,h(t)}^{2/3} \gamma_{h(t)}$$

$$\gamma_{h(t)} \sim \text{Beta}(2.29, 0.80)$$

Adult annual survival is raised to the 2/3 power to reduce it to the same temporal scale as juvenile survival (~8 months). Adult survival during this shortened period is multiplied by an annual adjustment ratio ($\gamma_{h(t)}$) which has an informative prior distribution from Apa et al. (2017) who reported a mean ratio of juvenile to adult September–March survival for radio-marked adult and juvenile sage-grouse of 0.70 over 3 years at 2 study sites in Colorado.

The observation component of the state-space model follows Ross et al. (2018)

$$y_{h(t)} \sim \text{Normal}(N_{1,h(t)} + N_{2+,h(t)}, h_{h(t)})$$

where $y_{h(t)}$ is the population estimate for a given area in a given year from the N -mixture model, $N_{1,h(t)}$ and $N_{2+,h(t)}$ are the estimates of yearling and adult abundance, respectively, at breeding, and $h_{h(t)}$ is the precision of the estimates from the N -mixture model.

I used age ratio adjusted abundance estimates for 2008 from the N -mixture model as initial values of yearling ($N_{1,h(1)}$) and adult abundance ($N_{2+,h(1)}$) for the state process. The age ratio is based on the mean productivity estimate of 1.58 from hunter-donated sage-grouse wings ($n = 7,986$) in Oregon from 1993 to 2005 reported by Hagen and Loughin (2008). I implemented the IPM in the Bayesian framework using JAGS (Plummer 2012) in R version 3.2.2 (R Core Team 2015). Three parallel chains ran for 30,000 iterations, and the first 25,000 iterations were

discarded resulting in 5,000 saved iterations. I determined convergence by $\hat{R} < 1.1$ (Gelman et al. 2004) and visual inspection of history plots (Link and Barker 2010).

Contributions of Vital Rates to Population Dynamics

I estimated the contributions of given vital rates to the observed dynamics in λ by correlating the differences (Treatment-Control) in the annual estimates of a given vital rate with the corresponding differences in λ (Treatment-Control) following Kéry and Schaub (2012). The strength of these correlations is indicative of the strength of the contribution of annual variation in the difference in vital rates to the annual variation in λ (Schaub et al. 2011). I used the mode of the posterior distributions of the correlation coefficients to describe these relationships because most of the posterior distributions were skewed (Schaub et al. 2011). Additionally, I derived the probability that the correlation was positive from the output of the analysis following Kéry and Schaub (2012).

Results

Integrated Population Model

Over the course of the project, 417 hens were captured and marked, 378 nests were observed, and 223 broods were monitored. Annual estimates from the IPM for the Treatment and Control of adult survival ranged 0.506–0.876, yearling survival ranged 0.541–0.918, nest survival ranged 0.282–0.731, chick survival ranged 0.124–0.507, and juvenile survival ranged 0.517–0.861 (Table 2.1). Lambda in the Treatment and Control generally followed the same pattern through time with both areas experiencing population increase ($\lambda > 1$), population decrease ($\lambda < 1$), and stable populations ($\lambda = 1$) during the same years (Figure 2.2). However, the magnitude of differences in λ between the Treatment and Control increased steadily from 2013 to 2016 resulting in λ that was 0.122 (95% CI: –0.055–0.304) higher in the Treatment

relative to the Control by 2016 (Figure 2.3). Lambda remained higher in the Treatment in 2017 with a 0.112 difference (95% CI: -0.034–0.267; Figure 2.3). Population growth exhibited greater stochasticity during the 2 pre-removal years and the first years of removals (2010–2012) and these were the only years when 95% credible intervals associated with differences in λ did not overlap zero (Figure 2.3). Differences in λ during this period indicated that the Treatment λ was greater than the Control in 2010 (0.203, 95% CI: 0.040-0.371) and 2012 (0.188, 95% CI: 0.072–0.308) and lower in 2011 (-0.210, 95% CI: -0.329—0.092; Figure 2.3).

Contributions of Vital Rates to Population Dynamics

Of the vital rates estimated separately for the Treatment and Control, higher juvenile survival in the Treatment relative to the Control had the greatest contribution (correlation coefficient) to $\Delta\lambda$ (0.73, 95% CI: 0.14–0.89) followed closely by adult survival (0.72, 95% CI: 0.20–0.89), first nest survival (0.71, 95% CI: 0.07–0.88), and yearling survival (0.16, 95% CI: 0.14–0.88; Figure 2.4). Renest survival had a lower, but still positive contribution (0.53, 95% CI: -0.07–0.80) and chick survival had a negative contribution (-0.48, 95% CI: -0.79–0.15; Figure 2.4). Based on their posterior distributions, the probability that the contributions were positive was ≥ 0.93 for juvenile, adult, first nest, yearling, and renest survival (Figure 2.4). Given the negative contribution of difference in chick survival, there was only a probability of 0.11 that its contribution was >1 (Figure 2.4).

Discussion

This is the first study to integrate lek and vital rate data to quantify the population response of sage-grouse to conifer removal. The population response adds to the body of evidence that targeted juniper removal serves as a potential conservation tool to increase sage-grouse populations. The overall trends in λ in the Treatment and Control generally tracked each

other temporally and a long-term data set was needed to assess the treatment effect on λ (Figure 2.2). This pattern indicated that both areas experienced the same climate and were as similar as possible as required of a BACI study design and a representative control area (Block et al. 2001). Although there was some uncertainty around estimates of λ in the Treatment and Control, the positive trend in the treatment point estimates relative to the control suggested a population-level response to juniper removals and credible intervals of the difference in λ overlapped zero by <10% in 2017 (Figure 2.3; Dugger et al. 2016).

The treatment effect on λ in 2016 and 2017 was not as high as that reported by Severson et al. 2017 (25%). However, Severson et al. (2017) inputted study area estimates of nest and adult survival into population projection matrices that used range wide averages for all other vital rates and did not estimate those rates directly. A sustained difference in λ of ~12%, as estimated in 2016 and 2017, could have a tremendous impact on sage-grouse abundance in the Treatment relative to the Control. These differences in λ occurred 5 and 6 years after removals were initiated, respectively. Given the lower reproductive output and long lifespan of adult sage-grouse relative to other galliformes, it may be biologically unfeasible for sage-grouse populations to respond to habitat management as rapidly as other galliformes. McKenzie (2017) modelled lek data from 1980–2015 in relation to conifer removals in a study area that encompassed predominantly eastern Oregon. The findings suggested a 5–10 year lag before an effect of conifer removals is realized in measurable, increased lek counts (McKenzie 2017). Similarly, analysis of time-lag effects from lek data collected at 704 leks over 12 years in Wyoming indicated a delay of 2–10 years between energy development and measurable negative effects on lek attendance (Harju et al. 2010). Short-term (2–3 years post-removal) studies may not capture population-level effects of conifer removals or other conservation actions on sage-

grouse and the lag effects observed in this study and others highlight the importance of long-term data sets to best assess the response of sage-grouse populations to management actions or disturbance.

Sub-models for individual vital rates generally produced reasonable estimates and did not differ substantially from what has been reported in the literature (Table 2.1). A notable exception was re-nest survival which was <0.2 in the Treatment and Control 2010–2015 (Table 2.1). However, the sample size was limited ($n \leq 5$) in several of these years and the estimates should be interpreted cautiously. Improved detection of nests with the increased use of GPS transmitters, particularly in 2016 and 2017, improved the sample size of re-nests and likely increased the precision and accuracy of estimates.

The sensitivity analysis suggested that juvenile, adult, first nest, and yearling survival had the greatest contributions to the observed changes in population dynamics in the Treatment relative to the Control. This finding supported my initial prediction that increases in adult and nest survival would contribute to increases in λ in the Treatment relative to the Control. Similar findings have been reported from larger data sets and Leslie-matrix style sensitivity analyses (Taylor et al. 2012; Dahlgren et al. 2016). However, these studies also reported chick survival as one of the top contributors to population dynamics among sage-grouse vital rates. Additionally, Sanford et al. (2017) documented increased brood success (≥ 1 chick at 50 days post-hatch) for female sage-grouse that selected brooding locations that were closer to conifer removals and in areas with minimal conifer cover in Utah. However, counter to my predictions, chick survival actually had a negative correlation with $\Delta\lambda$ and the juniper removals may not have benefited chick survival as much as other vital rates as evidenced by the 95% credible interval associated with the correlation coefficient for chick survival which overlapped zero (Figure 2.4). The

primary predators of sage-grouse chicks are largely unknown (Hagen 2011b). If reduction of avian predator perch sites and hunting efficiency is a mechanism for increases in sage-grouse vital rates following conifer removal, it is possible that the primary predators of chicks in the project area are not avian and/or were not affected by the removal. It is also possible that the deleterious effects on chick survival of wet, cold weather events in June 2016 and 2017 masked any benefits of juniper removal on this vital rate (Table 2.1). The sensitivity of $\Delta\lambda$ to differences in juvenile survival was not predicted, but complimented the findings of Prochazka et al. (2017) who documented increases in age-specific risk of daily mortality while moving through pinyon-juniper, with juveniles having the greatest increase in mortality risk (56% increase) compared to yearlings (42%) and adults (16%). Other retrospective analyses of the sensitivity of λ in the project area to the estimated vital rates such as life table response experiments (Caswell 1996, 2001) or transient population dynamics (Yearsley 2004) may better investigate the mechanism behind observed increases in λ .

As previously stated, mechanisms behind the response of sage-grouse to juniper expansion and removal may be related to predators and/or vegetation. Although understory dynamics vary across ecological gradients after juniper removal, understory vegetation cover can generally be increased by removing juniper (Roundy et al. 2014). Removal of encroaching juniper by hand cutting at a long-term study site in Oregon increased understory herbaceous biomass and cover and generally increased the productivity of these plant communities post-removal (Bates et al. 2000; 2005; 2007). Additionally, burning individual cut trees during the winter increased herbaceous and perennial grass cover 150% and 200%, respectively; while increasing the density of perennial grasses and reducing annual grass cover compared to areas that were cut but not burned (Bates and Svejcar 2009). Given the role of sage-grouse as

indicators of sagebrush ecosystem function and the positive understory vegetation response often associated with juniper removal, projects directed toward sage-grouse may benefit other species, particularly sagebrush obligates and near-obligates (Rowland et al. 2005; Copeland et al. 2014; Donnelly et al. 2017; Holmes et al. 2017). The population response of sage-grouse in this study may be indicative of the efficacy of the juniper management actions for the sagebrush ecosystems in the Treatment as a whole.

Using sage-grouse as a surrogate and indicator of sagebrush ecosystem health, the findings of this study highlight the efficacy of targeted juniper removal as a tool for ecosystem restoration and conservation in the Great Basin. In southern Oregon, Holmes et al. (2017) found abundances of Brewer's sparrow (*Spizella breweri*), green-tail towhee (*Pipilo chlorurus*), and vesper sparrow (*Poocetes gramineus*) more than doubled following mechanical conifer removal. Annual increases each year post-removal suggest that Brewer's sparrows use may increase even more with time. These findings illustrated that conifer removal conducted for sage-grouse that retained shrub cover could result in immediate benefits for other sagebrush birds of high conservation concern. Donnelly et al. (2017) advanced these findings to regional scales by using count data from North American Breeding Bird Survey (2004–2014) to show that strongholds for sagebrush songbirds and sage-grouse coincide; songbirds were 13–19% more abundant near large leks, which support half of all known sage-grouse populations.

The lag from the onset of juniper removal to measurable sage-grouse population effects emphasizes the importance of long-term population monitoring by managers employing juniper removal as a tool to bolster sage-grouse populations and restore ecosystem function in encroached landscapes. Adaptive management based on population assessments <5 years post-removal may underestimate the benefits of conifer removal.

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Table 2.1. Summary of posterior distributions of population parameters for greater sage-grouse (*Centrocercus urophasianus*) in the treatment and control study areas, 2010–2017, Lake County, Oregon, Modoc County, California, and Washoe County, Nevada, USA.

	2010						2011						2012						2013					
	Control			Treatment			Control			Treatment			Control			Treatment			Control			Treatment		
Vital rate	μ^a	0.025 ^b	0.975 ^c	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975
Adult Survival (12 mo) ^d	0.842	0.663	0.951	0.876	0.778	0.948	0.649	0.544	0.762	0.506	0.384	0.630	0.508	0.401	0.613	0.536	0.426	0.649	0.529	0.427	0.632	0.540	0.419	0.663
Yearling Survival (12 mo) ^d	0.896	0.746	0.976	0.918	0.821	0.978	0.673	0.424	0.859	0.541	0.262	0.773	0.590	0.403	0.765	0.615	0.423	0.790	0.607	0.410	0.779	0.617	0.433	0.785
Juvenile Survival (8 mo) ^e	0.838	0.675	0.945	0.861	0.709	0.946	0.633	0.379	0.781	0.535	0.326	0.678	0.517	0.304	0.671	0.535	0.323	0.687	0.597	0.462	0.702	0.605	0.458	0.726
Chick Survival (34 d)	0.282	0.130	0.507	0.299	0.232	0.369	0.328	0.223	0.438	0.414	0.320	0.517	0.359	0.259	0.473	0.358	0.242	0.477	0.386	0.300	0.476	0.447	0.360	0.537
Nest Survival (37 d)	0.441	0.289	0.606	0.518	0.369	0.670	0.431	0.294	0.577	0.393	0.242	0.550	0.329	0.171	0.496	0.510	0.358	0.666	0.561	0.415	0.711	0.372	0.222	0.536
Renest Survival (37 d)	0.061	0.000	0.314	0.091	0.000	0.375	0.076	0.000	0.347	0.060	0.000	0.304	0.048	0.000	0.264	0.117	0.001	0.428	0.166	0.006	0.485	0.066	0.000	0.295
Egg Hatchability	0.889	0.785	0.951	0.905	0.857	0.944	0.869	0.779	0.937	0.808	0.736	0.872	0.951	0.909	0.981	0.941	0.883	0.977	0.900	0.846	0.941	0.912	0.848	0.962
Nest Clutch Size*	7.393	6.865	7.936	7.393	6.865	7.936	7.391	6.864	7.944	7.391	6.864	7.944	7.276	6.622	7.685	7.276	6.622	7.685	7.315	6.765	7.723	7.315	6.765	7.723
Renest Clutch Size*	5.230	3.053	7.790	5.230	3.053	7.790	4.778	2.888	6.953	4.778	2.888	6.953	5.167	3.283	7.384	5.167	3.283	7.384	5.780	3.835	8.053	5.780	3.835	8.053
Adult Nest Propensity*	0.799	0.707	0.875	0.799	0.707	0.875	0.722	0.619	0.811	0.722	0.619	0.811	0.794	0.685	0.883	0.794	0.685	0.883	0.861	0.771	0.930	0.861	0.771	0.930
Yearling Nest Propensity*	0.661	0.452	0.834	0.661	0.452	0.834	0.739	0.535	0.897	0.739	0.535	0.897	0.511	0.312	0.707	0.511	0.312	0.707	0.888	0.736	0.982	0.888	0.736	0.982
Adult Renest Propensity*	0.295	0.152	0.467	0.295	0.152	0.467	0.407	0.250	0.583	0.407	0.250	0.583	0.321	0.158	0.528	0.321	0.158	0.528	0.233	0.096	0.401	0.233	0.096	0.401
Yearling Renest Propensity*	0.316	0.120	0.598	0.316	0.120	0.598	0.147	0.020	0.342	0.147	0.020	0.342	0.126	0.001	0.338	0.126	0.001	0.338	0.129	0.002	0.352	0.129	0.002	0.352
*Vital rate was estimated across pooled data from the treatment and control areas																								
^a Mean of the posterior distribution																								
^b 0.025 quantile of the posterier distribution																								
^c 0.975 quantile of the posterier distribution																								
^d Survival period for adult and yearlings is April–March																								
^e Survival period for juveniles is August–March																								

Table 2.1. *Continued.*

	2014						2015						2016						2017					
	Control			Treatment			Control			Treatment			Control			Treatment			Control			Treatment		
Vital rate	μ^a	0.025 ^b	0.975 ^c	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975	μ	0.025	0.975
Adult Survival (12 mo) ^d	0.667	0.548	0.777	0.638	0.513	0.752	0.789	0.678	0.882	0.827	0.713	0.923	0.664	0.527	0.785	0.750	0.632	0.852	0.614	0.485	0.735	0.644	0.504	0.771
Yearling Survival (12 mo) ^d	0.745	0.578	0.879	0.721	0.536	0.863	0.764	0.584	0.890	0.807	0.645	0.920	0.759	0.549	0.911	0.822	0.653	0.944	0.774	0.606	0.914	0.792	0.618	0.926
Juvenile Survival (8 mo) ^e	0.710	0.562	0.816	0.688	0.543	0.797	0.727	0.377	0.882	0.750	0.385	0.912	0.703	0.539	0.820	0.763	0.589	0.872	0.560	0.219	0.758	0.577	0.231	0.782
Chick Survival (34 d)	0.405	0.301	0.509	0.507	0.405	0.615	0.183	0.110	0.263	0.282	0.202	0.376	0.233	0.118	0.399	0.180	0.102	0.270	0.124	0.067	0.202	0.151	0.074	0.248
Nest Survival (37 d)	0.387	0.245	0.527	0.362	0.227	0.506	0.304	0.171	0.445	0.282	0.139	0.450	0.610	0.350	0.916	0.731	0.426	0.963	0.417	0.082	0.777	0.502	0.035	0.896
Renest Survival (37 d)	0.162	0.035	0.366	0.144	0.030	0.338	0.079	0.009	0.227	0.073	0.004	0.240	0.383	0.000	0.930	0.516	0.004	0.965	0.204	0.000	0.797	0.279	0.000	0.888
Egg Hatchability	0.893	0.830	0.939	0.896	0.844	0.938	0.943	0.899	0.976	0.957	0.912	0.988	0.915	0.853	0.958	0.936	0.884	0.975	0.967	0.922	0.994	0.970	0.922	0.995
Nest Clutch Size [*]	7.297	6.718	7.709	7.297	6.718	7.709	7.359	6.832	7.830	7.359	6.832	7.830	7.393	6.862	7.933	7.393	6.862	7.933	7.326	6.674	7.832	7.326	6.674	7.832
Renest Clutch Size [*]	5.335	2.850	8.392	5.335	2.850	8.392	5.945	3.692	8.637	5.945	3.692	8.637	6.708	4.336	9.502	6.708	4.336	9.502	5.364	3.857	7.103	5.364	3.857	7.103
Adult Nest Propensity [*]	0.900	0.822	0.959	0.900	0.822	0.959	0.896	0.808	0.962	0.896	0.808	0.962	0.885	0.803	0.949	0.885	0.803	0.949	0.663	0.531	0.779	0.663	0.531	0.779
Yearling Nest Propensity [*]	0.716	0.562	0.846	0.716	0.562	0.846	0.849	0.690	0.961	0.849	0.690	0.961	0.746	0.530	0.912	0.746	0.530	0.912	0.678	0.471	0.848	0.678	0.471	0.848
Adult Renest Propensity [*]	0.178	0.049	0.340	0.178	0.049	0.340	0.199	0.058	0.378	0.199	0.058	0.378	0.135	0.022	0.292	0.135	0.022	0.292	0.256	0.124	0.413	0.256	0.124	0.413
Yearling Renest Propensity [*]	0.132	0.002	0.369	0.132	0.002	0.369	0.176	0.022	0.422	0.176	0.022	0.422	0.273	0.071	0.649	0.273	0.071	0.649	0.148	0.019	0.343	0.148	0.019	0.343
*Vital rate was estimated across pooled data from the treatment and control areas																								
^a Mean of the posterior distribution																								
^b 0.025 quantile of the posterier distribution																								
^c 0.975 quantile of the posterier distribution																								
^d Survival period for adult and yearlings is April–March																								
^e Survival period for juveniles is August–March																								

Figure 2.1. Treatment and control study areas used in the “Before-After-Control-Impact” framework to assess the effect of western juniper (*Juniperus occidentalis*) management on greater sage-grouse (*Centrocercus urophasianus*), 2010–2017, Lake County, Oregon, Modoc County, California, and Washoe County, Nevada, USA.

