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Source: Rangeland Ecology and Management, 70(4) : 493-503

Published By: Society for Range Management

URL: https://doi.org/10.1016/j.rama.2017.01.007

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Rangeland Ecology & Management 70 (2017) 493–503

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Original Research

Resource Selection by Greater Sage-Grouse Reveals Preference for Mechanically-Altered Habitats☆

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ARTICLE INFO

Article history:
Received 7 May 2016
Received in revised form 4 January 2017
Accepted 16 January 2017

Keywords:
cross validation
information theoretic approach
mechanical treatment
mountain big sagebrush
sagebrush removal
Strawberry Valley

ABSTRACT

Effective conservation requires an understanding of how species respond to management actions. For species of conservation concern such as greater sage-grouse *(Centrocercus urophasianus)*, this understanding is urgently needed. We developed resource selection functions to assess the influence of mechanical treatments of mountain big sagebrush *(Artemisia tridentata vaseyana)* on habitat selection by greater sage-grouse during the critical brooding period. We measured multiple vegetation components, including shrub, grass, and forb cover, at random locations before and after sagebrush treatments. We then used model selection and a 19-yr telemetry data set (1998−2016) to evaluate response of greater sage-grouse to treatments. Statistical models were built using 418 locations from 72 females with broods (333 locations, 61 females pretreatment; 85 locations, 11 females post treatment). Using a difference in means comparison, we found shrub canopy cover decreased (mean ± SE) from 31.81% ± 0.70% to 16.16% ± 0.89% following mechanical treatment. Grass cover increased from 12.02% ± 0.51% to 31.33% ± 1.52% after treatment. Post-treatment forb cover (12.58% ± 1.23%) did not differ from pretreatment estimates (12.39% ± 0.61%). Overall, greater sage-grouse selected areas that were 1) distant from trees, paved roads, and powerlines; 2) high in elevation; 3) near treatment edges; and 4) consisting of gentle slopes. Post-treatment sage-grouse showed stronger selection for treatments and treatment edges than did pretreatment sage-grouse. Maps predicting probability of selection by brood-rearing sage-grouse showed increased use in and around mechanically treated areas. This altered pattern of selection by sage-grouse with broods suggests mechanical treatments may be a suitable way to increase use of mountain big sagebrush during the brooding period.
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Introduction

Loss and degradation of habitat threaten species across the globe (Pimm and Raven, 2000; Dirzo and Raven, 2003; Foley et al., 2005). The quantity and quality of habitats available to wildlife, including the rangelands of western North America, continue to decline due to the impacts of anthropogenic development, wildfires, climate change, and invasive species (Wisdom et al., 2005; Bradley, 2010). Obligate species are more sensitive to habitat alterations and are at increased risk of extinction compared with generalist species, especially when habitats are lost or degraded (Saab and Rich, 1997; Julliard et al., 2003; Colles et al., 2009). Obligate species often have low adaptive ability and require effective, species-based management actions to mitigate impacts of habitat fragmentation and loss (Goble et al., 2012). Examining how species respond to management actions, whether through experimental or observational studies, is essential to guide effective conservation of vulnerable and imperiled species and their habitats.

The distribution of sagebrush (*Artemisia* spp.) has dramatically decreased across western North American rangelands in recent decades, creating one of North America's most pressing conservation challenges (Knick, 1999; Connelly et al., 2004). Big sagebrush (*A. tridentata* ssp.) once dominated 400 000−600 000 km^2 in western North America (Beetle, 1960; McArthur and Stevens, 2004). Recent estimates suggest there has been a 50−60% reduction in sagebrush since the beginning of the 19th century (Schroeder et al., 2004). Anthropogenic impacts are recognized as having the greatest influence on this decline in sagebrush (Walker et al., 2007; Leu and Hanser, 2011; Wisdom et al., 2011). Additionally, encroachment by juniper (*Juniperus* spp.) woodlands and invasion by species such as cheatgrass *(Bromus tectorum)* have further impacted sagebrush ecosystems (Miller et al., 2011; Knick et al., 2013). Such a significant reduction and alteration in