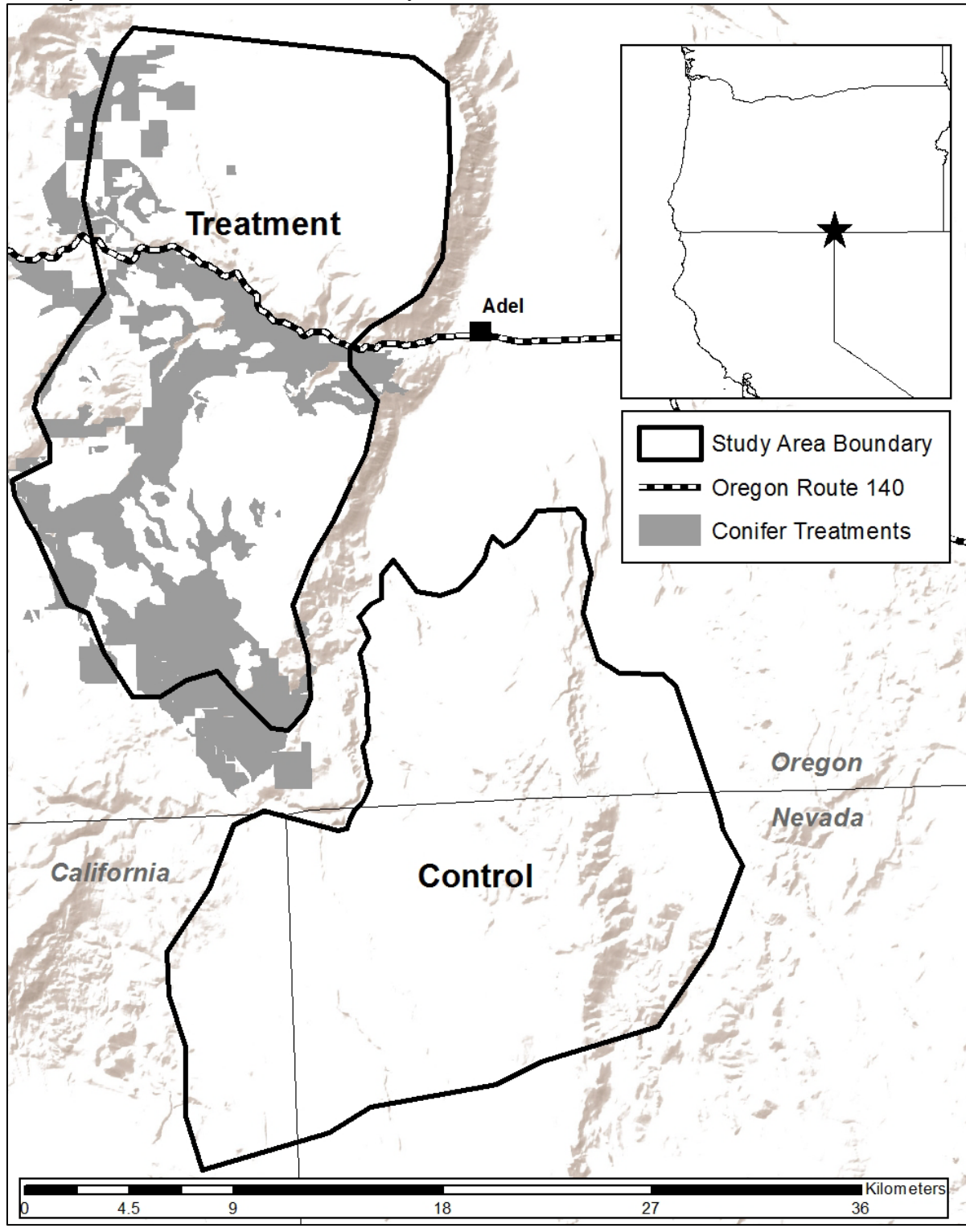


Figure 2.2. Population growth rates (λ) from the integrated population model for greater sage-grouse (*Centrocercus urophasianus*) in treatment and control study areas, 2010–2017, Lake County, Oregon, Modoc County, California, and Washoe County, Nevada, USA. Vertical lines are 95% credible intervals and the shaded area represents the pre-treatment period.

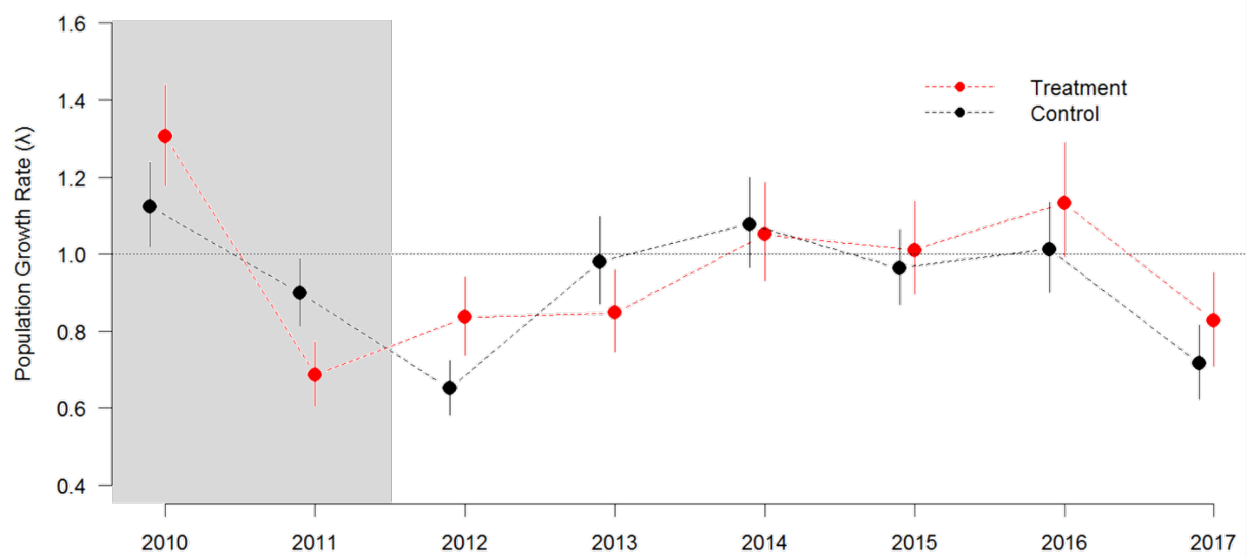


Figure 2.3. Difference (treatment-control) in population growth rates (λ) from the integrated population model for greater sage-grouse (*Centrocercus urophasianus*) in the treatment and control study areas, 2010–2017, Lake County, Oregon, Modoc County, California, and Washoe County, Nevada, USA. Vertical lines are 95% credible intervals and the shaded area represents the pre-treatment period, points above 0 indicate years in which λ was greater in the treatment area.

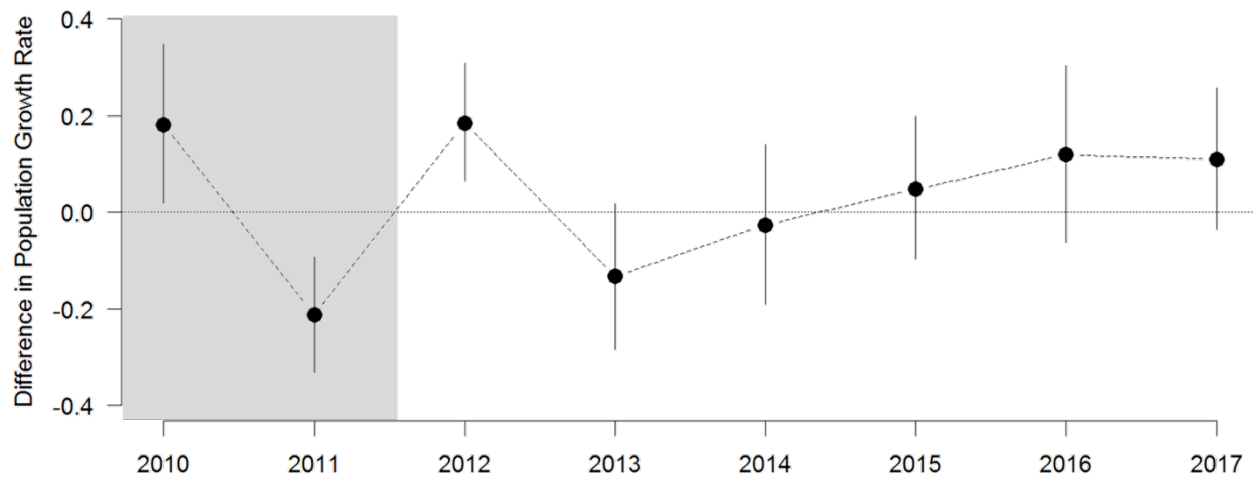
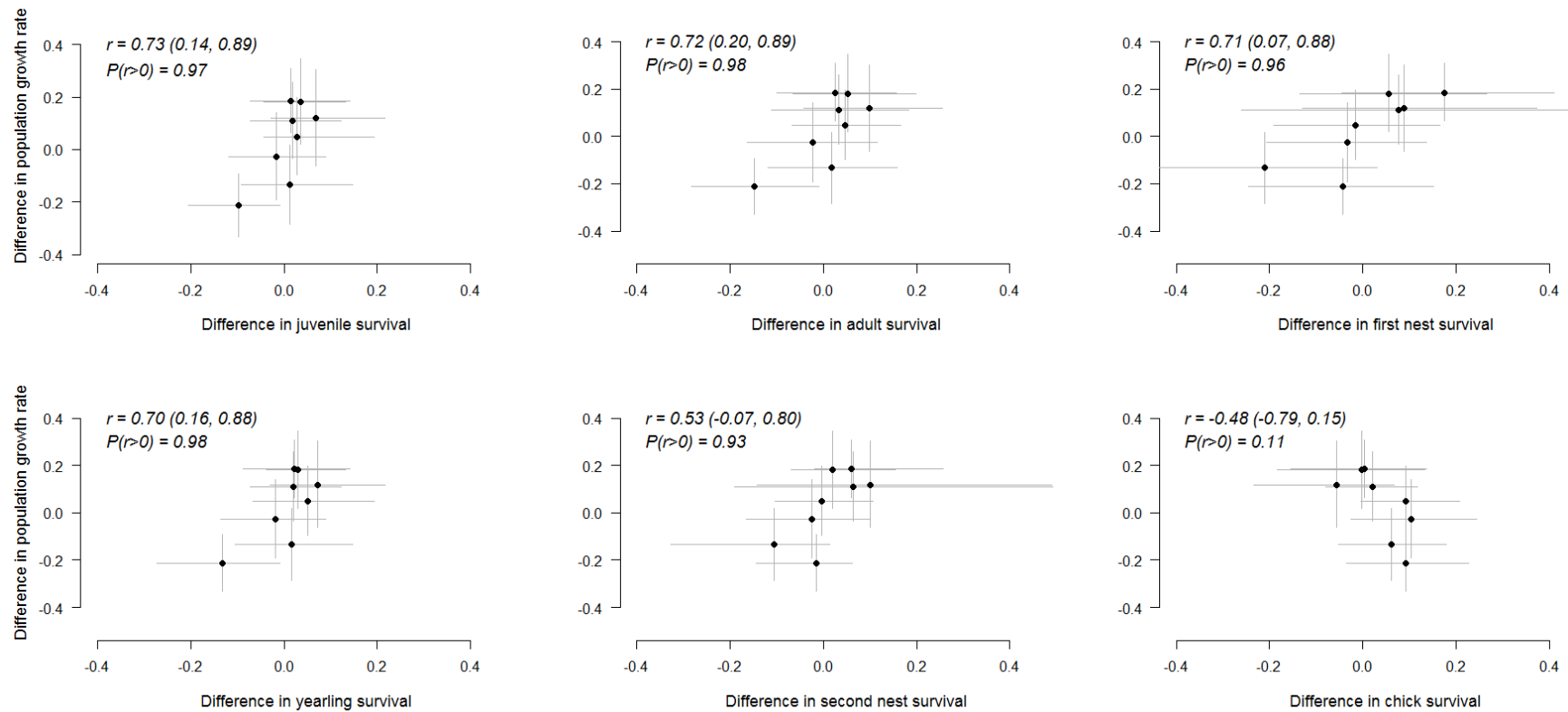


Figure 2.4. Differences (treatment-control) in annual estimates of vital rates for greater sage-grouse (*Centrocercus urophasianus*) plotted against annual estimates of differences (treatment-control) in population growth rates (λ) between the treatment and control study areas, 2010-2017, Lake County, Oregon, Modoc County, California, and Washoe County, Nevada, USA. Vertical and horizontal lines around points are 95% credible intervals association with these differences. The mode and 95% credible of posterior distributions for coefficients of correlation (r) are reported in addition to the probability that the correlation is positive [$P(r > 0)$].



3 – LANDSCAPE-SCALE RESTORATION OF GREATER SAGE-GROUSE HABITAT WITH CONIFER REMOVAL

Abstract

The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a sagebrush obligate gallinaceous bird, occupies approximately 56% of its pre-European settlement distribution as a result of declining habitat. In the Great Basin of western North America, western juniper (*Juniperus occidentalis*) has expanded its range 10-fold since European settlement, a rate higher than any other time during the Holocene. Most (90%) of the expansion since European settlement has occurred in sagebrush (*Artemisia* spp.) ecosystems. Expansion of conifers into sagebrush ecosystems is considered a primary threat to sage-grouse habitat in the Great Basin. Using a long-term (2010–2017) telemetry data set ($n = 399$ females) from a treatment area with conifer removal (Treatment; $n = 232$) and a control area (Control; $n = 167$), resource selection functions were estimated for nest site ($n = 463$) selection and breeding season (April–July) habitat selection with mixed effects logistic regression. Conifer and conifer removal variables were among the most influential predictors of nest site and breeding season selection. Sage-grouse selected nest sites in and near older conifer removal areas and were 16% less likely to nest in an area for every 1% increase in conifer cover within 400 m of the nest. During the breeding season, sage-grouse selected habitat closer to conifer removals and were 26% more likely to use a removal each year after removal. They were most likely to select areas where conifer cover had been reduced by ~10%. By 2017, 75% of the Treatment was categorized as medium-high and high probability of use as a result of conifer removal, up from 49% in 2010. These findings demonstrated the efficacy of conifer removal for increasing usable space for sage-grouse in landscapes affected by conifer expansion.

Introduction

The expansion of native, woody plants is a global phenomenon with characteristics and effects that are often indistinguishable from exotic invasions (Nackley et al. 2017). Trees have rapidly expanded into shrub and grassland ecosystems driven largely by changes in fires regimes, land use patterns, climate, and CO₂ concentrations (Miller and Wigand 1994; Van Auken 2009; Staver et al. 2011). In the Great Basin of western North America, a coniferous tree, western juniper (*Juniperus occidentalis*), has expanded its range 10-fold since European settlement and at a rate higher than any other time during the Holocene (Miller and Wigand 1994; Miller et al. 1999). It currently occupies approximately 3.6 mil ha (Azuma et al. 2005; Miller et al. 2005) and most (90%) of the expansion since European settlement has occurred in sagebrush (*Artemisia* spp.) ecosystems (Davies et al. 2011; Miller et al. 2011).

The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a sagebrush obligate gallinaceous bird, has declined 0.83% per year range-wide since 1965 and commensurate with trends in 8 of the 11 states where it occurs (Western Association of Fish and Wildlife Agencies 2015). It currently occupies approximately 56% of its pre-European settlement distribution (Schroeder et al. 2004). Expansion of western juniper and other conifers into sagebrush ecosystems is considered a primary threat to sage-grouse habitat, particularly in the Great Basin, and has likely contributed to its range contraction (Miller et al. 2011; Baruch-Mordo et al. 2013). Radio telemetry studies indicate sage-grouse are more likely to select sagebrush habitats with conifer cover levels $\leq 4\%$ and as low as $\leq 1.5\%$, indicating a low tolerance for conifers even in areas with intact sagebrush understories (Severson 2016; Coates et al. 2017; Severson et al. 2017b).

The impact of conifer expansion in shrub and grassland ecosystems in North America is not unique to sage-grouse and extends to Greater and Lesser Prairie-Chickens (*Tympanuchus*

cupido and *T. pallidicinctus*, respectively). Conifer cover is an influential predictor of Greater Prairie-Chicken lek presence (Merill et al. 1999; Niemuth 2003) and one study found 9% conifer cover as a threshold to suitability of prairie habitat for lek sites (Gregory et al. 2011). In addition to influencing probability of lek occurrence and occupation, increased conifer cover is associated with lower probability of nesting and reduced nest survival (Matthews et al. 2013; Hovick et al. 2015). Lesser Prairie-Chickens also avoid conifers year-round and select nest sites in areas with low tree densities (Boggie et al. 2017; Lautenbach et al. 2017)

Sage-grouse occupy habitats during the breeding season (defined as April–July for my study) critical to nesting/early brood and late brood/summer life history needs (Connelly et al. 2011). Brood habitat is limiting to the carrying capacity of sage-grouse habitat and loss of brood habitat is considered a major factor in the decline of sage-grouse populations (Connelly et al. 2004; Atamian et al. 2010; Donnelly et al. 2016). Lek (i.e., breeding arena) count data indicate that the mesic resources (e.g. wet meadows and riparian areas) that support brood habitats significantly influence sage-grouse breeding distributions (Donnelly et al. 2016). Conifer removal near potential brood and nesting habitat or along seasonal migration routes from early to late brood habitat may increase carrying capacity and usable space for sage-grouse (Reinhardt et al. 2017; Sandford et al. 2017).

My study expanded previous resource selection analyses (2010–2014; Severson 2016; Severson et al. 2017b, Severson et al. 2017d) for sage-grouse in a treatment area (area with conifer removal; hereafter Treatment) and a control area (area without conifer removal; hereafter Control; see Study Area). These analyses assessed the short-term (1-3 years post-removal) response of sage-grouse nest site and seasonal habitat selection to conifer and conifer removal (Severson 2016, Severson et al. 2017b, Severson et al. 2017d). Nest site selection analyses

indicated that sage-grouse readily nested in conifer removal areas, evidenced by 29% of the marked population that had shifted nests to removal areas by the third year after removals began (Severson et al. 2017d). Available nesting habitat increased 3,201 ha as a result of conifer removals in the project area (Severson et al. 2017d). Marked sage-grouse selected older removal areas (relative probability of use >50% 2 years after removal; Severson et al. 2017d), nest sites closer to or inside of removal areas (relative probability of use >50% within 1,163 m of removal; Severson et al. 2017d) and with conifer cover <4% within 800 m (Severson et al. 2017b). They demonstrated avoidance of conifers within 400 m during all times of the year, but avoidance was weakest during the late summer (July–August; Severson 2016).

Building on this foundational data set, my study assessed the longer term response (3–7 years post-removal) of sage-grouse nest site and breeding season habitat selection to conifer and conifer removal. Additionally, location data from GPS technology with greater temporal resolution and increased sample size was incorporated to improve parameter estimation in the breeding season models (see Methods: Field techniques). My specific objectives were 1) to assess nest site selection in response to conifer and conifer removal across all years (2010–2017) of the project in the Treatment and Control, 2) assess breeding season habitat selection in response to conifer and conifer removal across all years, and 3) to quantify the dynamics in landscape-level probability of breeding season habitat use in the Treatment as a result of conifer removal.

Study Area

The majority of the study area was in Lake County, Oregon within the Lakeview BLM Resource Area (Figure 3.1). The Treatment encompassed approximately 40,000 ha and lay entirely in Lake County, Oregon. The Control encompassed approximately 33,000 ha and

extended south into extreme northwest Washoe County, Nevada and northeast Modoc County, California. The elevation in these areas ranged from 1,200 to 2,200 m with an average of approximately 1,700 m. Although the majority of the study area was dominated by uplands characterized by sagebrush-bunchgrass and mountain big sagebrush (*A. tridentata* subsp. *vaseyana*)-bunchgrass plant associations, mesic resources indicative of sage-grouse summer habitat such as wet meadows, irrigated fields, riparian areas, and high elevation habitats with higher soil moisture content were also available in the study area.