☆ This work was supported by the Utah Reclamation, Mitigation, and Conservation Commission; Western Association of Fish and Wildlife Agencies; Sportsmen for Fish and Wildlife; Utah Division of Wildlife Resources; US Forest Service; and Brigham Young University.
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http://dx.doi.org/10.1016/j.rama.2017.01.007
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sagebrush systems has had profound effects on the distribution and abundance of sagebrush-obligate or near-obligate species, such as greater sage-grouse *(Centrocercus urophasianus;* hereafter, sage-grouse) (Connelly et al., 2004; Crawford et al., 2004; Wisdom et al., 2011). Sage-grouse have become a species of great conservation concern following their range-wide decline over recent decades. Loss of quality brood-rearing habitat, in particular, has been implicated as a major factor in the range-wide decline (Aldridge and Brigham, 2002; Connelly et al., 2004; Crawford et al., 2004). Due to the decline in the amount and contiguity of sagebrush in North America, conservation and restoration of remaining suitable habitat have become increasingly important for sage-grouse.

Sage-grouse require sagebrush throughout all phases of their life cycle, but specific needs vary by season. Nesting and winter habitats are predominantly characterized by tall, dense stands of sagebrush (Connelly et al., 2000). In contrast, a productive and diverse understory of grasses and forbs with relatively sparse sagebrush cover is more typical of brood-rearing habitat (Klebenow, 1969; Wallestad, 1971; Drut et al., 1994). In some areas where brood-rearing habitat may be limiting, managers have reduced sagebrush cover using chemical, mechanical, or other (e.g., fire or grazing) means in an attempt to improve quality of brood-rearing habitat (Utah DWR, 2013; BLM, 2015). Plant community response to these sagebrush treatments, however, is highly variable and often dependent on the method used, subspecies of big sagebrush, and environmental conditions (e.g., precipitation, soil moisture) following treatment. Prescribed fire and mechanical treatments in Wyoming big sagebrush *(Artemisia tridentata wyomingensis)* generally produced either neutral or negative (e.g., invasion of exotic annual grasses) responses in herbaceous cover and understory (Davies et al., 2011; Beck et al., 2012; Davies et al., 2012b; Hess and Beck, 2012). Annual grass cover, for example, increased sevenfold by the third year following mowed treatments in Oregon (Davies et al., 2011). In Wyoming, perennial grass cover and height in mowed treatments did not differ from reference sites (Hess and Beck, 2012). In contrast, production of forbs and grasses favored by sage-grouse increased in the immediate years following mechanical treatment in mountain big sagebrush *(Artemisia tridentata vaseyana)* (Dahlgren et al., 2006; Davies et al., 2012c).

These studies produced data on the response of vegetation following treatments in sagebrush, yet little is known about how sage-grouse respond to these changes. Some evidence suggests that females with broods used areas where sagebrush cover was reduced (40% down to 10 − 15%), particularly within 30 − 90 m of treatment edges (Klebenow, 1970; Dahlgren et al., 2006; Thacker, 2010; Dahlgren et al., 2015). Female sage-grouse with broods favored treated areas if they contained increased availability of herbaceous plants (e.g., forbs) and associated arthropods, which are linked to improved nutrition for sage-grouse (Gregg et al., 2008; Dahlgren et al., 2015). If these nutritional components were not present following treatment of sagebrush, sage-grouse avoided treated areas (Martin, 1970). To our knowledge, however, there are no published reports examining habitat selection both before and after sagebrush removal, including using a geographic information system (GIS) to account for other features that may influence habitat selection. We took advantage of a 19-yr telemetry data set that spanned periods before and after mechanical treatment of sagebrush to assess response of sage-grouse to these actions.

The objectives of our study were to assess the effectiveness of mechanical treatments by 1) measuring shrub and herbaceous cover in treated and untreated sagebrush communities and 2) evaluating the influence of mechanical treatments on habitat selection by female sage-grouse with chicks during the brooding period (June − August) in a high-elevation (2 300 − 2 600 m) system dominated by mountain big sagebrush. We predicted that 1) herbaceous understory cover would increase with decreasing shrub cover resulting from mechanical treatment and 2) sage-grouse would demonstrate increased use of areas in and near treatments during the brood-rearing period following mechanical treatments. Our results present important findings with implications for the management of sagebrush throughout the West and for the conservation of greater sage-grouse.

Methods

Study Area

Strawberry Valley was located in Wasatch County, Utah, south and east of the Uinta and Wasatch mountain ranges, respectively. Strawberry Reservoir was the dominant feature in the valley comprising nearly 7 000 surface ha at full pool. At elevations ranging from 2 300 to 2 600 m, the climate was characterized by cool summers (13.5°C mean air temperature) and cold winters (−8.7°C mean air temperature) with annual precipitation of 77.5 cm (NRCS National Water and Climate Center, 2015). The majority of precipitation fell as snow from December to March, with snowpack often lasting into the early brood-rearing period (late May). No severe droughts or fires occurred in Strawberry Valley during our study years. No grazing by domestic livestock occurred in the study area, and the population of sage-grouse was not subject to hunting pressure by humans.

Mountain big sagebrush and silver sagebrush *(Artemisia cana)* were the dominant shrubs in the area, typical of mesic sagebrush ecosystems. Common forbs found in our study area included silvery lupine *(Lupinus argenteus),* sticky purple geranium *(Geranium viscosissimum),* and sulphur-flower buckwheat *(Eriogonum umbellatum).* Common grasses included needle-and-thread *(Stipa comata),* Kentucky bluegrass *(Poa pratensis),* and prairie Junegrass *(Koeleria cristata).*

Defining availability of habitats to animals has the potential to influence resource selection functions (RSFs). Thus, it is important to delineate an area that is biologically relevant to the species of interest and appropriate for the question asked. We limited our study area for the RSF in our analysis to a 50% minimum convex polygon (MPC; Worton, 1989) derived from 19 years of brood locations, centered on the lek nearest to the treated areas (Fig. 1). We then added a 1-km buffer (Aldridge and Boyce, 2007; Carpenter et al., 2010; Sovern et al., 2015) to the MCP, which represented the approximate upper end of daily brood movements (Wallestad, 1971). This buffer allowed us to capture additional areas likely associated with those broods found on the MCP boundary. We created the MCP using Home Range Tools 2.0 (Rodgers et al., 2012) in ArcMap 10.3 (ESRI, Redlands, CA). With this process, we delineated a total study area of 10 080 ha, which was then reduced by 33.7% to 6 680 ha after subtracting unavailable areas (i.e., Strawberry Reservoir).

Our objective with this delineation was not to estimate home range size or assess habitat selection across the broad area used by semimigratory sage-grouse in this population. Instead, our goal was to delineate an area available to brooding female sage-grouse in and around the areas mechanically altered and subsequently to determine if grouse with broods in this area selected for or against mechanical treatments (Gillies et al., 2006; Tardy et al., 2014; Losier et al., 2015). With this approach, we achieved a study area that was biologically relevant to sage-grouse with broods and appropriate for our particular study objectives while avoiding overestimations that can occur with 95% MCPs (Burgman and Fox, 2003).

Mechanical Treatments

The Utah Division of Wildlife Resources (UDWR) and US Forest Service (USFS) mechanically treated sagebrush using either a chain harrow (chain with sections of railroad tracks welded to it) or brushhog (mower). Approximately 165.7 ha of mountain big sagebrush were treated in 2009, 177.6 ha in 2011, and 91.9 ha in 2014, totaling 435.2 ha (6.5% of study area). Individual treatment plots (polygons) ranged in size from 0.4 ha to 14.9 ha, with an overall mean (± SE) of 3.6 ± 0.2 ha (Fig. 1). Treatments were implemented in September of each year, avoiding the critical period of brood-rearing and in association with seed set by sagebrush. These treatments were designed to