Conifer woodlands comprised predominantly of western juniper covered approximately 43% (17,000 ha) of the Treatment prior to removals and the Lakeview District of the Bureau of Land Management (BLM) designated 14,000 ha as expanding into bitterbrush (*Purshia tridentata*)-sagebrush habitats, low sagebrush (*A. arbuscula*) habitats, and aspen (*Populus tremuloides*) stands (Bureau of Land Management 2011). Following the definitions of transitional – phases described by Miller et al. (2005), the Treatment conifer cover (17,000 ha) was comprised of Phase I ~ 3,000 ha, Phase II ~ 12,000 ha, and Phase III ~ 2,000 ha (Bureau of Land Management 2011). The BLM initiated removal of approximately 9,983 ha of conifers in the Treatment in 2012 consisting of 1,566 ha of Phase I, 7,864 ha of Phase II, and 553 ha of Phase III conifers (Table 3.1). Additionally, the Natural Resource Conservation Service (NRCS) completed approximately 3,683 ha of removals on private lands within the study area. The majority (81%) of removals (11,177 ha) were completed by the end of 2014 and all remaining removals were completed by 2017 (Table 3.1). Hand cutting was the primary removal technique employed (Bureau of Land Management 2011). When trees were sparse, cut trees were left where they fell or branches were lopped to < 1.2 m to minimize their utility as perch sites for avian predators after felling (Bureau of Land Management 2011). When trees were dense, felled

individual trees were burned or slash was piled and burned. Cut trees were dried for ~1 year prior to burning and most burning took place during winter months when impacts from fire to non-target habitat were minimized (Bureau of Land Management 2011).

Methods

Field techniques

Radio collars (22-g VHF, Advanced Telemetry Systems, Isanti, MN, USA) or rump-mounted GPS backpacks (22-g PTT-100 solar Argos/GPS PTT, Microwave Telemetry, Inc., Columbia, MD, USA) were fitted to female sage-grouse that we captured using a traditional spotlighting technique (Giesen et al. 1983; Wakkinen et al. 1992). The goal was to maintain a sample size of 40 individuals in both the Treatment and Control prior to the start of the breeding season (1 April). Rump-mounted GPS backpacks were not deployed until 2015, but by 2017, all females were marked with GPS transmitters and VHF radio collars were no longer in use. Females marked with VHF transmitters were located twice per week and locations were collected from females marked with GPS transmitters 4–5 times per day. Nests of females marked with VHF transmitters were identified by 2 consecutive locations in the same location and then visual confirmation of the female on a nest at <30 m without flushing. Nests of females marked with GPS transmitters were identified by ≥ 3 consecutive points at the same location and subsequent visual confirmation as above.

Vegetation surveys were conducted at each sage-grouse nest location and at paired available nest locations (see Methods: Nest site selection) within 1 week of nest termination (hatched, depredated, or abandoned) 2010–2016. During 2017, all nests and paired available nest locations were sampled within 3 days of estimated hatch. This correction was made after Gibson et al. (2016) highlighted the potential bias induced on demographic model estimates by sampling

vegetation at date of nest fate, which varies by nest, rather than a standardized sampling date such as projected hatch. Two perpendicular 10-m transects oriented in random directions were centered on each nest or random point (Gregg et al. 1994). Shrub foliar line-intercept cover was recorded in 1-m intervals along each transect (Gregg et al. 1994). Grass and forb cover were estimated in 5 equally spaced 0.1-m² frames along each transect (Daubenmire 1959, Gregg 1992). Key forbs considered important components of sage-grouse diets were differentiated from other forbs and included *Lomatium* spp., *Crepis* spp., *Agoseris* spp., *Astragalus* spp., *Orobancha* spp., *Trifolium* spp., *Phlox gracilis*, *Erigeron* spp., *Taraxacum officinale*, *Tragopogon dubius*, *Achillea millefolium*, *Aster* spp., *Mimulus* spp., *Gayophytum* spp., *Antennaria* spp., and *Blepharipappus* spp. (Barnett and Crawford 1994, Drut et al. 1994, Gregg 2006).

Nest site selection

Separate resource selection functions (RSF) of nest site selection were estimated for the Treatment and Control in the use-availability framework using mixed effects logistic regression (MELR) in the lme4 package (Bates et al. 2015) in R (R Core Team 2015). Inclusion of random effects can improve model fit and account for the spatial and temporal autocorrelation inherent to many resource selection studies using telemetry data (Gillies et al. 2006; Bolker et al. 2009).

Available nest locations were generated annually in ArcMap 10.2 (ESRI 2011) at a 1:1 ratio to used nest locations and randomly placed in the area between the 75% and 95% contours from kernel densities of all nest sites from previous years which were generated in the adehabitat package (Calenge 2006) in R (R Core Team 2015). This placement ensured that the available nest locations were spatially related to nesting habitat but minimized placement in areas of high nest density thereby reducing sample contamination (Hagen et al. 2005). However, RSFs

estimated using logistic regression in use-availability studies are robust to sample overlap and contamination (Johnson et al. 2006).

A combination of remotely sensed and physically measured variables were considered as covariates in the nest site selection models. Percent conifer cover was calculated in buffers of radii 50, 100, 200, 400, 800, and 1,200 m (conifer-50, conifer100, etc.) around used and available nest sites and was derived using the Spatial Analyst extension in ArcMap 10.2 (ESRI 2011) from remotely sensed, annual, 30-m rasters of percent cover (Jones et al. 2018; Appendix table B1). These extents followed Severson et al. (2017b) and encompassed the potential range of spatial scales found to be important for sage-grouse in previous studies (Doherty et al. 2010; Casazza et al. 2011; Baruch-Mordo et al. 2013). A 10-m digital elevation model (DEM) was used to assign elevation to used and available nest locations. Using the DEM, the Geomorphometry and Gradient metrics Toolbox 2.0 (Evans et al. 2014) was used to calculate slope and aspect at used and available nest locations as well as the terrain landform and ruggedness in buffers of radii 56, 400, and 800 m (rugged-56, landform-56, etc.) around points following Severson (2016). Ruggedness (or roughness) is a measurement of topographic heterogeneity (Riley et al. 1999) and landform is an index of landscape curvature (Bolstad and Lillesand 1992). Ruggedness values are ≥ 0 and larger values indicate greater topographic roughness (Riley et al. 1999). Positive values of landform indicate convex features (ridges), negative values indicate concave features (depressions), and values at or near 0 indicate flat features (Bolstad and Lillesand 1992). Covariates from vegetation plots included perennial grass cover (perennial), annual grass cover (annual), shrub cover (shrub), key forb cover (key forb), other forb cover (other forb), and species richness of key forbs (K-forb; see Methods: Field Techniques; Appendix table B1). Conifer removal variables included distance to nearest conifer

removal (removal-distance), years since nearest conifer removal (removal-years), and change in conifer cover. Using conifer removal area polygons obtained from the BLM and NRCS, the distance (m) to nearest removal polygon and years since the nearest removal were assigned to used and available nest sites in the Treatment in ArcMap 10.2 (ESRI 2011). Using 2008 as a reference, the change in percent conifer cover within buffers of radii 50, 100, 200, 400, 800, and 1,200 m (Δ conifer-50, Δ conifer-100, etc.) was derived from the percent conifer cover metrics described above for used and available nests. Larger, positive values of Δ conifer indicate greater reduction in conifer cover since 2008, negative values indicate increases in conifer cover, and values near 0 indicate no change in conifer cover. Prior to inclusion in MELR models, the correlation of candidate covariates was assessed with Spearman rank-order correlations. Highly correlated variables ($|r| \geq 0.60$) were excluded or transformed prior to inclusion in models.

The *a priori* random effects structure for all candidate nest site selection models was a random intercept for the effect year. This structure accounted for any correlation in space use due to annual changes in the availability and quality of nesting habitat as a result of conifer removal and annual variation in understory vegetation. A random effect for individual was not considered because re-nesting attempts represented a small portion (17%) of all samples and models with this more complex structure did not converge due to the limited sample size of nests relative to the number of parameters estimated in the models. An information-theoretic approach using Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to evaluate nest site selection models in a 3-stage process: stage-1) selection of the most parsimonious scale for variables that were measured at multiple buffers, stage-2) selection of the most parsimonious *a priori* habitat model incorporating variables from stage-1 and all other non-conifer removal variables, and stage-3) selection of the most parsimonious *a priori* conifer removal model

incorporating removal variables into the most parsimonious habitat model from stage-2 (for the Treatment only).

The marginal (only fixed effects) and conditional (fixed and random effects combined) R^2 of the most parsimonious models for the Treatment and Control from stage-2 and for the Treatment from stage-3 were calculated following Nakagawa and Schielzeth (2013) using the MuMIn package (Bartón 2014) in R (R Core Team 2015). Additionally, the variance explained by the random and fixed effects from these top models was calculated using the sjstats package (Lüdtke 2018) in R (R Core Team 2015). I report coefficient estimates and 95% confidence intervals for standardized and non-standardized predictor variables from the top habitat and conifer removal models as well as partial effects plots for the top conifer removal model. Odds ratios and 95% confidence intervals are reported for conifer and conifer removal variables.

Breeding season selection

Resource selection functions of breeding season (April–July) habitat selection, regardless of nest or brood success, were estimated for the Treatment and Control using MELR and model selection followed the 3-stage process described for nest site selection. The *a priori* random effects structure for all models was a random intercept for the effect of year and a random intercept for the effect of individual sage-grouse. Available locations for the Treatment and Control were randomly generated at a 3:1 ratio to used locations in ArcMap (ESRI 2011) in minimum convex polygons of pooled, used locations from all years of the project (2010–2017).

All of the predictor variables included in the breeding season habitat selection analysis were derived from remote sensing data. Following the methods described for nest site selection, slope, aspect, and elevation were assigned to used and available locations. Landform and ruggedness were calculated in buffers of radii 56, 400, and 800 m around used and available

points. Percent cover of conifers, shrubs, perennial forbs and grasses, and annual forbs and grasses was calculated in buffers of radii 56, 400, and 800 m (conifer-56, shrub-56, perennial-56, annual-56, etc.) around used and available points following Severson (2016) and was derived from annual, 30 m rasters of percent cover (Jones et al. 2018; Appendix table B3). Conifer removal variables included distance to nearest conifer removal, years since nearest conifer removal, and change in conifer cover in buffers of radii 56, 400, and 800 m. Prior to inclusion in MELR models, the correlation of candidate covariates was assessed with Spearman rank-order correlations. Highly correlated variables ($|r| \geq 0.60$) were excluded from models.

Conditional and marginal R^2 and the variance explained by fixed and random effects were calculated for the most parsimonious models following the methods described for nest site selection. I report coefficient estimates and 95% confidence intervals for the standardized and non-standardized predictor variables from the top habitat and conifer removal models as well as partial effects plots for the top conifer removal model. Odds ratios and 95% confidence intervals are reported for conifer and conifer removal variables.

Breeding season predictive surfaces

Predictive surfaces for the Treatment bounded by the minimum convex polygon (see Methods: Breeding season selection) were generated for each year (2010–2017) of the project using the coefficients from the most parsimonious conifer removal model for the Treatment where fitted values for individual 30-m pixels were:

$$Fitted\ value_{pixel_i} = \exp(\beta_1 x_{1i} + \beta_2 x_{2i} + \dots + \beta_k x_{ki})$$

Predicted values for each 30-m pixel were assigned selection categories of “low”, “medium-low”, “medium-high,” and “high” using the quartiles of the distribution of predicted values across all years and symbolized accordingly in ArcMap (Morris et al. 2016; ESRI 2011).

Results

Nest site selection

Four-hundred and sixty-three nests were monitored in the Treatment ($n = 199$) and Control ($n = 264$), 2010–2017. The model selection results indicated that the appropriate scale of selection were landform-400, rugged-100, and conifer-400 for the Control. The coefficients from the top habitat model for the Control indicated selection for nest sites on more north facing aspects ($\beta = 0.007$, 95% CI: 0.002–0.012), with greater species richness of key forbs ($\beta = 0.232$, 95% CI: 0.090–0.375), greater shrub cover ($\beta = 0.058$, 95% CI: 0.039–0.078), and lower conifer-400 ($\beta = -0.140$, 95% CI: -0.211–0.068; Table 3.2). The confidence interval for the coefficient for annual grass cover overlapped zero by $< 10\%$ indicating weak support for selection of areas with lower cover ($\beta = -0.103$, 95% CI: -0.212–0.006; Table 3.2; Dugger et al. 2016). The random effects structure of a random intercept for the effect of year was not significant in the control area nest site selection model. Subsequently, both the marginal and conditional R^2 values were 0.307 and the variance decomposition indicated that the fixed effects (i.e. predictor variables) explained all of the variance in the data.

The most parsimonious scales for the Treatment nest site selection model were landform-400, rugged-100, conifer-400, and Δ conifer-800. The coefficients from the top habitat model for the Treatment indicated selection of nest sites with greater values of landform-400 (ridges; $\beta = 13.056$, 95% CI: 2.550–23.562), with greater annual grass cover ($\beta = 0.054$, 95% CI: 0.011–0.096), greater shrub cover ($\beta = 0.061$, 95% CI: 0.045–0.076), and lower conifer-400 ($\beta = -0.216$, 95% CI: -0.315–0.118; Table 3.2). The marginal R^2 for this model was 0.283 and the conditional R^2 was 0.306. Of the variance explained by the fixed and random effects, the random effect of year explained 7% of the variance and the fixed effects explained 93%. After

adding conifer removal variables in stage-3 of the modeling process, the coefficients for the top model indicated selection for nest sites in or near older conifer removal areas ($\beta = 0.341$, 95% CI: 0.106–0.576) and for reductions in conifer cover since 2008 $\leq 1\%$ ($\beta = -4.118$, 95% CI: -7.796–-0.441; Table 3.3; Figure 3.2). The odds ratio ($e^{\text{coefficient}}$) indicated a 40.6% (95% CI: 11.2–78.0%) annual increase in the probability of nesting in a conifer removal area. Additionally, there was a 16.4% (95% CI: 4.5–29.7%) decrease in probability of use for each 1% increase in conifer-400. The direction and significance (95% CI not overlapping 0) of effects of variables from the habitat model remained the same after adding the conifer removal variables (Table 3.3). The conditional R^2 for this model was 0.480 and marginal R^2 was 0.528. Of the variance explained by the fixed and random effects combined, the fixed effects explained 90.9% and the random effect of year explained 9.1%.

Breeding season selection

Three-hundred ninety-nine female sage-grouse were monitored during the breeding season in the Treatment ($n = 232$) and Control ($n = 167$), 2010–2017. Perennial and annual herbaceous cover were highly correlated ($|r| \geq 0.60$) and were combined to create a new variable: herbaceous cover (herb-56, etc.). The scale selection process for the Control indicated that landform-400, rugged-400, herb-56, and conifer-56 were the most parsimonious scales. The top habitat model for the Control indicated selection for higher elevations ($\beta = 0.002$, 95% CI: 0.002–0.002), more north facing aspects ($\beta = 0.003$, 95% CI: 0.003–0.003), greater landform-400 (ridges; $\beta = 5.038$, 95% CI: 4.493–5.582), lower rugged-400 ($\beta = -0.028$, 95% CI: -0.029–-0.027), lower herb-56 ($\beta = -0.005$, 95% CI: -0.006–0.004), greater shrub-400 ($\beta = 0.003$, 95% CI: 0.003–0.003), and lower conifer-56 ($\beta = -13.249$, 95% CI: -13.757–-12.742; Table 3.4). The conditional and marginal R^2 were 0.278 and 0.291, respectively. The variance decomposition

indicated that of the variance explained by the fixed and random effects combined, the random effect of year explained 1.7%, the random effect of individual explained 3.2%, and the fixed effects explained 95.1%.

The most parsimonious scales for the Treatment were landform-800, rugged-56, herb-800, conifer-56, and Δ conifer-800. The top habitat model for the Treatment indicated selection for lower elevations ($\beta = -0.004$, 95% CI: -0.004--0.003), more north facing aspects ($\beta = 0.001$, 95% CI: <0.001--0.001), greater landform-800 (ridges; $\beta = 5.464$, 95% CI: 4.658--6.270), lower rugged-56 ($\beta = -0.009$, 95% CI: -0.010--0.008), greater herb-800 ($\beta = 0.003$, 95% CI: 0.002--0.003), greater shrub-400 ($\beta = 0.004$, 95% CI: 0.002--0.005), and conifer-56 ($\beta = -17.277$, 95% CI: -17.904--16.650; Table 3.4). The conditional and marginal R^2 of the model were 0.265 and 0.277, respectively. Of the variance explained by the fixed and random effects combined, the fixed effects explained 95.6%, the random effect of year explained 4.4%, and the random effect of individual explained 0%. The top conifer removal model indicated selection for areas in or near older conifer removal areas ($\beta = 0.235$, 95% CI: 0.218--0.251), areas closer to conifer removal areas ($\beta = <-0.001$, 95% CI: <-0.001--<-0.001), and for changes in conifer cover $\pm 10\%$ since 2008 ($\beta = -0.055$, 95% CI: -0.059--0.040; Table 3.5; Figure 3.3). The odds ratio indicated a 26.5% annual increase in probability of use of removal areas (95% CI: 24.4--28.6%). There was a decrease in probability of use of 4.1% (95% CI: 4.0--4.2%) for each 100 m distance from a removal area and a 26.5% (95% CI: 23.3--25.1%) decrease in probability of use for each 1% increase in conifer-56. The direction and significance of the effects from the habitat model were unchanged after addition of these variables (Table 3.5). The conditional and marginal R^2 of the model were 0.409 and 0.625, respectively. Of the variance explained by the fixed and random

effects combined, the fixed effects explained 50.0%, the random effect of individual explained 1.3%, and the random effect of year explained 48.7%.

Breeding season predictive surfaces

Annual predictive surfaces for the Treatment breeding season RSF were generated from the most parsimonious conifer removal model (Figure 3.4). The percentage of 30-m pixels in each probability of use category were approximately proportional in 2010; however, by 2017, 75% of pixels had transitioned to the medium-high or high probability of use categories (Figure 3.5). This shift suggested an increase of 10,229 ha of breeding season habitat in these higher relative probability of use categories with lower conifer cover (Figure 3.5). The percentage of pixels in the low category decreased from 27% in 2010 to 7% in 2017, a reduction of 6,521 ha (Figure 3.5). Of the individual pixels that were in the low category in 2010, only 21% remained in the low category by 2017 (Table 3.6). Similarly, of the pixels in the medium-low category in 2010, only 21% remained in the medium-low category by 2017 and 73% had shifted to the medium-high or high categories (Table 3.6).

Discussion

My study represents the first long-term, landscape-scale analysis of sage-grouse habitat selection in relation to conifer removals. As conifer removals continue across the Great Basin, findings of my research provide valuable insight into the response of sage-grouse to these broad-scale management actions which historically lacked empirical evidence for their efficacy (U.S. Fish and Wildlife Service 2015). Conifer removal projects are variable and occur in a variety of landscapes, even within the Great Basin, and caution should be used when drawing inference from these results to other projects. However, it is my goal that these findings will aid in planning future conifer removals and provide some insight into what type of response can be

expected from sage-grouse. The removals in the project area targeted Phase I and II conifers and employed hand-cutting and slash removal when necessary as the primary modes of removal (Bureau of Land Management 2011). When fire was used to remove slash, effort was made to limit the effect of fire to the slash piles for individual trees and their stumps (i.e. pile burning) and burning took place during winter and early spring months when the risk of fire spreading to non-target fuels was minimal. Conifers that established prior to European settlement were not removed (Bureau of Land Management 2011). The findings of my research may be inferred to other projects targeting Phase I and II conifers with low disturbance techniques.

Although conifer expansion is a widespread and serious threat to sagebrush ecosystem function in the Great Basin (Chambers and Wisdom 2009; Davies et al. 2011; Baruch-Mordo et al. 2013), my findings indicated that large-scale conifer removals, such as those employed in this project, can be an effective method of restoring these imperiled ecosystems. My findings may support land managers that are continuing to employ these landscape restoration methods and benefit the species that inhabit landscapes affected by post-European settlement conifer expansion. Previous research indicates that the benefits of conifer removal can extend beyond sage-grouse to other terrestrial vertebrates such as sagebrush obligate songbirds (Donnelly et al. 2017; Holmes et al. 2017) and mule deer (*Odocoileus hemionus*; Bender et al. 2013, Bergman et al. 2014a, b, 2015).

The understory response after conifer removal has been well documented and often results in rapid increase in perennial grasses and forbs after removal (Bates et al. 2000, Bates et al. 2005; Miller et al. 2005; Severson et al. 2016a, Bates et al. 2017). These are important components of sage-grouse habitat and diet which may be drivers of the utilization of conifer removal areas by sage-grouse documented in my study and previous analyses (Commons et al.