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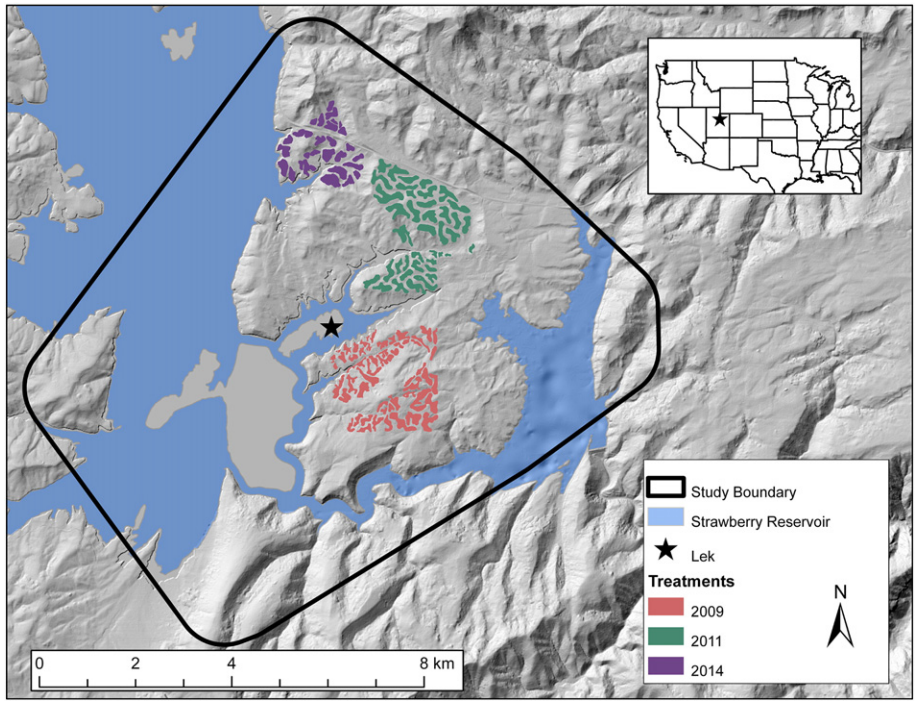


Figure 1. Map of Strawberry Valley in north central Utah, United States, where we assessed habitat selection by greater sage-grouse *(Centrocercus urophasianus)* with broods in response to mechanical treatment of mountain big sagebrush *(Artemisia tridentata vaseyana)*. The boundary (black outline) of the study area was based on a 1-km buffer around a 50% minimum convex polygon of all greater sage-grouse brood locations from 1998 to 2016, centered on the lek nearest to the mechanical treatments.

increase productivity of the herbaceous understory by reducing sagebrush canopy cover in dense (>40% sagebrush canopy cover) stands of sagebrush (Utah Watershed Restoration Initiative projects #1360 and #1816). Treatments followed a mosaic pattern, focusing on areas of high sagebrush canopy cover while avoiding rocky outcrops, riparian areas, and crucial winter habitat (thick cover on south and west slopes).

Sage-Grouse Capture and Monitoring

From 1998 to 2016 we captured female sage-grouse during March—May using a spotlight method (Wakkinen et al., 1992) and ATV or backpack generator. After capture, we identified age of females (adult or yearling) based on feather characteristics (Crunden, 1963; Bihrle, 1993). We then placed a 22-g necklace radio-transmitter (Advanced Telemetry Systems, Inc., Isanti, MN and Sirtrack, New Zealand) on each female and released them at the point of capture. Following capture and release, we attempted to locate radio-marked females twice per week using a four-element Yagi antenna and TR-2 receiver (Telonics Incorporated, Mesa, AZ) or R-1000 digital radio receiver (Communication Specialists Incorporated, Orange, CA). We did not use triangulation to estimate locations of sage-grouse broods. We flushed females after locating them using radiotelemetry, searched the immediate vicinity (20 m) for chicks, and then recorded the location using a handheld Global Positioning System (GPS) in the NAD83 datum. Brood locations were collected from June to August during daylight hours (0700—2000 h) up to 7 wk post hatch. Broods were not checked on specific days post hatch (e.g., days 7, 14). Trapping and handling of sage-grouse were permitted and approved by the Utah Division of Wildlife Resources (Certificate of Registration numbers 1COLL6817 and 4BAND9604) and by the Institutional Animal Care and Use Committee at Brigham Young University (most recent protocol number 16-0404).

Vegetation Measurements and Analysis

We quantified changes in vegetation within treatment polygons using data collected at random locations before (PRET, 1998—2009) and after (POST, 2010—2016) implementation of mechanical treatments. Before implementation of the 2009 treatment, we measured multiple vegetative components at random locations ($N = 175$) in and around polygons to be treated in 2009 and 2011 (Bunnell et al., 2004; Baxter et al., 2009). We collected post-treatment habitat data during the summers of 2013 and 2014 at random locations throughout both the 2009 and 2011 treatment polygons. For this POST analysis, we generated 40 random locations each year (80 total) using the random points tool in ArcMap 10.2 (ESRI, Redlands, CA). We used T^2 analysis (Bonham, 1989) and the line intercept method (Ludwig and Reynolds, 1988) to measure shrub overstory components, including shrub crown area (Bunnell et al., 2004), shrub height, horizontal obscurity, and shrub decadence. We used a modified 0.25-m^2 quadrat (Daubenmire, 1959) and ocular estimation (Bunnell et al., 2004; Baxter et al., 2009) to measure percent cover and species richness of grasses and forbs in the understory.

Before making an overall comparison between PRET and POST vegetation components, we first compared PRET habitat data collected in the 2009 treatment with that collected in the 2011 treatment. We used a difference in means comparison with 95% confidence intervals for each vegetation component. Differences were considered significant if the confidence interval did not overlap zero. We followed the same procedure and compared POST habitat data collected in the 2009 treatment and 2011 treatment. No differences were found in either case. Therefore, we pooled PRET vegetation data for the 2009 and 2011 treatments, doing the same for POST vegetation data. We then made the overall comparison between PRET and POST vegetation data using the same difference in means comparison.

Resource Selection Functions

We evaluated brood habitat selection by sage-grouse at the population level (i.e., Johnson's second order; Johnson, 1980) within a use-availability study design (Manly et al., 2002). We used a mixed-effects, logistic regression with a random intercept for individuals, comparing descriptive variables at use versus available (random) locations within

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Table 1
Geographic information system (GIS) predictor variables potentially associated with greater sage-grouse *(Centrocercus urophasianus)* use sites in Strawberry Valley, Utah, USA 1998−2016. Topographic data are 10-m resolution. Anthropogenic, vegetation, and treatment data are 1-m resolution

Variable name	Description
Topographic	
ASPECTBIN	Aspect binned to the 4 cardinal directions
ELEV	Elevation in meters
SLOPE	Slope in degrees
TPI25	Topographic Position Index[1] with a 25-cell neighborhood
TPI50	Topographic Position Index[1] with a 50-cell neighborhood
TPI100	Topographic Position Index[1] with a 100-cell neighborhood
VRM5	Vector Ruggedness Measure[2] with a 5-cell neighborhood
VRM7	Vector Ruggedness Measure[2] with a 7-cell neighborhood
VRM11	Vector Ruggedness Measure[2] with a 11-cell neighborhood
Anthropogenic	
D.PLINE	Distance to power lines
D.PSTRUCT	Distance to permanent structure
D.ROAD2T	Distance to 2-track road
D.ROADHUD	Distance to high-use dirt road
D.ROADPAV	Distance to paved road
Vegetative	
HabType	Land cover class[3] (shrub, riparian, etc.)
D.BA.TR	Distance to an edge consisting of bare ground and trees
D.BAREG	Distance to bare ground
D.GRASS	Distance to grass
D.RI.TR	Distance to an edge consisting of riparian and trees
D.RIP	Distance to riparian
D.SH.GR	Distance to an edge consisting of shrub and grass
D.SH.RI	Distance to an edge consisting of shrub and riparian
D.SH.TR	Distance to an edge consisting of shrub and trees
D.SH.WA	Distance to an edge consisting of shrub and water
D.SHRUB	Distance to shrub
D.TREE	Distance to tree
D.WATER	Distance to water
Treatment	
IN.OUT	Binary variable where 0 = outside a treatment and 1 = inside a treatment
PERIOD	Binary variable where 0 = Pre and 1 = Post
N.TREAT	Distance to treatment
N.TREAT2	Distance to treatment, squared
PRE.POST	Interaction between *PERIOD* and *N.TREAT*
PRE.POST2	Interaction between *PERIOD* and *N.TREAT2*