1999; Frey et al. 2013; Severson et al. 2016b; Sandford et al. 2017). However, annual grasses such as cheatgrass (*Bromus tectorum*) may also increase in conifer removal areas (Bates et al. 2000; Bates et al. 2005; Severson et al. 2016c), and may have contributed to the unexpected positive effect of annual grass cover on nest site selection in the Treatment conifer removal model (Table 3.3). Although the effect had the smallest magnitude of the predictor variables in the model (Appendix table A2), the odds ratio indicated a 4.5% (95% CI: 0.1–8.9%) increase in probability of use for each 1% increase in annual grass cover. Localized increases in exotic annual grass cover associated with conifer removal in the project area were documented 1-3 years after removals, but were not statistically significant (Severson et al. 2016c). These increases may have been driven by infill from annual grass that was present at low levels prior to conifer removal. However, establishment of annual grasses in conifer removal areas is driven by multiple factors and may not always be immediate, as evidenced by the delayed establishment (4–6 years post conifer removal) at a study site in Oregon (Bates et al. 2005). Conifer removal sites with high ecosystem resistance and resilience (Chambers et al. 2014) and adequate pre-removal perennial grass density have the greatest chance of native understory reestablishment post-removal (Bates et al. 2005).

In addition to increases in important vegetation components, sage-grouse can experience demographic benefits from conifer removals (Sandford et al. 2017; Severson et al. 2017a, chapter 2). Conifer expansion may increase perch sites for avian predators of sage-grouse (Paton 1994; Wolff et al. 1999) and contribute to environments with higher risk of mortality, even when trees are sparse and scattered (Coates et al. 2017; Prochazka et al. 2017). This risk may be the mechanism behind the strong avoidance of conifers in my study and others (Baruch-Mordo et al. 2013; Severson 2016; Coates et al. 2017; Severson et al. 2017b). Conifer cover was the effect

with the largest magnitude in all of models in my analysis except the nest site conifer removal model (Appendix tables A1, A2, A3, and A4) and seems to be a primary driver of sage-grouse space use in areas affected by conifer expansion in the Great Basin. Sage-grouse habitat management that seeks to increase available habitat in these landscapes is unlikely to be successful if it does not address conifer expansion.

My analysis was the first to apply the Jones et al. (2018) annual vegetation rasters to sage-grouse habitat selection analyses and the temporal resolution of these data captured the annual variability of herbaceous cover. Severson et al. (2016a) examined the effect of conifer clustering index on sage-grouse nest site selection. An index of >1 indicated a dispersed arrangement of conifers and index <1 indicated a clustered arrangement of conifers (Severson et al. 2016a). This index, at the 800 m scale, was an important predictor of sage-grouse nest site selection and indicated selection for increasingly clustered conifers and an interaction between clustering index and conifer indicated selection for areas of low conifer cover and high conifer clustering (Severson et al. 2016a). The conifer cover data used for their analysis consisted of individual tree locations and their associated crown diameters, which is necessary for calculation of the index (Severson et al. 2016a; Falkowski et al. 2017). The clustering index could not be derived from the 30-m rasters of conifer cover used in my analysis (Jones et al. 2018). This may limit the interpretation of selection for lower conifer cover in my analyses, as the findings of Severson et al. (2016a) indicated differential selection within the same level of conifer cover based on a clustering index. However, the temporal resolution of these layers was coarse (3-year resolution; Falkowski et al. 2017) compared to that of the layers of used in my analysis.

The incorporation of Δ conifer as a predictor variable in conifer removal models was a novel approach to assessing the degree of landscape change as result of conifer removal on sage-

grouse resource selection. The quadratic effect of change in conifer cover ($\Delta\text{conifer-800}^2$) had a large effect relative to other predictor variables in the top conifer removal models for nest site and breeding season habitat selection (Figures 3.2, 3.3; Appendix tables A2, A4). The breeding season model indicated selection for a broader range of $\Delta\text{conifer-800}$ relative to the nest site selection model (Figures 3.2, 3.3). Sage-grouse occupy a variety of seasonal habitats during breeding season and may exhibit more plasticity in selection for removal areas when assessing use availability data across this larger time-frame (April–July) relative to the nesting season (April–May). Sage-grouse nesting habitat is characterized by 15–25% sagebrush cover and $\geq 15\%$ grass/forb cover at arid sites such as my study area (Connelly et al. 2000). Conifer removal areas with understories providing adequate nesting vegetation may have had limited conifer cover prior to removal, driving the selection for nest sites in areas where conifer cover had been reduced $< 1\%$ (Figure 3.2). However, given the selection for older removals (Table 3.3; Figure 3.2), this effect on nest site selection may dampen with time.

The results of the variance partitioning for the top breeding season model were unexpected and indicated that the random effect of year explained far more variation than that of individual. This indicated that individual sage-grouse used the landscape similarly and that despite using GPS data, which are subject to temporal and spatial autocorrelation, these effects were minimal. The primary annual changes in the landscape were attributed to herbaceous cover, conifer cover, and conifer removal metrics. Dynamics in these predictors may have driven the larger amount of variance explained by the random effect of year relative to the random effect of individual.

The percentage of pixels in the low category of probability of use increased and the high category decreased on predictive surfaces for 2013 and 2014 (Figure 3.5). This pattern may have

been driven by reduced herbaceous cover across the Treatment during those years, which was a positive effect in the breeding season conifer removal model (Table 3.5). The mean herbaceous cover for 30-m pixels in 2013 and 2014 was 16.3% and 15.1%, respectively. The annual mean for all other years of the project ranged from 19.5-23.0%.

The findings of my study further demonstrate the efficacy of conifer removal as a landscape restoration tool. Although reduced frequency of fire was a primary driver of post-European settlement conifer expansion in the Great Basin (Miller and Wigand 1994; Miller and Tausch 2001; Miller et al. 2005), the role of fire as a mechanism to limit conifer expansion has been forever altered by the widespread invasion of exotic annual grasses which further contributes to altered successional dynamics and limits the extent to which treatments incorporating fire can be applied to expanding conifers (Miller and Tausch 2001; Miller et al. 2005). The need for targeted, mechanical, conifer removal to maintain and restore ecosystem function will persist as the accelerated expansion of conifers in the Great Basin continues at ~0.4–1.5% annually (Sankey and Germino 2008) and limits the space use of sagebrush obligates and near-obligates.

Management implications

Management that seeks to improve sage-grouse breeding season habitat should target post-European settlement conifers at <10% cover and create treeless habitat patches with a minimum area of 200 ha for the greatest probability of use by sage-grouse in the time frame examined in my analysis (1–5 years post-removal; Figure 3.3). However, conifer removal areas should be proximate to existing, occupied habitat and collective, contiguous removals leading to watershed-scale restoration will likely have the greatest long-term benefits to sage-grouse (Sandford et al. 2017; Severson et al. 2017d). If improving nesting habitat is the management

objective, the findings of my research indicate the greatest increases in probability of use occur when targeting conifers at even lower cover levels (<1%; Figure 3.2). Sage-grouse are increasingly likely to utilize areas where conifers were removed year after year and this pattern is more pronounced in nesting habitat (Figures 3.2, 3.3). Given these temporal dynamics in relative probability of use of conifer removal areas, long-term monitoring data may be needed to assess the change in sage-grouse space use as a result of conifer removal as short-term (1-3 years post-removal) monitoring may underestimate the effects of conifer removal on sage-grouse space use. Seeding with natives and/or application of appropriate herbicides may reduce the localized increase in exotic annual grasses that may be associated with burning slash (i.e. burning individual trees or piling and burning; Severson et al. 2017c).

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Table 3.1. Annual and cumulative area of conifers removed on public and private lands at a treatment study area, 2010–2017, Lake County, Oregon, USA.

Year	Annual Hectares Removed¹	Cumulative Hectares Removed (% of total) ¹
2010	0	185 (1%) ²
2011	240	425 (3%)
2012	710	1135 (8%)
2013	5113	6248 (45%)
2014	4929	11177 (81%)
2015	359	11536 (83%)
2016	656	12192 (88%)
2017	1659	13851 (100%)

¹Includes removals within 3 km of the study area boundary

²Includes area removed 2007–2009

Table 3.2. Coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) nest site selection functions in a treatment area with conifer removal and a control area, 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA.

Control				Treatment			
Predictor Variable	β	0.025	0.975	Predictor Variable	β	0.025	0.975
Intercept	-0.195	-0.433	0.043	Intercept	-0.854	-1.52	-0.187
shrub	0.058	0.039	0.078	shrub	0.061	0.045	0.076
annual	-0.103	-0.212	0.006	annual	0.054	0.011	0.096
conifer-400	-0.140	-0.211	-0.068	conifer-400	-0.216	-0.315	-0.118
K-forb	0.232	0.09	0.375	landform-400	13.056	2.55	23.562
aspect	0.007	0.002	0.012				

Table 3.3. Coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) nest site selection function in a treatment area with conifer removal incorporating conifer removal variables, 2010–2017, Lake County, Oregon, USA.

Predictor Variable	β	0.025	0.975
Intercept	-1.727	-3.024	-0.429
landform-400	13.733	2.806	24.659
shrub	0.064	0.048	0.081
annual	0.044	0.002	0.086
conifer-400	-0.152	-0.260	-0.044
removal-years	0.341	0.106	0.576
Δ conifer-800	1.517	-1.727	4.761
Δ conifer-800 ²	-4.118	-7.796	-0.441

Table 3.4. Coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) breeding season (April–July) resource selection in a treatment area with conifer removal and a control area, 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA.

Control				Treatment			
Predictor Variable	β	0.025	0.975	Predictor Variable	β	0.025	0.975
Intercept	-1.23	-1.353	-1.108	Intercept	5.188	4.79	5.586
elevation	0.002	0.002	0.002	elevation	-0.004	-0.004	-0.003
landform-400	5.038	4.493	5.582	landform-800	5.464	4.658	6.27
aspect	0.003	0.003	0.003	aspect	0.001	<0.001	0.001
rugged-400	-0.028	-0.029	-0.027	rugged-56	-0.009	-0.01	-0.008
conifer-56	-0.132	-0.138	-0.127	conifer-56	-0.173	-0.179	-0.167
shrub-400	0.003	0.003	0.003	shrub-400	0.004	0.002	0.005
herb-56	-0.005	-0.006	-0.004	herb-800	0.003	0.002	0.003

Table 3.5. Coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) breeding season (April–July) resource selection in a treatment area with conifer removal incorporating conifer removal variables, 2010–2017, Lake County, Oregon, USA.

Predictor Variable	β	0.025	0.975
Intercept	-2.211	-3.151	-1.271
elevation	0.001	0.001	0.002
landform-800	1.971	1.176	2.766
aspect	<0.001	<0.001	0.001
rugged-56	-0.012	-0.013	-0.011
herb-800	0.002	0.002	0.002
shrub-400	0.010	0.008	0.011
conifer-56	-0.217	-0.224	-0.210
removal-distance	<-0.001	<-0.001	<-0.001
removal-years	0.235	0.218	0.251
Δ conifer-800	-0.037	-0.053	-0.021
Δ conifer-800 ²	-0.055	-0.059	-0.04

Table 3.6. Percent change in probability of use categories from predictive surfaces for Greater Sage-grouse (*Centrocercus urophasianus*) in a treatment study area with conifer removal, 2010–2017, Lake County, Oregon, USA.

2010 category	Year	Sage-grouse probability of use category			
		Low	Medium-low	Medium-high	High
Low	2011	74%	19%	5%	2%
	2012	75%	18%	6%	2%
	2013	86%	10%	2%	1%
	2014	78%	16%	4%	2%
	2015	54%	33%	10%	3%
	2016	24%	38%	26%	11%
	2017	21%	39%	30%	11%
Medium-low	2011	31%	39%	22%	8%
	2012	32%	39%	21%	7%
	2013	55%	31%	11%	3%
	2014	40%	38%	17%	5%
	2015	14%	50%	30%	7%
	2016	4%	25%	46%	25%
	2017	6%	21%	47%	26%
Medium-high	2011	4%	32%	39%	24%
	2012	5%	32%	39%	23%
	2013	21%	43%	26%	11%
	2014	10%	41%	36%	14%
	2015	3%	28%	51%	19%
	2016	1%	10%	44%	46%
	2017	2%	10%	39%	49%
High	2011	0%	5%	20%	76%
	2012	1%	6%	22%	71%
	2013	3%	16%	21%	60%
	2014	2%	13%	25%	60%
	2015	1%	7%	25%	67%
	2016	0%	3%	15%	82%
	2017	0%	2%	12%	86%

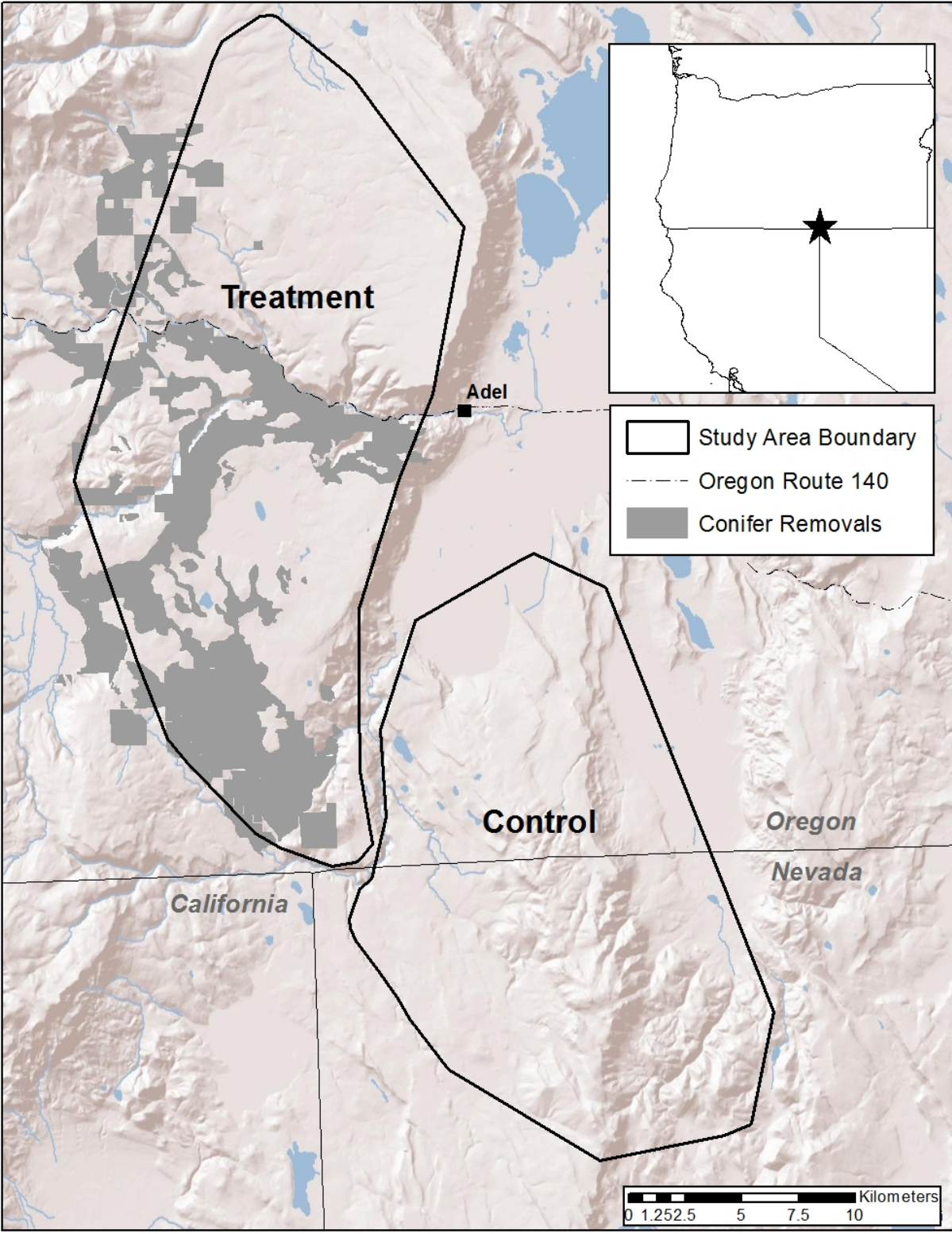


Figure 3.1. Treatment and control study areas for research on Greater Sage-grouse (*Centrocercus urophasianus*) habitat use in relation to conifer removals, 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA.

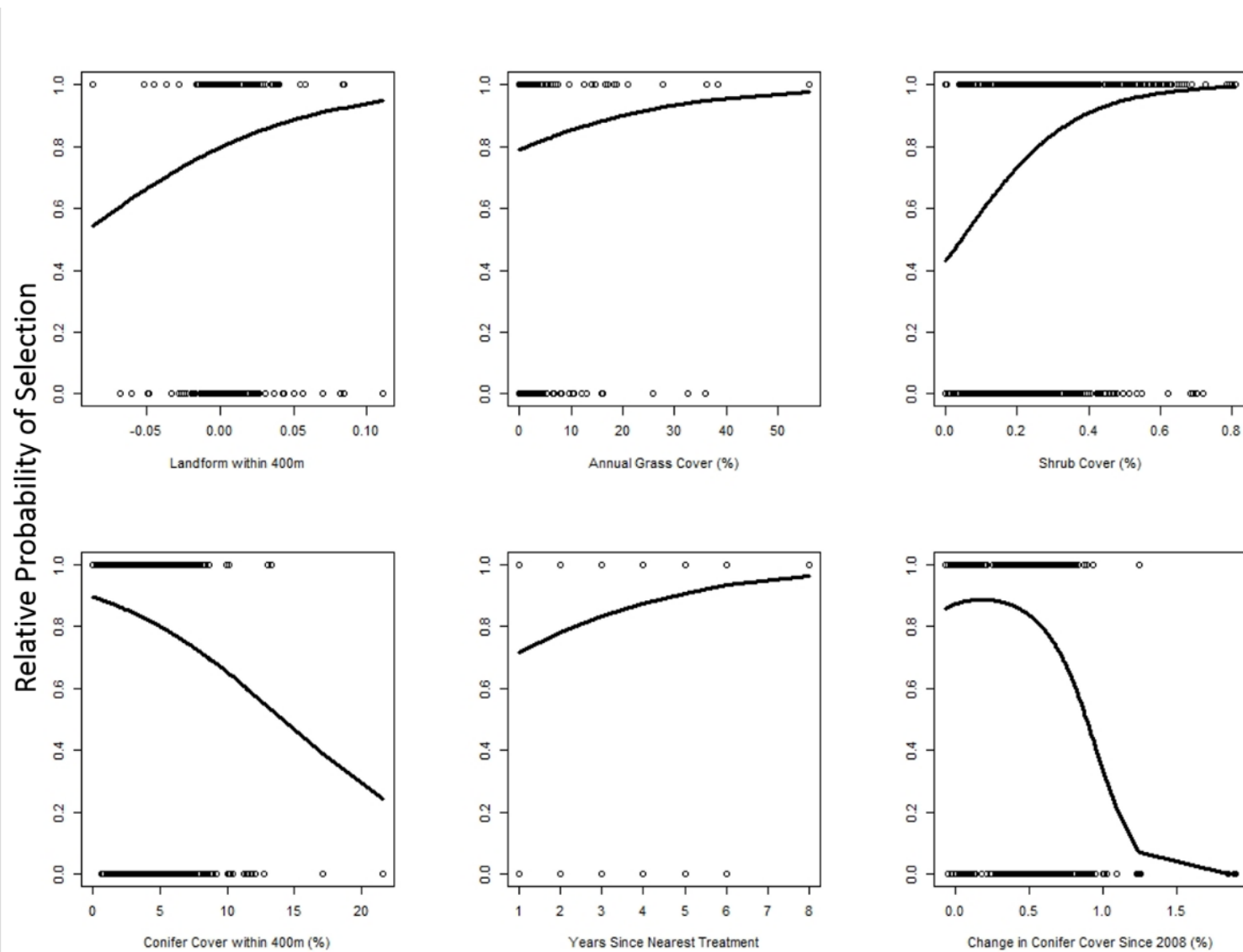


Figure 3.2. Partial effects plots for a Greater Sage-grouse (*Centrocercus urophasianus*) nest site resource selection function for a treatment area with conifer removal, 2010–2017, Lake County, Oregon, USA.

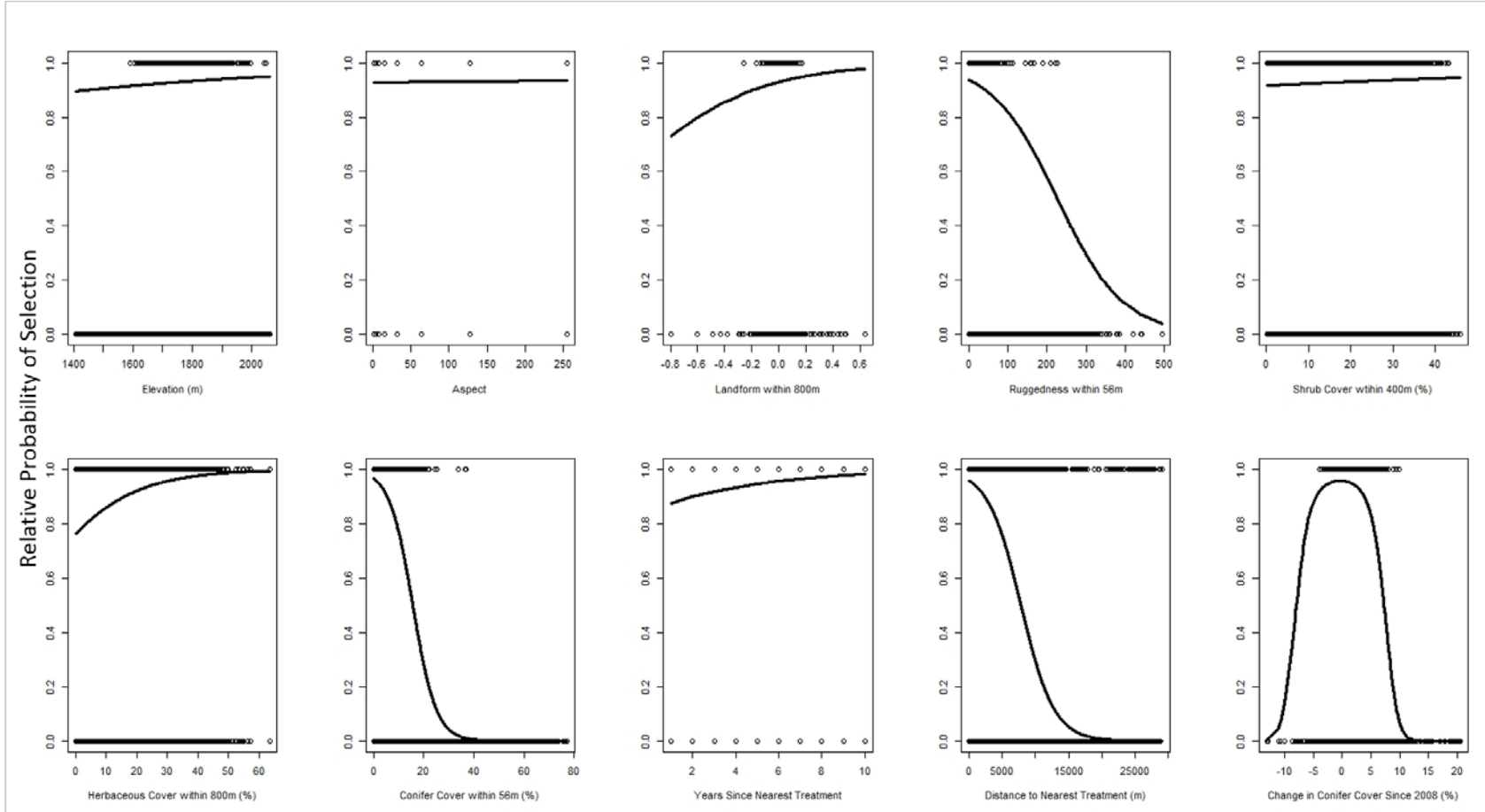


Figure 3.3. Partial effects plots for a Greater Sage-grouse (*Centrocercus urophasianus*) breeding season (April–July) resource selection function for a treatment area with conifer removal, 2010–2017, Lake County, Oregon, USA.

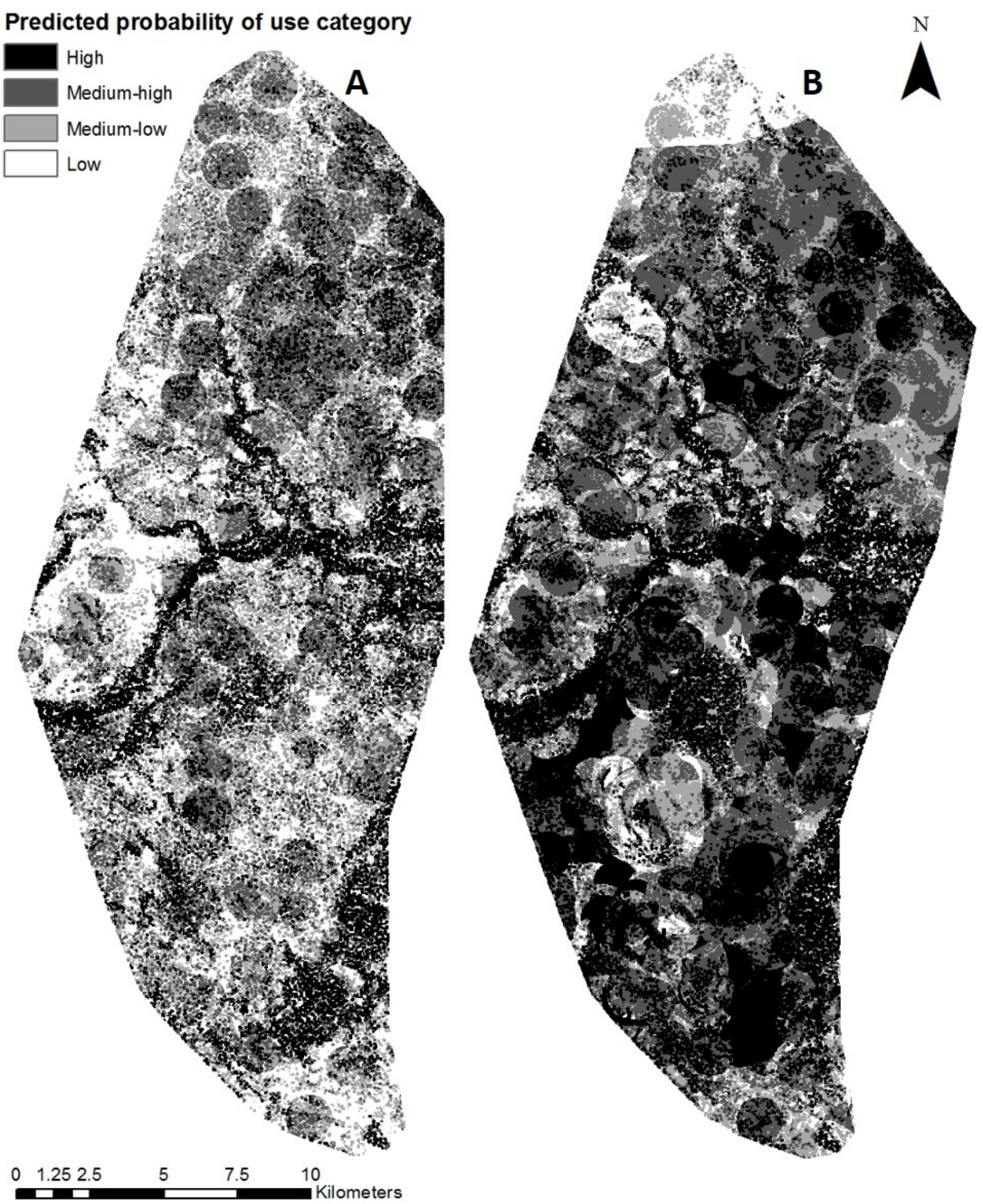


Figure 3.4. Predictive surfaces for Greater Sage-grouse (*Centrocercus urophasianus*) breeding season habitat before (A; 2010) and after (B; 2017) conifer removals, Lake County, Oregon, USA. Circular patterns are an artifact of predictor variables measured in circular buffers and the reduction in probability of use at the northern end of the study area in 2017 was driven by a conifer removal in the area which reduced the age of nearest removal.

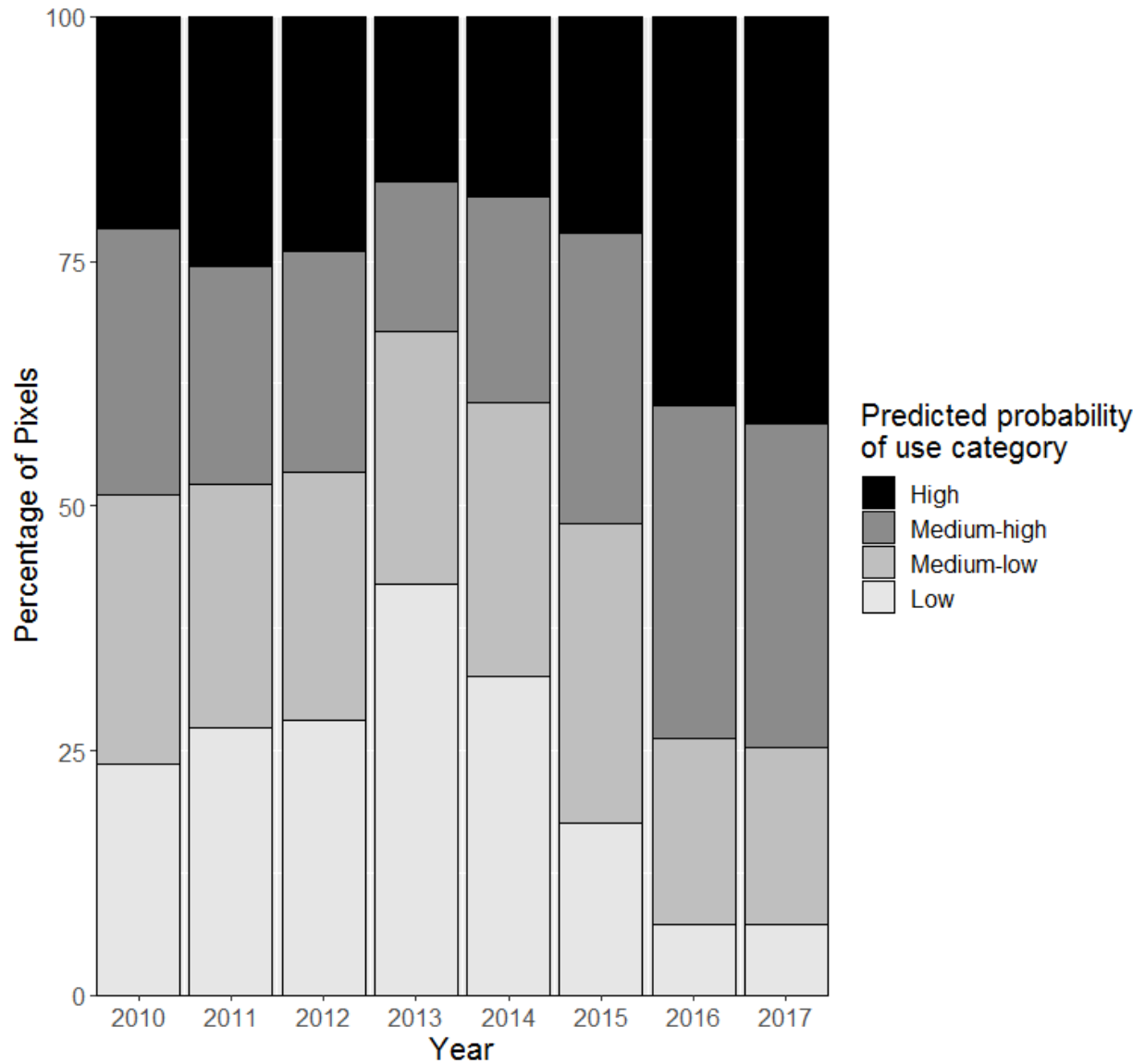


Figure 3.5. Percentage of pixels in each predicted probability of use category from predictive surfaces for Greater Sage-grouse (*Centrocercus urophasianus*) in a treatment study area with conifer removal, 2010–2017, Lake County, Oregon, USA.

4 – CONIFER REMOVAL REDUCES LANDSCAPE RESISTANCE TO GREATER SAGE-GROUSE MOVEMENT

Abstract

Landscape connectivity plays a critical role in many aspects of animal movement and ecology. The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a sagebrush (*Artemisia* spp.)-obligate gallinaceous bird, has undergone dramatic population declines and range contraction since European settlement of the American West. Movement between seasonal ranges is an important aspect of sage-grouse behavior and ecology for many sage-grouse populations. A primary threat to the sage-grouse habitat in the Great Basin is expansion of conifers such as western juniper (*Juniperus occidentalis*) into sagebrush ecosystems, which may reduce landscape connectivity due to the avoidance of conifers by sage-grouse. Using a long-term (2010–2017) telemetry data set ($n = 232$), resistance surfaces were generated with a resource selection function for a conifer removal study area for a pre-conifer removal year (2010) and 3 post-removal years when data from GPS transmitters were available. Brownian bridge movement models and movement paths were generated with the GPS data and the change in landscape resistance in the habitat utilized by sage-grouse during the post-removal years was quantified. Additionally, comparisons were made between the resistance experienced by females with broods and those without broods. Regardless of resistance metric, there was an increase (up to 76% increase) in landscape connectivity in the breeding season home ranges of sage-grouse as a result of conifer removal. Home ranges of females without broods experienced greater increases (up to 81% increase) in connectivity than those of females with broods. Within post-removal years, females without broods experienced greater landscape connectivity (up to 18% greater) in their breeding season home ranges than females with broods. Conifer removal was an effective tool for increasing landscape connectivity, but disproportionately benefited females

without broods which may have demographic consequences for females with broods and their chicks potentially due to the difference in movement strategies between females with and without broods.

Introduction

Understanding the spatial-temporal distribution of animals is a critical component to the study of wildlife ecology and is inextricably linked to hierarchical patterns of movement. At broad scales this hierarchy includes migration, dispersal, gene flow, and adaptation, and at finer scales foraging, thermal refugia, and predator avoidance (Fahrig 2007; Zeller et al. 2012; Wade et al. 2015). However, unprecedented loss and fragmentation of habitat has decoupled this hierarchy and led to deleterious effects on various wildlife populations (Kareiva and Wennergren 1995; Wilcove et al. 1998; Fahrig 2007). Landscape connectivity is “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). A common technique for modeling landscape connectivity is the development of resistance surfaces (Zeller et al. 2012; Wade et al. 2015). Resistance surfaces quantify variables across a continuum of resistance (or cost) to movement and assume a relationship between these variables and the ease of animal movement across the landscape (Zeller et al. 2012, Wade et al. 2015). Resistance surfaces have been broadly applied across conservation and management issues and are an important tool in genetic studies that seek to model genetic isolation and gene flow as functions of landscape connectivity (Spear et al. 2010; Zeller et al. 2012; Wade et al. 2015).

The data types and analytical methods employed to develop resistance surfaces are extremely variable. In a review, Zeller et al. (2012) reports data types including expert opinion, detection data, relocation data, movement pathway data, genetic data, and combinations of these data types have been used to develop resistance surfaces. The analytical approaches used to generate

resistance surfaces are as variable as their data types and include models developed using expert opinion alone and a variety of resource selection functions (Zeller et al. 2012; Wade et al. 2015). Generally, resistance surfaces based on empirical data are considered superior to those based on expert opinion alone (Clevenger et al. 2002; Shirk et al. 2010). However, conservation decisions that consider landscape connectivity are often needed even when empirical data are not available (e.g. rare species; Zeller et al. 2012).

The Greater Sage-grouse (*Centrocercus urophasianus*; sage-grouse), a sagebrush (*Artemisia* spp.)-obligate gallinaceous bird, has undergone dramatic population declines and range contraction since European settlement of the American West (Western Association of Fish and Wildlife Agencies 2015; Schroeder et al. 2004). Movement between seasonal ranges is an important aspect of sage-grouse behavior and ecology for many sage-grouse populations (Figure 4.1; Gill and Glover 1965, Connelly et al. 2011a, Fedy et al. 2012). The species exhibits a variety of migration strategies to meet their life history requirements within each seasonal range (Connelly et al 2000). Seasonal ranges may include winter, nesting/early brood rearing, and summer/late brood rearing (Connelly et al 2011b). Breeding habitat, which includes nesting/early brood rearing and summer/late brood rearing habitats collectively, supports important sage-grouse vital rates such as nest and chick survival, which are leading drivers of sage-grouse population dynamics (Taylor et al. 2012; Dahlgren et al. 2016). Brood habitat, characterized by mesic resources such as riparian areas and wet meadows, is considered a limiting factor to sage-grouse distribution in the Great Basin (Figure 4.1; Donnelly et al. 2016).

A primary threat to sage-grouse is the reduction and fragmentation of suitable habitat in the Great Basin resulting from such factors as the expansion of conifers, particularly pinyon-juniper (*Pinus monophylla*-*J.* spp.), and invasive weeds into sagebrush ecosystems (Davies et al. 2011;

Baruch-Mordo et al. 2013; Miller et al. 2017). In the northwestern region of the semi-arid Intermountain West, western juniper has been expanding at a higher rate since the 1870s than past episodes during the Holocene (Miller and Wigand 1994; Miller and Tausch 2001). This rapid expansion is largely driven by climate and human altered fire regimes (Miller and Rose 1999; Miller et al. 2005) and as much as 90% of conifer expansion is occurring in the sagebrush ecosystems (Davies et al. 2011, Miller et al. 2011).

Recent studies have documented sage-grouse avoidance of conifers at low levels ($\leq 4\%$ cover; Severson 2016; Coates et al. 2017; Severson et al. 2017a). However, less is known about the effect of conifer expansion on sage-grouse movements and no published work exists that examines the influence of conifer removal on sage-grouse habitat connectivity. Using GPS data from marked sage-grouse in Nevada and California ($n = 233$), Prochazka et al. (2017) modeled survival rates of adult, yearling, and juvenile sage-grouse when encountering pinyon-juniper. Encounters with pinyon-juniper increased the risk of mortality across age classes, with juveniles experiencing the greatest risk, followed by yearlings and adults (Prochazka et al. 2017). These results support the hypothesis that perceived risk from visually acute predators serves as a mechanism for sage-grouse avoidance of conifers, which may serve as perch and nest sites for raptors (Dwight and Murphy 1973; Wolff et al. 1999; Prochazka et al. 2017). Models of landscape connectivity that quantify the change in resistance as a result of management actions such as conifer removal are needed to provide valuable insight into the efficacy of conifer removal for sage-grouse conservation and to tie these actions to the ecology of the bird.

Using a telemetry location dataset (2010–2017) from marked sage-grouse at a conifer removal study site in Oregon (see Study Area), my objectives were to 1) develop resistance surfaces for a pre-removal year (2010) and 3 post-removal years (2015–2017) that incorporate

conifer and conifer removal landscape variables, 2) quantify the change in landscape resistance between the pre- and post-removal years using post-removal GPS data from marked sage-grouse, and 3) quantify differences in resistance experienced by female sage-grouse with broods and those without broods.

Study Area

The majority of the study area was in Lake County, Oregon within the Bureau of Land Management (BLM) Lakeview Resource Area (Figure 4.2). The study area encompassed ~40,000 ha and extended ~15 km north and ~20 km south of Oregon Route 140. Elevation ranged from 1,408 to 2,061 m with a mean of 1,757 m. The dominant plant associations in the study area were low sagebrush (*A. arbuscula*)-bunchgrass and mountain big sagebrush (*A. tridentata* subsp. *vaseyana*)-bunchgrass. Mesic habitats used by sage-grouse during the late brood rearing period and summer in the study area were characterized by riparian vegetation and wet meadows.

Conifer woodlands comprised predominantly of western juniper covered approximately 43% (17,000 ha) of the study area prior to removals, of which, 14,000 ha was considered post-European settlement expansion into sagebrush habitats based on visual inspection of stand structure and tree morphology (Bureau of Land Management 2011). Conifer expansion can be described in 3 transitional phases: Phase I woodlands are dominated structurally and functionally by shrubs and herbs, Phase II woodlands exhibit codominance between conifers, shrubs and herbs, and Phase III woodlands are dominated by conifers (Miller et al. 2005). Of the area where conifers were removed by the Lakeview BLM, 16% was Phase I, 79% was Phase II, and 5% was Phase III (Bureau of Land Management 2011). The Natural Resource Conservation Service (NRCS) facilitated an additional 3,683 ha of removals on private lands within the study area.