[1] Jenness and Beier (2013).
[2] Sappington et al. (2007).
[3] Westover et al. (2016).

the study area. Females with broods in multiple years were considered in our analysis but represented a relatively small number ($N = 12$; 10 PRET, 2 POST) of individuals. To capture availability, we generated 1 000 random locations and then removed those that fell within the reservoir, leaving 914 random locations (13.7 locations per km^2). To ensure we adequately characterized the study area, random locations were generated at densities equal to or greater than those used in previous studies of habitat selection by sage-grouse (1–2 km^{-2}) (Aldridge and Boyce, 2007; Aldridge et al., 2008; Carpenter et al., 2010; Fedy et al., 2014; Fedy et al., 2015). We then down-weighted random locations to have the same weight as use locations (Hirzel et al., 2006). Because our study was based on a use-availability and not a presence-absence design, our RSFs represented relative probabilities of use, given our data (1998−2016) and the available resource units in our study area.

We did not assess habitat selection for both early and late brood-rearing periods, which in some areas has been shown to differ (Wallestad, 1971; Drut et al., 1994; Atamian et al., 2010). In the majority of these cases, broods moved to more mesic areas at higher elevations as herbaceous plants desiccated at lower elevations. Strawberry Valley as a whole is characterized as a high-elevation, high-precipitation, mesic area. Thus, brood habitat selection in our study area was unlikely to differ between early and late brood-rearing periods.

GIS Explanatory Variables

We extracted landscape-level variables potentially influencing sage-grouse habitat selection using a GIS (Westover et al., 2016). We separated variables into one of four categories: topographic, anthropogenic, vegetative, and treatment (Table 1). Topographic features were derived from a 10-m National Elevation Dataset (NED). Anthropogenic variables included distances to different landscape features associated with humans (e.g., power lines, roads). Vegetative variables were derived from a National Agriculture Imagery Program (NAIP) classification (Westover et al., 2016). From the classification, we estimated distance to vegetation types, as well as to edges consisting of two contrasting vegetation types (e.g., riparian and trees). For treatment variables, distance to treatment edge was set up such that locations falling inside a treatment polygon were given a negative distance and locations outside polygons were given positive distances, with a location on a treatment edge a distance of 0 m. We squared these values to create a second variable that, in combination with the first, allowed us to capture a nonlinear relationship between relative probability of use and distance to treatment edge. We tested for a difference between pretreatment and post-treatment habitat selection of sage-grouse by including an interaction term between a binary predictor (0 for pretreatment, 1 for post-treatment) and distance to treatment (continuous). A significant negative coefficient for the interaction term would indicate that post-treatment females selected for areas nearer treatment edges than did pretreatment females. To estimate distance to the edge of a feature (e.g., water, treatment), we used the Euclidean distance tool in the Spatial Analyst extension in ArcMap 10.3 and then intersected use and available points with the layer. For all other variables, we simply

Table 2
Mean (±SE) vegetation measurements taken at random locations before and following mechanical treatments of mountain big sagebrush *(Artemisia tridentata vaseyana)* in Strawberry Valley, Utah, United States. Difference in means with 95% confidence intervals is also shown.