The majority (81%) of removals were completed 2012–2014 (Table 4.1). Hand cutting was the primary removal technique employed (Bureau of Land Management 2011). When trees were sparse, cut trees were left where they fell or branches were lopped to < 1.2 m to minimize their utility as perch sites for avian predators after felling (Bureau of Land Management 2011). When trees were dense, felled individual trees were burned or slash was piled and burned. Cut trees were dried for ~1 year prior to burning and most burning took place during winter months when impacts from fire to non-target habitat were minimized (Bureau of Land Management 2011).

Methods

Sage-grouse capture and location data

Radio collars (22-g VHF, Advanced Telemetry Systems, Isanti, MN, USA) or rump-mounted GPS backpacks (22-g PTT-100 solar Argos/GPS PTT, Microwave Telemetry, Inc., Columbia, MD, USA) were fitted to female sage-grouse that were captured using spotlighting techniques (Giesen et al. 1983; Wakkinen et al. 1992) with the sample size goal of 40 individuals prior to the start of each breeding season (1 April; 2010–2017). Prior to 2015, only VHF transmitters were deployed and by 2017, a transition to GPS transmitters was completed and VHF transmitters were no longer in use. Females marked with VHF transmitters were located twice per week and locations were collected from females marked with GPS transmitters 4–5 times per day.

Resistance surfaces

Breeding season resistance surfaces for a pre-removal year (2010) and the years when GPS transmitters were deployed (2015–2017) were bounded by the minimum convex polygon of all breeding season locations across all years (2010–2017). These were generated using a resource selection function (RSF) estimated with mixed effects logistic regression (MELR) in the

lme4 package (Bates et al. 2015) in R (R Core Team 2015). The random effects component of MELR can account for the spatial and temporal autocorrelation of animal location data as well as improve model fit (Breslow and Clayton 1993; Gillies et al. 2006; Bolker et al. 2009). The *a priori* random effects structure of all models was random intercepts for the effects of year and individual sage-grouse. The random effect of year accounted for the annual variation in breeding season habitat driven by dynamics in herbaceous vegetation and conifer removals. The random effect of individual accounted for the spatial and temporal autocorrelation of location data from marked sage-grouse. Breeding season location data from all years of the project (2010–2017) and available locations randomly generated at a 3:1 ratio to pooled used locations from all years in ArcMap (ESRI 2011) were used to estimate the RSF. For details on model development and selection, see chapter 2.

Topographic variables considered for inclusion in *a priori* models included slope, aspect, elevation, landform, and ruggedness. Ruggedness (rugged) and landform were calculated in buffers of radii 56, 400, and 800 m around used and available points following Severson (2016). Ruggedness (or roughness) is a measurement of topographic heterogeneity (Riley et al. 1999) and landform is an index of landscape curvature (Bolstad and Lillesand 1992). Ruggedness values are ≥ 0 and larger values indicate greater topographic roughness (Riley et al. 1999). Positive values of landform indicate convex features (ridges), negative values indicate concave features (depressions), and values at or near 0 indicate flat features (Bolstad and Lillesand 1992). Vegetation variables included percent cover of conifers (conifer), shrubs (shrub), and forbs and grasses (herb) in buffers of radii 56, 400, and 800 m around used and available points following Severson (2016) and were derived from annual, 30-m rasters of percent cover (Jones et al. 2018). Conifer removal variables included distance to nearest conifer removal (m; removal-distance),

years since nearest conifer removal (removal-years), and change in conifer cover ($\Delta\text{conifer}$) since 2008 in buffers of radii 56, 400, and 800 m. Larger, positive values of $\Delta\text{conifer}$ indicated greater reduction in conifer cover.

The model fit of the most parsimonious model was assessed using the marginal (only fixed effects) and conditional (fixed and random effects combined) R^2 following Nakagawa and Schielzeth (2013) using the MuMIn package (Bartón 2014) in R (R Core Team 2015). Additionally, the variance explained by the random and fixed effects was calculated using the sjstats package (Lüdecke 2018) in R (R Core Team 2015). I report coefficient estimates and 95% confidence intervals for the predictor variables from the top model.

Predictive resistance surfaces for 2010 and 2015–2017 were calculated using the coefficients from the most parsimonious RSF mode where the resistance units (RU) for 30-m pixels was calculated as:

$$RU_{\text{pixel}_i} = \exp(\beta_1 x_{1i} + \beta_2 x_{2i} + \dots + \beta_k x_{ki})$$

For visualization, predicted resistance values for each 30-m pixel were assigned resistance categories of “low”, “medium-low,” “medium-high,” and “high” using the quartiles of the distribution of predicted values across all years with greater RU values indicating lower resistance (Morris et al. 2016).

Change in resistance after conifer removal

Brownian bridge movement models account for the time (and subsequent uncertainty) between successive locations when estimating utilization distributions and are recommended for home range estimation for serially correlated data from GPS transmitters (Horne et al. 2007; Walter et al. 2011). Breeding season BBMMs were calculated for all sage-grouse marked with GPS transmitters (2015–2017) using the BBMM package (Nielson et al. 2013) in R (R Core

Team 2015). Rasters representing the 50% and 95% BBMM contours were derived from BBMMs for individual sage-grouse (Figure 4.3). I used the 95% contour to represent the broadest extent of sage-grouse breeding season home range and the 50% contour to represent the core breeding season home range. I calculated the mean differences and percent changes in RU for the 30-m pixels in the contour rasters between 2010 and the respective post-removal year for each sage-grouse. Additionally, the mean differences and percent changes in RU between females with broods (≥ 1 chick at 14 days post-hatch) and females without broods are reported.

Rasterized, straight line movement paths during the breeding season for each sage-grouse marked with a GPS transmitter were generated in ArcMap (ESRI 2011; Figure 4.3). I used these paths to model finer scale landscape resistance experienced by sage-grouse during the breeding season as well as resistance more closely tied individual movements and seasonal migrations, rather than home range. As described above, mean differences and percent changes RU along these paths between 2010 and each sage-grouse's post removal year are reported as well as for females with broods and females without broods.

Results

Resistance surfaces

Two-hundred and thirty-two female sage-grouse were monitored during the breeding season in the study area, 2010–2017. The coefficients for the most parsimonious RSF model indicated lower landscape resistance (higher relative probability of use) at higher elevations ($\beta = 0.001$, 95% CI: 0.001–0.002), more north facing aspects ($\beta = <0.001$, 95% CI: <0.001 –0.001), greater landform-800 (ridges; $\beta = 1.971$, 95% CI: 1.176–2.766), lower rugged-56 ($\beta = -0.012$, 95% CI: -0.013–0.011), greater herb-800 ($\beta = 0.002$, 95% CI: 0.002–0.002), greater shrub-400 ($\beta = 0.010$, 95% CI: 0.008–0.011), less conifer-56 ($\beta = -0.217$, 95% CI: -0.224–0.210), areas in or near

older conifer removal areas ($\beta = 0.235$, 95% CI: 0.218–0.251), areas closer to conifer removal areas ($\beta = <-0.001$, 95% CI: <-0.001 – <-0.001), and for change in conifer cover $\pm 10\%$ since 2008 ($\beta = -0.055$, 95% CI: -0.059–0.040). The most influential (largest, standardized magnitude) predictor variables were conifer-56 and removal-distance (Appendix table A4). The conditional and marginal R^2 of the model were 0.409 and 0.625, respectively. Of the variance explained by the fixed and random effects combined, the fixed effects explained 50.0%, the random effect of individual explained 1.3%, and the random effect of year explained 48.7%. Resistance surfaces generally depicted an increase in connectivity from 2010 to the post-removal period 2015–2017 (Figure 4.4).

Change in resistance after conifer removal

Brownian bridge movement models and movements paths were generated from the breeding season location data for 69 female sage-grouse marked with GPS transmitters. Annual sample sizes were 13, 27, and 29 for 2015, 2016, and 2017, respectively. Of these marked sage-grouse, 14 had broods with at least 1 chick at 14 days post-hatch with annual sample sizes of 5, 4, and 5 for 2015, 2016, and 2017, respectively. The mean change in resistance for 95% BBMM contours in the post-removal period (2015–2017) compared to the pre-removal year (i.e., 2010) was -61.4 RU (-73%), indicating a reduction in landscape resistance since 2010 for all females regardless of brood status (Figure 4.5). The change in resistance for females without broods was -65.3 RU (-78%) and for female with broods was -40.0 RU (-46%; Figure 4.5). At the 50% BBMM contour scale, the change in resistance was -57.7 (-76%) for females regardless of brood status (Figure 4.5). The change in resistance for females without broods was -61.1 (-81%) and for female with broods was -39.9 (-52%; Figure 4.5).

The mean change in resistance along movement paths from 2010 to the post-removal period, regardless of brood status, was -31,951 RU (-4,523%; Table 4.3A). The large magnitude of this change in the combined data set was driven by movement paths for females without broods (-40,556; -4,735%; Table 4.3A). The change for females with broods was -183.6 RU (-120.7%; Table 4.3A).

Females with broods experienced greater resistance than those without broods across all metrics and across all post-removal years. At the 95% BBMM contour scale, the raw annual mean differences (no brood-brood) in resistance and corresponding percent differences were -11.0 RU (-11%), -7.4 RU (-5%), and -16.4 RU (-11%) for 2015, 2016, and 2017, respectively, indicating that the landscape utilized by females with broods had a higher resistance than that used by females without broods (Figure 4.6). Differences at the 50% BBMM contour scale were -8.7 RU (-9%), -19.8 RU (-18%), and -23.0 RU (-17%) for 2015, 2016, and 2017, respectively (Figure 4.6). Differences in mean resistance along movement paths were -83.4 RU (-41%), -85,165 RU (-12,980%), and -2,494 RU (-1,155%) for 2015, 2016, and 2017, respectively (Table 4.3B).

Discussion

My findings suggest that conifer removal reduced landscape resistance of breeding season habitat, but disproportionately benefited habitat utilized by females without broods versus those with broods. Landscape resistance occurs at multiple scales for sage-grouse and has been investigated range-wide (Knick et al. 2013; Row et al. 2018), regionally (Shirk et al. 2010; Row et al. 2015), and at finer spatial extents (i.e. individual study areas such as that of my study; Harju et al. 2013). My study highlights the finer scale processes that collectively influence regional and range-wide dynamics in landscape connectivity. In a state-wide analysis of genetic

resistance in Wyoming, model selection indicated that large-scale (radii of 6,440 or 17,330 m) patterns in habitat structure, specifically nesting and winter habitat with high resistance, were the most influential drivers of landscape connectivity (Row et al. 2015). However, findings of my study indicated that finer scale changes (1–200 ha) in habitat structure due to conifer removal had dramatic effects on the landscape resistance in the project area (Figure 4.4). Given that sage-grouse exhibit avoidance of conifers at low canopy levels (Severson 2016; Coates et al. 2017; Severson et al. 2017a; chapter 2), the value of conifer removals at finer spatial scales should not be overlooked. Additionally, the most supported scale of conifer cover as a predictor variable in this analysis was the finest spatial scale: 56-m (~ 1 ha; Table 4.2; chapter 2). This indicated that sage-grouse perceived the landscape in relation to conifers at a finer scale than previously documented on this project (Severson 2016; Severson et al. 2017b) and that broader scale patterns in conifer and conifer removal may not explain the behavioral responses of sage-grouse to these variables during the breeding season. This fine scale pattern in selection holds for lesser prairie chickens (*Tympanuchus pallidicinctus*), which avoided conifers at the 16 ha scale for nest sites and at the 36 ha scale seasonally (Lautenbach et al. 2017). While sage-grouse may select habitat at fine scales, the importance of large-scale removals should be not discounted as sage-grouse require large tracts of intact habitat to support their life history and seasonal habitat requirements. The collective scale of removals employed in my study area (13,851 ha; ~31% of the Treatment) was adequate to provide a variety of connected, habitat patches for sage-grouse to select.

The varied migratory strategies of sage-grouse populations (and individual heterogeneity) to meet their life-history needs requires land managers to consider perturbations that may affect connectivity between seasonal habitats (Gill and Glover 1965, Connelly et al. 2011a, Fedy et al.

2012). Because conifer presence can limit connectivity, effective, targeted conifer removal should be considered when there is a need to increase potential movement pathways between seasonal habitats. With the increasing availability of remotely sensed products and the increased utilization of GPS technology to monitor sage-grouse movement and habitat use, tools necessary to identify these pathways are becoming widely available (Reinhardt et al. 2017). A recent case study demonstrated the use of the Marxan framework to optimize conifer removal in Oregon and incorporated sage-grouse movement between breeding and brood-rearing habitats in addition to improving seasonal habitat quality as model priorities (Reinhardt et al. 2017). I believe the approach employed by Reinhardt et al. (2017) is more comprehensive in addressing the breeding biology needs of sage-grouse than lek-centric models or models that only consider certain seasonal habitats, particularly at finer spatial scales.

As Prochazka et al. (2017) demonstrated, there are demographic costs to sage-grouse vital rates when encountering conifers. Adult and yearling survival are important drivers of sage-grouse population dynamics (Taylor et al. 2012; Dahlgren et al. 2016; chapter 1). These vital rates could be affected by encounters with conifer during seasonal migrations in addition to conifer expansion in nesting/early brood and summer/late brood habitats. I have demonstrated that the 2 vital rates with the largest impact on dynamics in population growth rates in the study area were juvenile and adult survival (chapter 1). Specifically, increases in these vital rates contributed to increases in population growth rates in the study area relative to a “control” area without conifer removal. The matrix of habitat that sage-grouse navigate during seasonal migration in landscapes affected by conifer expansion should not be discounted when targeting removals.

The differential effects of conifer removal and the subsequent reduction in landscape resistance on females with broods versus those without broods was a novel finding (Table 4.3A; Figures 4.5, 4.6). This pattern may have implications for demographic rates (Prochazka et al. 2017) and may have been driven by differential mobility. Females tend to move their broods primarily on foot for the first 5 weeks post-hatch until they are capable of strong, sustained flight (Schroeder et al. 1999). As females walk with their chicks to mesic areas for late brood habitat, steep and rugged topography may limit the movement path and force them utilize terrain which may be more heavily impacted by conifer. Alternatively, females without broods are able to navigate by flying and walking and experience different landscape resistance when migrating. Females with broods move at a slower pace to summer habitat than females without broods (Connelly et al. 1988). Fortunately, BBMM models account for the time between locations as part of the estimated area of use. When encountering conifers, the slower pace of females with broods may have inflated the BBMM density in those areas relative to faster moving females without broods, driving the differences in resistance within BBMM contour polygons. The magnitude of differences was larger along movement pathways (Table 4.3A). Although, the movement pathways modeled simple, straight line travel between known locations and assumed pseudo-locations along each leg of the pathway (Harju et al. 2013), they may have better captured the resistance experienced by sage-grouse during seasonal migration. These differences further support the hypothesis that differences in mobility may have driven the differential reductions in landscape resistance in the portions of the study area used by females with and without broods. These patterns held when comparing females with and without broods in the post removal landscape with females without broods utilizing breeding season habitat with lower resistance than those with broods (Table 4.3B; Figure 4.6). Regardless of the mechanism, the

elevated impacts of landscape resistance driven by conifers on females with broods highlighted the potential demographic impacts of conifer expansion through unbalanced impacts on these individuals. Assessing the heterogeneity in landscape resistance experienced by individuals (e.g., females with and without broods) is essential for a robust understanding of the connections between animal behavior and functional, landscape connectivity (Bélisle 2005).

A fundamental assumption of resistance surfaces based on RSFs is that lower probability of use habitat is more resistant to movement. The strength of this approach is that it infers resistance from actual animal habitat use data rather than non-empirical data sources such as expert opinion (Zeller et al. 2012; Wade et al. 2015). However, it may underestimate habitat resistance if sage-grouse are actually selecting resistant habitat. Coates et al. (2017) used telemetry data to evaluate pinyon-juniper impacts on sage-grouse along the Nevada/California border. Findings provided clear evidence that local sage-grouse distributions and demographic rates are negatively influenced by pinyon-juniper, especially in areas of higher primary productivity but relatively low conifer cover. Furthermore, they suggest that these productive, early-phase woodland sites may function as ecological traps that are attractive for grouse but adversely affect population vital rates. While these habitats might not be resistant to sage-grouse movement, they may have fitness consequences which could be considered another form of landscape resistance (Zeller et al. 2012).

My work provided initial insights into how connectivity may change with management and subsequent sage-grouse movements. Future work linking resistance to sage-grouse vital rates such as chick survival and adult survival would provide valuable insight into the fitness consequences of landscape connectivity. In addition to increasing usable space for sage-grouse (Severson et al. 2017c; chapter 2), conifer removal can increase vital rates and affect sage-grouse

population dynamics (Severson et al. 2017b; chapter 1). A logical next step is to model vital rates using covariates derived from the annual resistance layers, further linking impacts of conifer expansion and removal to sage-grouse fitness and identifying the degree to which landscape connectivity affects demography.

The findings of my research demonstrated the efficacy of conifer removal for increasing landscape connectivity in the landscape affected by post-European settlement conifer expansion in my study area. Although these effects were measured at a finer scale relative to regional and range-wide analyses, the benefits of conifer removal may extend to larger scales and removals can be targeted to have multi-scale benefits (Reinhardt et al. 2017). While the published literature is flooded with examples of reduced connectivity due to habitat fragmentation, my findings were an encouraging example of a reversal in this trend through conservation action. There is an increasing body of literature documenting the benefits for sage-grouse space use and demography, and the collective spatial extent and area of the ongoing conifer removal efforts in the Great Basin is increasing genetic connectivity as well (Row et al. 2018).

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Table 4.1. Annual and cumulative area of conifers removed on public and private lands at a conifer removal study area, 2010–2017, Lake County, Oregon, USA.

Year	Annual Hectares Removed¹	Cumulative Hectares Removed (% of total) ¹
2010	0	185 (1%) ²
2011	240	425 (3%)
2012	710	1135 (8%)
2013	5113	6248 (45%)
2014	4929	11177 (81%)
2015	359	11536 (83%)
2016	656	12192 (88%)
2017	1659	13851 (100%)

¹Includes removals within 3 km of the study area boundary

²Includes area removed in the treatment area 2007–2009

Table 4.2. Coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) breeding season (April–July) resource selection, 2010–2017, Lake County, Oregon, USA.

Predictor Variable	β	0.025	0.975
Intercept	-2.211	-3.151	-1.271
Elevation (m)	0.001	0.001	0.002
landform-800	1.971	1.176	2.766
aspect	<0.001	<0.001	0.001
rugged-56	-0.012	-0.013	-0.011
herb-800 (%)	0.002	0.002	0.002
shrub-400 (%)	0.010	0.008	0.011
conifer-56 (%)	-0.217	-0.224	-0.210
removal-distance (m)	<-0.001	<-0.001	<-0.001
removal-years	0.235	0.218	0.251
Δ conifer-800 (%)	-0.037	-0.053	-0.021
Δ conifer-800 ² (%)	-0.055	-0.059	-0.04

Table 4.3. Change in landscape resistance from pre-conifer removal (2010) to post-conifer removal (2015–2017; A) and difference in resistance between females with and without broods (no brood-brood; B) along breeding season (April–July) movement paths for female Greater Sage-grouse (*Centrocercus urophasianus*) marked with GPS transmitters post-conifer removal (2015–2017) at a conifer removal study area, Lake County, Oregon, USA.