		Pre	Post	Difference	95% Confidence interval
		Mean ± SE	Mean ± SE		
Crown Area*	cm^2	6118.8 ± 629.13	1095.55 ± 120.73	−5023.25	[−6278.84, −3767.66]
Horizontal obscurity	%	90.91 ± 0.96	87.75 ± 1.22	−3.2	[−6.2, −0.2]
Decadence*	%	24.82 ± 1.18	30.09 ± 1.95	5.26	[0.79, 9.73]
Shrub height	cm	36.38 ± 1.23	33.54 ± 1.52	−2.84	[−6.67, 0.99]
Shrub canopy cover*	%	31.81 ± 0.70	16.16 ± 0.89	−15.7	[−17.9, −13.5]
Grass richness*	# spp.	1.40 ± 0.04	1.73 ± 0.09	0.32	[0.14, 0.51]
Forb richness	# spp.	1.51 ± 0.06	1.31 ± 0.11	−0.19	[−0.43, 0.05]
Grass cover*	%	12.02 ± 0.51	31.33 ± 1.52	19.3	[16.2, 22.4]
Forb cover	%	12.39 ± 0.61	12.58 ± 1.23	0.2	[−2.5, 2.9]
Moss	%	3.02 ± 0.92	0.47 ± 0.15	−2.6	[−4.4, −0.8]
Bare ground	%	13.24 ± 0.92	13.15 ± 0.92	−0.1	[−2.6, 2.4]
Rock*	%	9.18 ± 1.33	2.00 ± 0.34	−7.2	[−9.9, −4.5]
Litter*	%	46.73 ± 1.04	34.67 ± 1.02	−12.1	[−14.9, −9.3]

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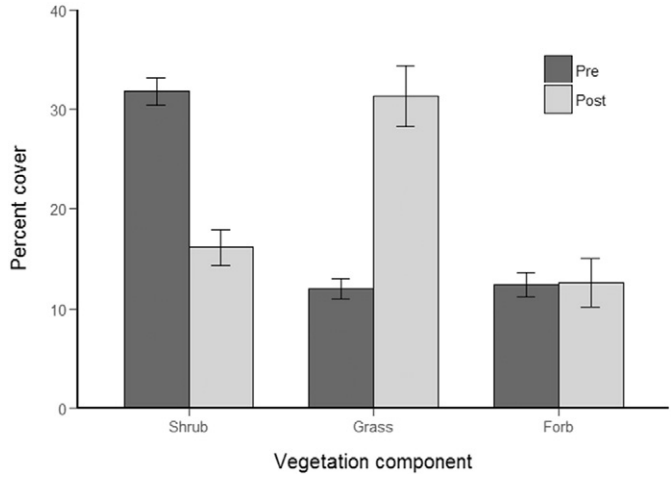


Figure 2. Percent cover of vegetation components before (1998–2009) and after (2010–2016) mechanical treatment of mountain big sagebrush *(Artemisia tridentata vaseyana)* in Strawberry Valley, Utah, United States. Error bars are 95% confidence intervals.

intersected the locations with the layer. We standardized all variables before model development $[(x_i - \bar{x})/s]$.

Model Development and Assessment

We developed a priori models (hypotheses) within an information theoretic framework (Burnham and Anderson, 2002). We selected hypotheses on the basis of sage-grouse brooding ecology (Crawford et al., 2004; Dahlgren et al., 2006; Aldridge et al., 2008) and previous research in Strawberry Valley (Westover et al., 2016). We used a 2-stage hierarchical approach. For each stage, we developed a unique set of univariable and multivariable a priori models, avoiding highly correlated variables ($r \geq |0.6|$) in the same model. In stage 1, we developed hypotheses for all four categories of variables. For each category we identified competitive (Akaike Information Criterion [AIC_c] ≤ 2.0) models and advanced those models (maintaining model structure) to the second step (Carpenter et al., 2010). In step 2, we generated a new set of a priori hypotheses based on combinations of model structures that advanced from step 1. We reported all models from step 2 with ≥ 1% of AIC_c weight. An entire list of models developed in each step can