A		
Change in resistance pre–post-conifer removal		
Brood status	Change in resistance	Percent change
Females with broods	-183.6	-120.7
Females without broods	-40556.6	-4735.2
All females	-31951.0	-4523.1

B		
Difference in resistance between hens with and without broods		
Year	Difference in resistance	Percent difference
2015	-83.4	-41.1
2016	-85165.9	-12980.6
2017	-2494.5	-1155.4

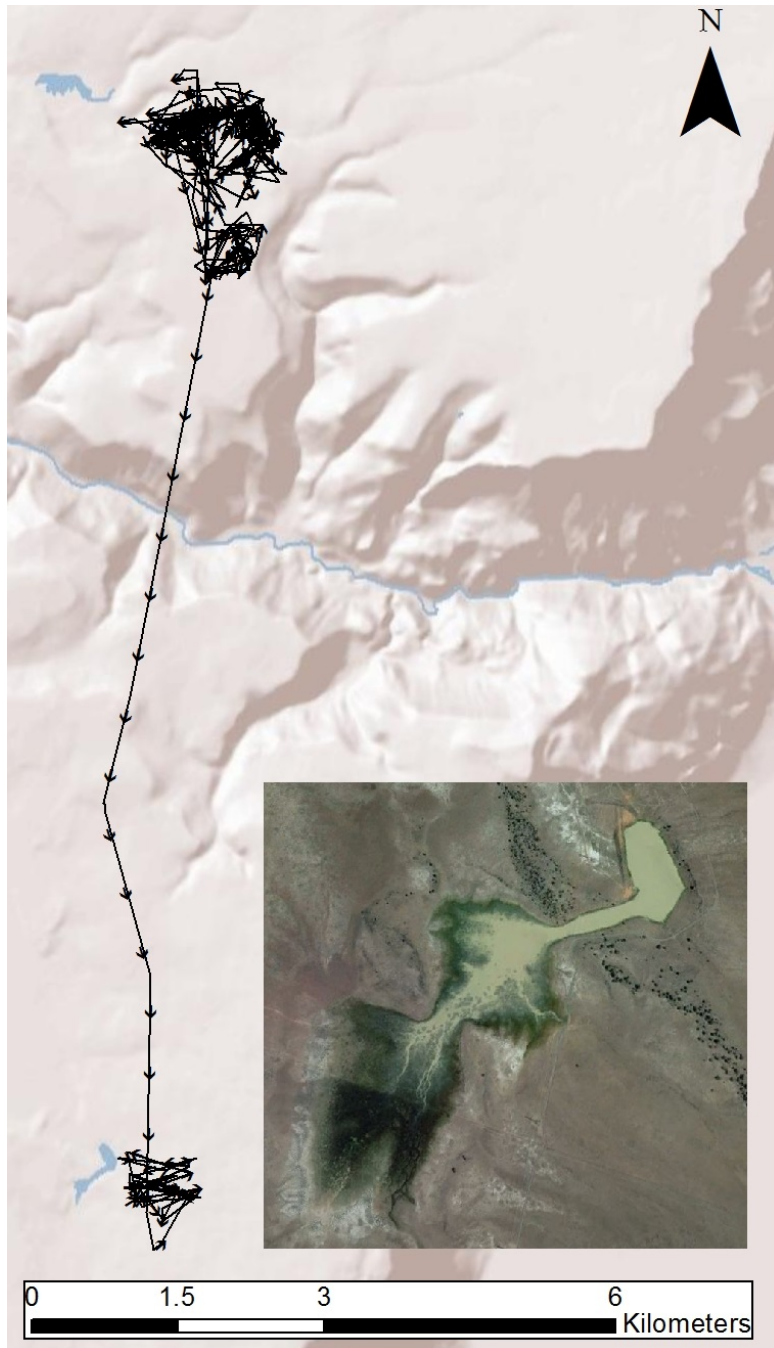


Figure 4.1. Example of a seasonal migration from nesting/early brood (north) to summer/late brood habitat (south) for a Greater Sage-grouse (*Centrocercus urophasianus*) marked with a GPS transmitter at a conifer removal study site, Lake County, Oregon, USA. The inset image is an aerial photo of the reservoir immediately west of the locations at the southern end of the migration and is an example of mesic habitat occupied during the summer months in the study area.

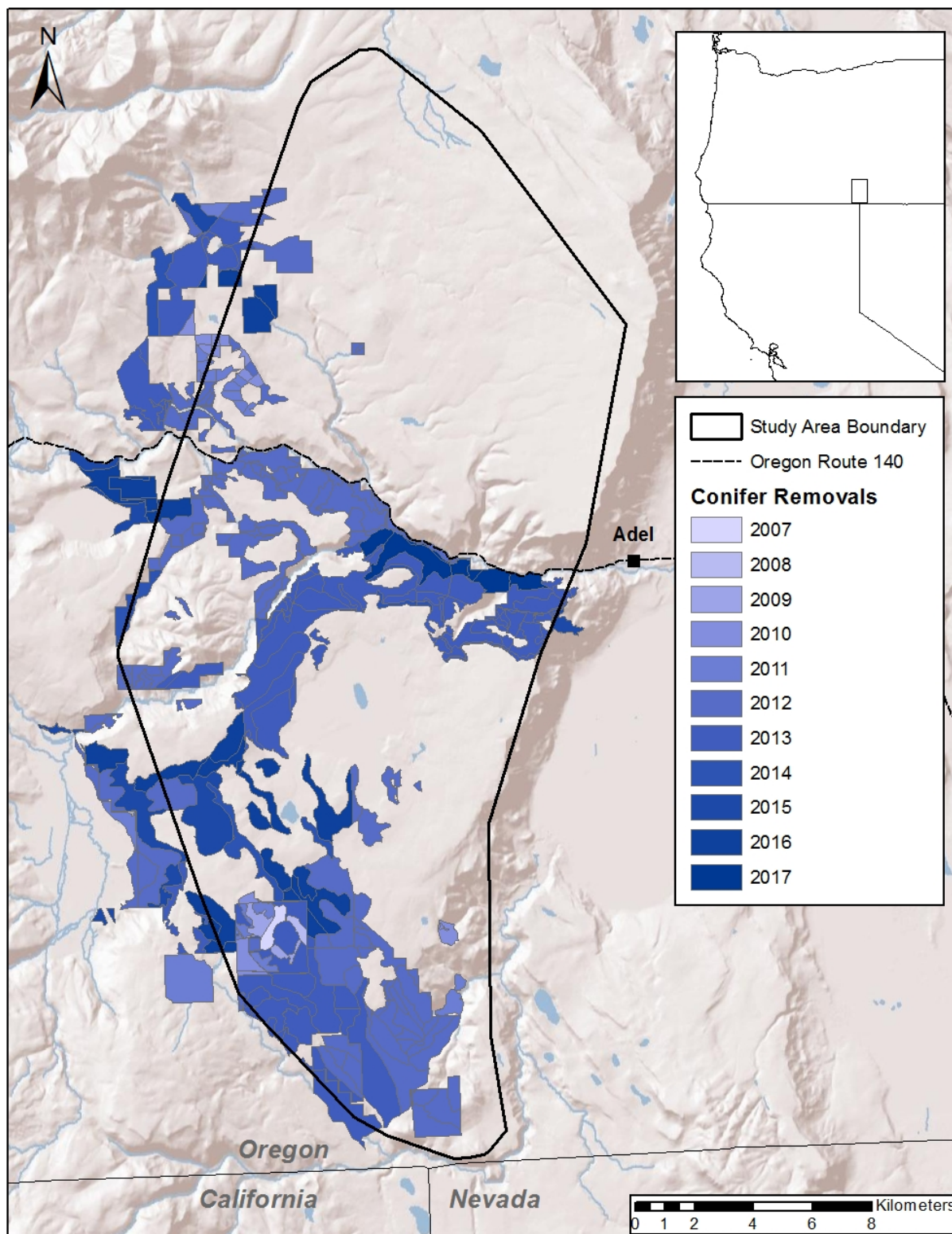


Figure 4.2. Study area for research on landscape resistance for Greater Sage-grouse (*Centrocercus urophasianus*), 2010–2017, Lake County, Oregon, USA.

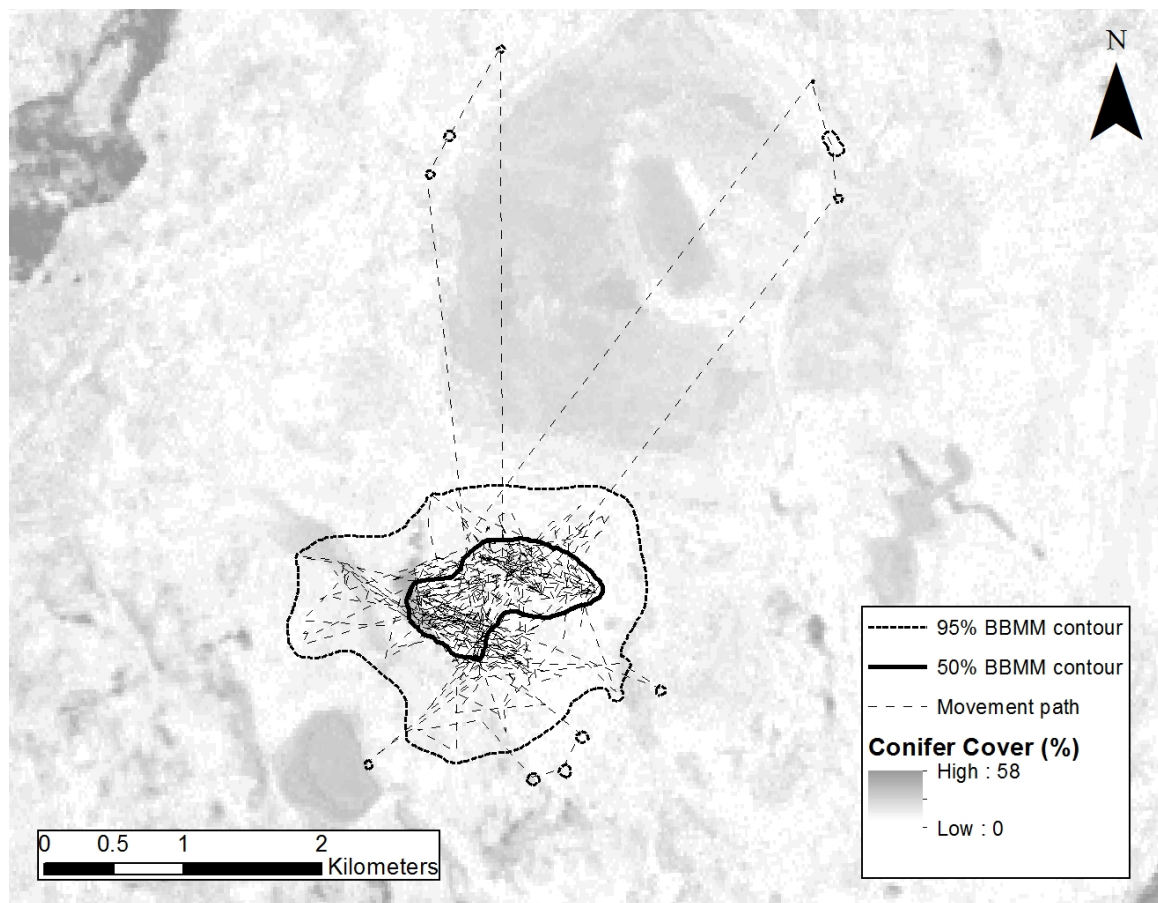


Figure 4.3. Example of movement paths and contours from Brownian bridge movement models (BBMM) for Greater Sage-grouse (*Centrocercus urophasianus*), Lake County, Oregon, USA.

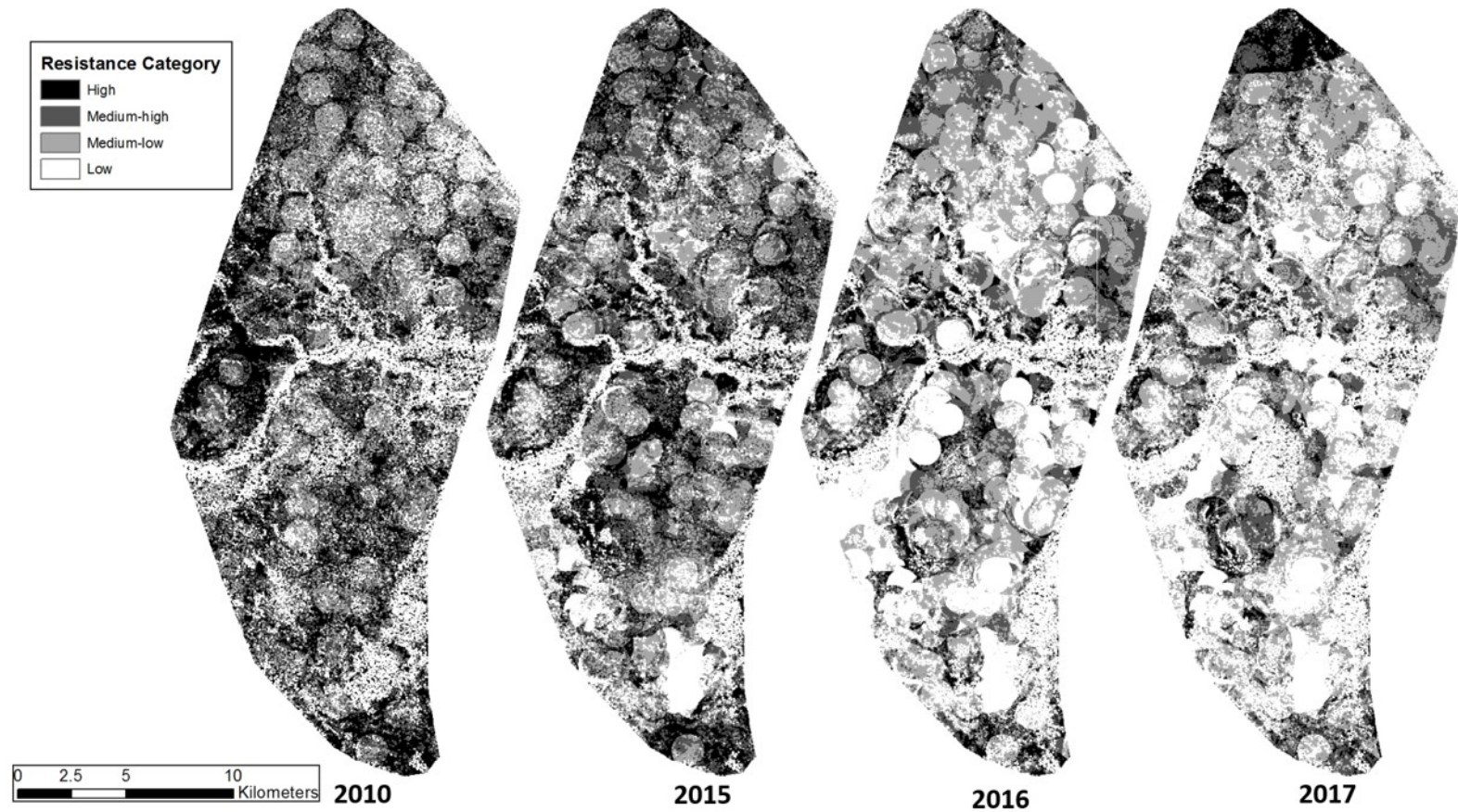


Figure 4.4. Landscape resistance surfaces for Greater Sage-grouse (*Centrocercus urophasianus*) at a conifer removal study area, Lake County, Oregon, USA. The increase in resistance at the extreme northern end of the study area in 2017 was driven by proximate and recent conifer removals in 2016. The circular patterns on the resistance surfaces are relicts of the predictor variables measured in buffers.

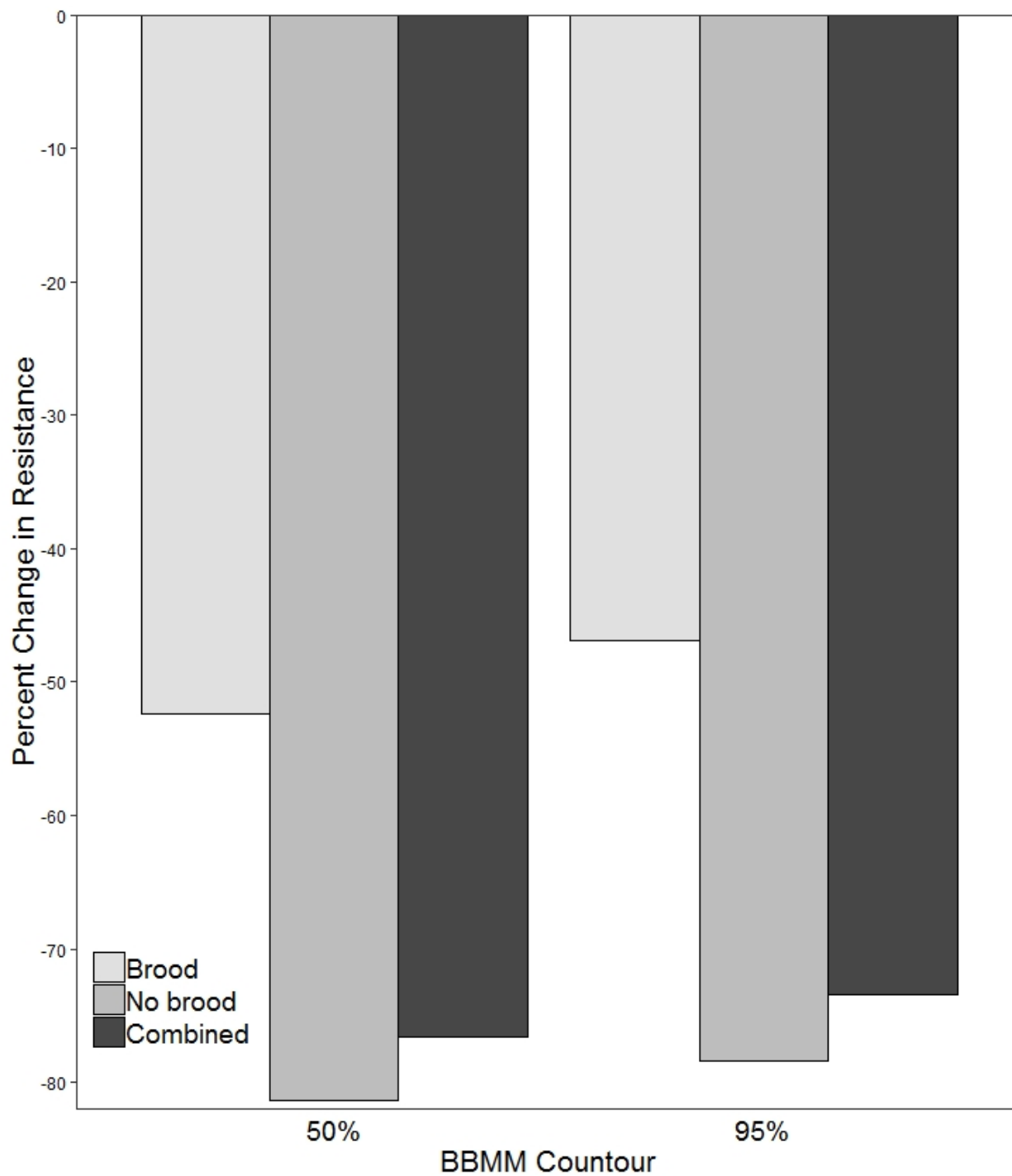


Figure 4.5. Percent change in landscape resistance since 2010 within 50% and 95% contours from Brownian bridge movement models for female Greater Sage-grouse (*Centrocercus urophasianus*) marked with GPS transmitters post-conifer removal (2015–2017) at a conifer removal study area, Lake County, Oregon, USA. Comparison were made for females with broods (≥ 1 chick at 14 days post-hatch), without broods, and regardless of brood status.

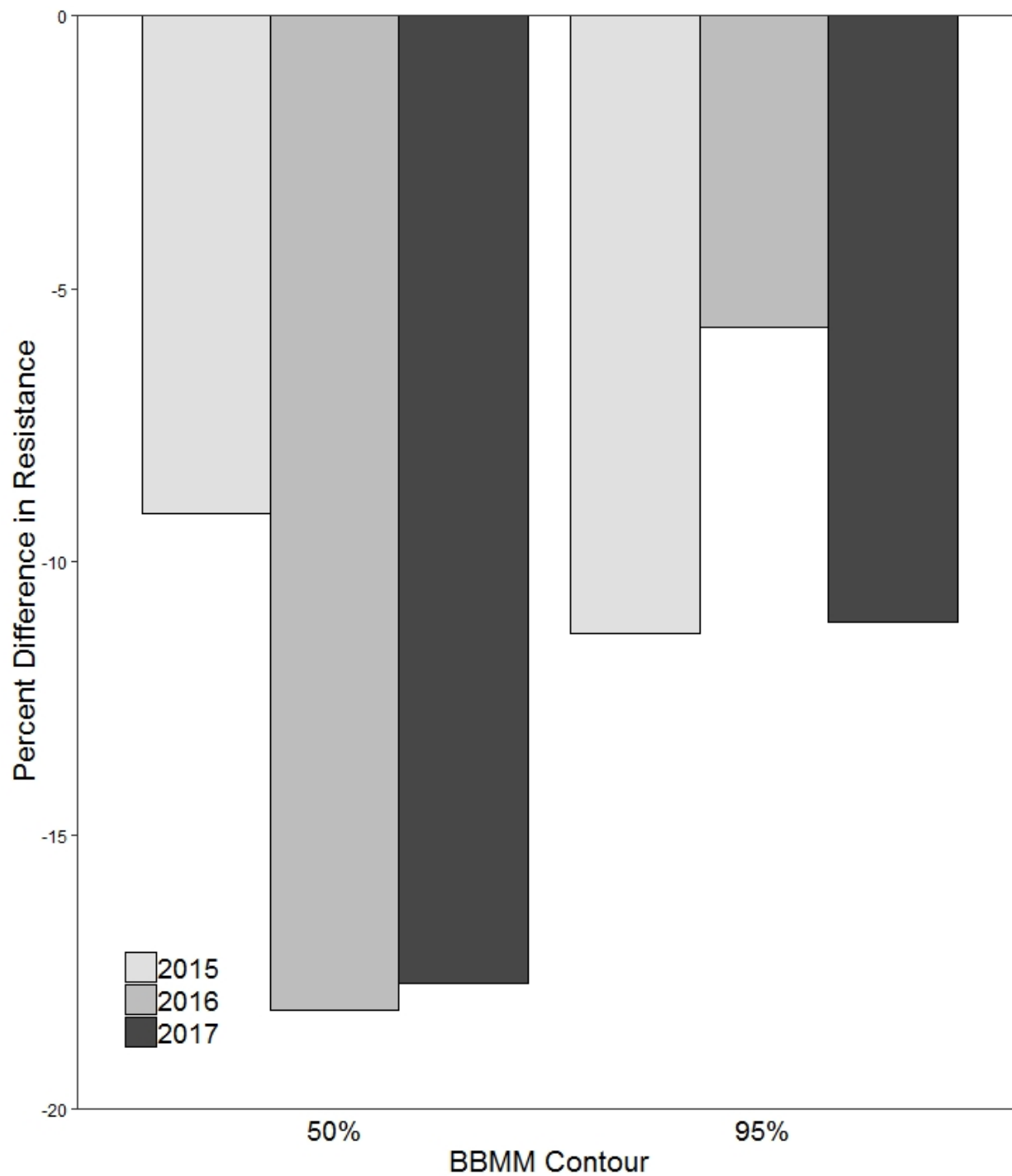


Figure 4.6. Percent difference in landscape resistance between female with broods (≥ 1 chick at 14 days post-hatch) and without broods within 50% and 95% contours from Brownian bridge movement models for female Greater Sage-grouse (*Centrocercus urophasianus*) marked with GPS transmitters post-conifer removal (2015–2017) at a conifer removal study area, Lake County, Oregon, USA. Differences are in reference to females with broods (no brood-brood).

5 – CONCLUSION

Although conifer expansion is a widespread and serious threat to sagebrush ecosystem function in the Great Basin (Chambers and Wisdom 2009; Davies et al. 2011; Baruch-Mordo et al. 2013), my findings indicated that large-scale conifer removals, such as those employed in this project, may be an effective method of restoring these imperiled ecosystems. My findings may support land managers that are continuing to employ these landscape restoration methods and benefit the species that inhabit landscapes affected by post-European settlement conifer expansion.

My study is the first to integrate lek and vital rate data to quantify the population response of sage-grouse to conservation actions and specifically, conifer removal. The population response as estimated in a Bayesian framework provided evidence that targeted conifer removal may serve as a beneficial conservation tool and contribute to increasing sage-grouse populations. If sage-grouse serve as indicators of sage-brush ecosystem health, the population responses measured in my study may be indicative of the efficacy of the conifer management actions for other species in the Treatment. Previous research indicated that the benefits of conifer removal can extend to other terrestrial vertebrates such as sagebrush obligate songbirds (Donnelly et al. 2017; Holmes et al. 2017) and mule deer (*Odocoileus hemionus*; Bender et al. 2013, Bergman et al. 2014a, b, 2015). Using sage-grouse as a surrogate and indicator of sagebrush ecosystem function, findings of my study highlight the efficacy of targeted conifer removal as a tool for ecosystem restoration and conservation in the Great Basin.

The impact of conifer expansion in shrub and grassland ecosystems in North America is not unique to sage-grouse and extends to Greater Prairie-Chickens (*Tympanuchus cupido*) and Lesser Prairie-Chickens (*T. pallidicinctus*). Conifer cover is an influential predictor of Greater

Prairie-Chicken lek presence (Merill et al. 1999; Niemuth 2003) and one study found 9% conifer cover as a threshold to suitability of prairie habitat for lek sites (Gregory et al. 2011). In addition to influencing probability of lek occurrence and occupation, increased conifer cover is associated with lower probability of nesting and reduced nest survival (Matthews et al. 2013; Hovick et al. 2015). Lesser Prairie-Chickens also avoid conifers year-round and select nest sites in areas with low tree densities (Boggie et al. 2017; Lautenbach et al. 2017).

My study represents the first long-term, landscape-scale analysis of sage-grouse habitat selection in relation to conifer removals. As conifer removals continue across the Great Basin, findings of my research provide valuable insight into the potential response of sage-grouse to these broad-scale management actions which historically lacked empirical evidence for their efficacy (U.S. Fish and Wildlife Service 2015). Conifer removal projects are variable and occur in a variety of landscapes, even within the Great Basin, and caution should be used when drawing inference from these results to other projects. However, one goal of this work was that these findings might aid in planning future conifer removals and provide insight as to the expected response of sage-grouse. The removals in the project area targeted Phase I and II conifers, that were primarily hand-cut (i.e., with chainsaws) and slash removed when necessary (Bureau of Land Management 2011). When fire was used to remove slash, it was limited to the slash piles and individual trees (i.e. pile burning). Burning occurred during winter and early spring months when the risk of fire spreading to non-target fuels was minimal. Conifers that established prior to European settlement were not removed (Bureau of Land Management 2011). Inference from my research may be most appropriately made to other removal projects that target Phase I and II conifers with low disturbance techniques.

Landscape resistance occurs at multiple scales for sage-grouse and has been investigated range-wide (Knick et al. 2013), regionally (Shirk et al. 2010; Row et al. 2015), and at finer spatial extents (Harju et al. 2013). My study highlights the finer scale processes that collectively influence regional and range-wide dynamics in landscape connectivity. In a state-wide analysis of genetic resistance in Wyoming, model selection indicated that large-scale (radii of 6,440 or 17,330 m) patterns in habitat structure, specifically nesting and winter habitat with high resistance, were the most influential drivers of landscape connectivity (Row et al. 2015). However, findings of my study indicated that finer scale changes in habitat structure due to conifer removal had dramatic effects on landscape resistance in the project area. Given that sage-grouse exhibit avoidance of conifers at low canopy levels (Severson 2016; Coates et al. 2017; Severson et al. 2017a; chapter 2), effects of conifer removals at finer spatial scales should not be overlooked. Additionally, the most supported scale of conifer cover as a predictor variable in this analysis was the finest spatial scale (56-m; ~ 1 ha). This finding indicated that sage-grouse may have perceived the landscape in relation to conifers at a finer scale than previously documented (Severson 2016; Severson et al. 2017b) and that broader scale patterns in conifer and conifer removal may not explain the behavioral responses of sage-grouse to these variables during the breeding season. This fine scale pattern in selection holds for Lesser Prairie-Chickens, which avoided conifers at the 16 ha scale for nest sites and at the 36 ha scale seasonally (Lautenbach et al. 2017). While sage-grouse may select habitat at fine scales, the importance of large-scale removals should be not overlooked as sage-grouse require large tracts of intact habitat to support their life history and seasonal habitat requirements. The collective scale of the removals employed in my study area (13,851 ha; ~31% of the Treatment) was adequate to provide a variety of connected, habitat patches for sage-grouse select.

My work provided initial insights into how connectivity may change with management. In addition to increasing usable space for sage-grouse (Severson et al. 2017c; chapter 2), conifer removal can increase vital rates and affect sage-grouse population dynamics (Severson et al. 2017b; chapter 1). Future work linking resistance to sage-grouse vital rates such as chick survival and adult survival would provide valuable insight into the fitness consequences of landscape connectivity.

Findings of my research demonstrated the efficacy of conifer removal for increasing landscape connectivity in landscapes affected by post-European settlement conifer expansion in the project area. Although these effects were measured at a finer scale relative to regional and range-wide analyses, benefits of conifer removal may extend to larger scales and removals can be targeted to have multi-scale benefits (Reinhardt et al. 2017). While the published literature is replete with examples of reduced connectivity due to habitat fragmentation, my findings were an example of a reversal in this trend through conservation action. There is an increasing body of literature documenting the benefits for sage-grouse space use and demography, and the collective spatial extent and area of the ongoing conifer removal efforts in the Great Basin could ultimately increase genetic connectivity as well.

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APPENDIX A

APPENDIX A– Standardized coefficients from resource selection models

Table A1. Standardized coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) nest site selection in a treatment area with conifer removal and a control area, 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA.

Control				Treatment			
Predictor Variable	β	0.025	0.975	Predictor Variable	β	0.025	0.975
Intercept	-0.195	-0.433	0.043	Intercept	-0.163	-0.471	0.145
shrub	0.836	0.559	1.114	shrub	1.062	0.793	1.331
K-forb	0.41	0.159	0.662	annual	0.294	0.060	0.528
aspect	0.322	0.0861	0.558	landform-400	0.256	0.050	0.461
annual	-0.428	-0.883	0.027	conifer-400	-0.572	-0.832	-0.312
conifer-400	-0.511	-0.775	-0.248				

Table A2. Standardized coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) nest site selection in a treatment area with conifer removal incorporating conifer removal variables, 2010–2017, Lake County, Oregon, USA.

Predictor Variable	β	0.025	0.975
Intercept	-0.316	-0.785	0.164
shrub	1.130	0.847	1.412
removal-years	0.451	0.149	0.813
Δ conifer-800	0.403	-0.458	1.263
landform-400	0.269	0.055	0.483
annual	0.241	0.011	0.471
conifer-400	-0.403	-0.688	-0.117
Δ conifer-800 ²	-1.440	-2.727	-0.154

Table A3. Standardized coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) breeding season (April–July) resource selection in a treatment area with conifer removal and a control area, 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA.

Control				Treatment			
Predictor Variable	β	0.025	0.975	Predictor Variable	β	0.025	0.975
Intercept	-1.230	-1.353	-1.108	Intercept	-1.068	-1.251	-0.884
elevation	0.425	0.405	0.444	herb-800	0.391	0.385	0.413
shrub-400	0.297	0.281	0.314	landform-800	0.124	0.105	0.143
landform-400	0.202	0.180	0.224	aspect	0.069	0.057	0.083
aspect	0.197	0.179	0.214	shrub-400	0.040	0.027	0.055
herb-56	-0.098	-0.115	-0.080	rugged-56	-0.237	-0.262	-0.215
rugged-400	-0.560	-0.589	-0.531	elevation	-0.283	-0.303	-0.27
conifer-56	-0.798	-0.829	-0.768	conifer-56	-0.903	-0.943	-0.875

Table A4. Standardized coefficients and 95% confidence intervals for Greater Sage-grouse (*Centrocercus urophasianus*) breeding season (April–July) resource selection in a treatment area with conifer removal incorporating conifer removal variables, 2010–2017, Lake County, Oregon, USA.

Predictor Variable	β	0.025	0.975
Intercept	-0.461	0.461	0.317
removal-years	0.310	0.288	0.332
herb-800	0.298	0.297	0.327
shrub-400	0.110	0.092	0.122
elevation	0.099	0.087	0.127
landform-800	0.045	0.026	0.064
aspect	0.034	0.022	0.050
Δ conifer-800	-0.080	-0.117	-0.046
rugged-56	-0.321	-0.345	-0.288
Δ conifer-800 ²	-0.954	-1.044	-0.912
removal-distance	-0.967	-1.016	-0.958
conifer-56	-1.131	-1.180	-1.103

APPENDIX B

APPENDIX B– Vegetation predictor variables for resource selection models

Table B1. Means and standard deviations (in parentheses) of vegetation variables measured at Greater Sage-grouse (*Centrocercus urophasianus*) nest sites (NEST) and random points (RAND) in a treatment area with conifer removal, 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA.

Vegetation Variable	2010		2011		2012		2013	
	NEST	RAND	NEST	RAND	NEST	RAND	NEST	RAND
Key forb cover (%)	1.2 (1.3)	1.8 (2.5)	2.2 (3.5)	2.9 (2.8)	1.2 (1.1)	2.2 (1.9)	1.1 (0.9)	1.6 (1.6)
Other forb cover (%)	1.4 (1.0)	2.4 (2.5)	3.4 (3.0)	2.8 (2.8)	2.3 (1.8)	3.4 (7.1)	1.7 (2.3)	2.0 (1.9)
Species richness key forbs	3.4 (1.6)	3.0 (1.9)	2.7 (1.7)	2.8 (1.5)	2.7 (1.6)	2.7 (1.6)	2.6 (1.6)	3.0 (2.1)
Annual grass cover (%)	0.3 (0.6)	0.4 (0.9)	0.5 (0.7)	0.7 (1.2)	4.2 (10.1)	1.6 (3.1)	1.0 (2.3)	0.4 (0.9)
Perennial grass cover (%)	9.3 (7.9)	7.4 (7.5)	6.4 (4.4)	8.0 (9.0)	5.3 (3.0)	5.1 (3.7)	6.5 (4.8)	7.1 (14.0)
Shrub cover (%)	37.3 (14.0)	24.7 (15.0)	41.5 (17.7)	41.5 (17.7)	47.4 (14.3)	47.3 (14.3)	37.4 (18.4)	23.3 (18.7)
Conifer cover within 400m (%)	4.7 (1.5)	5.9 (3.2)	7.3 (1.2)	6.7 (1.4)	5.5 (2.7)	6.7 (2.3)	4.9 (2.1)	5.1 (2.4)

Table B1. *Continued*

Vegetation Variable	2014		2015		2016		2017	
	NEST	RAND	NEST	RAND	NEST	RAND	NEST	RAND
Key forb cover (%)	1.1 (2.1)	1.2 (1.7)	1.8 (2.2)	2.1 (1.8)	3.0 (4.8)	2.1 (2.6)	4.4 (6.1)	9.9 (7.9)
Other forb cover (%)	1.3 (1.3)	1.4 (1.7)	1.4 (1.0)	2.8 (3.4)	4.5 (5.9)	5.0 (6.6)	6.0 (7.5)	5.0 (6.7)
Species richness key forbs	1.5 (1.4)	2.1 (1.9)	3.2 (1.7)	3.7 (2.1)	3.4 (2.2)	2.6 (1.9)	2.5 (1.7)	3.5 (1.6)
Annual grass cover (%)	0.8 (1.2)	0.7 (1.0)	1.1 (1.4)	0.5 (0.9)	4.6 (8.1)	3.5 (7.1)	10.5 (13.5)	4.8 (7.9)
Perennial grass cover (%)	6.7 (5.4)	6.6 (14.8)	5.1 (4.1)	6.5 (6.7)	9.6 (8.1)	10.0 (8.2)	12.9 (7.1)	12.2 (7.3)
Shrub cover (%)	32.4 (19.0)	20.9 (12.2)	18.1 (11.1)	11.0 (7.2)	23.6 (12.0)	15.2 (10.2)	19.6 (16.1)	20.6 (13.3)
Conifer cover within 400m (%)	5.2 (1.7)	6.3 (3.5)	3.2 (1.5)	4.1 (2.1)	2.0 (1.2)	3.9 (3.2)	2.8 (1.3)	3.6 (2.1)

Table B2. Means and standard deviations (in parentheses) of vegetation variables measured at Greater Sage-grouse (*Centrocercus urophasianus*) nest sites (NEST) and random points (RAND) in a control area, 2011–2017, Lake County, Oregon and Washoe County, Nevada, USA.

Vegetation Variable	2011		2012		2013		2014	
	NEST	RAND	NEST	RAND	NEST	RAND	NEST	RAND
Key forb cover (%)	2.3 (2.2)	1.6 (1.8)	2.0 (2.2)	1.1 (1.3)	1.1 (2.1)	0.7 (0.7)	1.0 (0.7)	0.6 (1.0)
Other forb cover (%)	2.5 (1.8)	2.8 (4.7)	2.3 (2.4)	2.4 (4.0)	1.3 (1.3)	2.1 (4.3)	1.2 (1.0)	0.5 (1.3)
Species richness key forbs	3.3 (1.8)	2.4 (1.9)	3.0 (1.6)	2.0 (1.4)	1.5 (1.4)	2.0 (1.4)	2.1 (1.5)	1.7 (1.7)
Annual grass cover (%)	1.1 (1.6)	5.8 (11.6)	0.6 (0.8)	1.1 (1.5)	0.8 (1.2)	0.8 (1.0)	0.7 (0.7)	0.9 (1.5)
Perennial grass cover (%)	5.3 (3.7)	4.9 (4.2)	7.9 (9.3)	5.7 (7.7)	6.7 (5.4)	4.4 (4.1)	5.5 (4.9)	3.2 (1.6)
Shrub cover (%)	28.0 (11.3)	22.6 (10.3)	31.7 (14.0)	24.1 (18.1)	32.4 (19.0)	25.2 (13.1)	34.6 (14.1)	26.7 (12.7)
Conifer cover within 400m (%)	6.7 (1.3)	6.4 (3.3)	6.4 (1.9)	6.3 (3.9)	5.2 (1.7)	7.2 (4.0)	6.0 (2.4)	8.2 (3.5)

Table B2. *Continued*

Vegetation Variable	2015		2016		2017	
	NEST	RAND	NEST	RAND	NEST	RAND
Key forb cover (%)	1.6 (1.1)	1.0 (0.9)	2.5 (1.9)	3.1 (2.5)	5.7 (4.9)	3.7 (2.9)
Other forb cover (%)	1.3 (0.8)	2.1 (2.9)	2.7 (2.6)	3.4 (3.2)	5.5 (3.2)	6.1 (3.7)
Species richness key forbs	4.0 (1.6)	3.0 (2.0)	4.4 (1.5)	2.7 (1.3)	3.2 (1.7)	2.9 (1.4)
Annual grass cover (%)	0.7 (0.5)	1.6 (2.1)	1.4 (1.9)	2.0 (3.5)	1.0 (2.3)	3.5 (8.1)
Perennial grass cover (%)	3.7 (4.4)	3.7 (9.2)	6.3 (9.4)	10.6 (8.1)	9.9 (4.0)	13.5 (6.9)
Shrub cover (%)	26.7 (10.1)	11.8 (9.4)	26.7 (9.7)	20.9 (12.0)	20.0 (9.8)	18.1 (11.3)
Conifer cover within 400m (%)	3.7 (2.7)	3.9 (2.4)	3.1 (2.2)	7.5 (4.5)	3.3 (3.0)	6.9 (4.7)

Table B3. Means and standard deviations (in parentheses) of vegetation cover within 30-m pixels for a treatment area (TRT) with conifer removal and a control area (CTRL), 2010–2017, Lake County, Oregon and Washoe County, Nevada, USA. Data available at rangelands.app.

Year	Herbaceous cover (%)		Shrub cover (%)		Conifer cover (%)	
	Control	Treatment	Control	Treatment	Control	Treatment
2010	36.3 (16.0)	32.1 (6.9)	21.6 (7.3)	24.1 (4.3)	4.6 (5.0)	5.4 (5.3)
2011	39.3 (16.0)	33.2 (7.7)	22.4 (8.3)	27.7 (5.8)	6.3 (5.3)	6.4 (5.5)
2012	36.7 (17.1)	28.1 (6.8)	20.6 (7.6)	24.8 (4.9)	5.5 (5.4)	6.4 (5.2)
2013	28.9 (13.4)	23.7 (5.9)	20.3 (6.6)	24.7 (5.4)	6.2 (6.1)	5.6 (5.5)
2014	24.2 (15.3)	21.9 (7.1)	19.1 (5.8)	22.5 (5.3)	7.1 (5.8)	5.6 (4.8)
2015	32.8 (14.0)	28.3 (6.7)	19.6 (6.0)	22.6 (4.6)	3.6 (4.9)	4.1 (5.1)
2016	39.9 (19.3)	31.7 (9.9)	17.8 (5.9)	23.0 (4.8)	5.4 (7.1)	3.4 (5.7)
2017	36.2 (14.8)	28.3 (6.7)	18.5 (6.7)	23.8 (4.9)	4.7 (6.4)	4.1 (5.7)