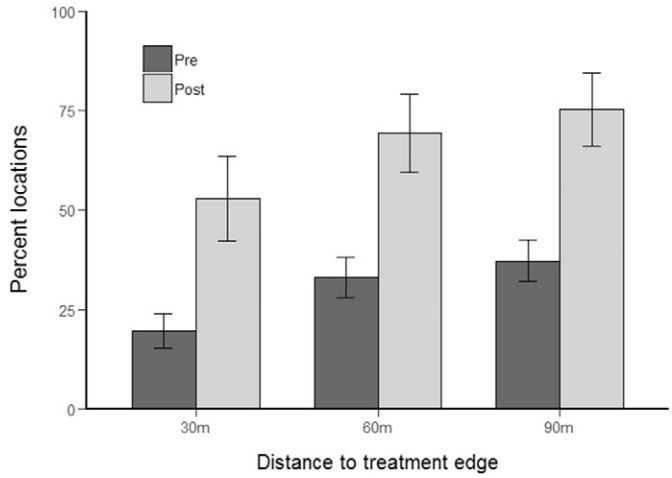


Figure 3. Percent of greater sage-grouse *(Centrocercus urophasianus)* brood locations in Strawberry Valley, Utah, United States found within 30 m, 60 m, and 90 m of a treatment edge both before (pretreatment, 1998–2009) and after (post-treatment, 2010–2016) mechanical alteration of mountain big sagebrush *(Artemisia tridentata vaseyana)*. Error bars are standard errors.

Table 3
Model results (≥ 0.01 model weight) for habitat selection by greater sage-grouse *(Centrocercus urophasianus)* with broods in Strawberry Valley, Utah, United States in relation to mechanical alteration of mountain big sagebrush *(Artemisia tridentata vaseyana)* showing number of parameters *(K)*, corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, model weight (ω_i), and log likelihood (LL). Variable names match those in Table 1.

Model number	Model structure	*K*	AIC_c	ΔAIC_c	ω_i	LL
47	D.GRASS + D.TREES + SLOPE + ELEV + D.ROADPAV + D.ROAD2T + D.PLINE + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2 + IN.OUT	14	815.62	0.00	0.41	−393.65
51	D.RI.TR + D.TREES + D.SH.WA + SLOPE + ELEV + D.ROADPAV + D.ROAD2T + D.PLINE + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2	14	817.22	1.60	0.18	−394.45
43[1]	D.GRASS + D.RI.TR + D.TREES + SLOPE + ELEV + D.ROADPAV + D.ROAD2T + D.PLINE + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2 + IN.OUT	15	817.61	1.99	0.15	−393.62
53	D.RI.TR + D.SHRUB + D.TREES + SLOPE + ELEV + D.ROADPAV + D.ROAD2T + D.PLINE + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2 + IN.OUT	15	819.01	3.39	0.07	−394.32
48	D.GRASS + D.TREES + SLOPE + VRM11 + ELEV + D.PLINE + D.ROADPAV + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2	13	820.09	4.47	0.04	−396.91
41	D.RI.TR + D.TREES + SLOPE + D.ROADPAV + D.ROAD2T + D.PLINE + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2 + IN.OUT	13	820.83	5.21	0.03	−397.28
44	D.RI.TR + D.TREES + D.SH.WA + SLOPE + VRM11 + ELEV + D.PLINE + D.ROADPAV + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2	14	821.04	5.42	0.03	−396.36
45	D.TREES + SLOPE + D.ROADPAV + D.ROAD2T + D.PLINE + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2 + IN.OUT	12	821.10	5.48	0.03	−398.43
54	D.RI.TR + D.TREES + SLOPE + VRM11 + ELEV + D.PLINE + D.ROADPAV + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2	13	821.35	5.73	0.02	−397.54
52[1]	D.GRASS + D.RI.TR + D.TREES + SLOPE + VRM11 + ELEV + D.PLINE + D.ROADPAV + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2	14	822.08	6.46	0.02	−396.88
49	D.SHRUB + D.TREES + SLOPE + D.ROADPAV + D.ROAD2T + D.PLINE + N.TREAT + N.TREAT2 + PRE.POST + PRE.POST2	12	823.06	7.44	0.01	−399.41
55	NULL	2	1138.18	322.56	0.00	−567.09

[1] Uninformative model based on AIC_c and variables.

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Table 4
β coefficients and 85% confidence intervals for variables in models (≥1% of model weight) explaining habitat selection by greater sage-grouse *(Centrocercus urophasianus)* with broods in Strawberry Valley, Utah, United States in relation to mechanical alteration of mountain big sagebrush *(Artemisia tridentata vaseyana)*. Blanks indicate the variable was not included in that model and asterisks (*) indicate the confidence interval did not overlap zero. Model numbers match those in Table 3. Variable names match those in Table 1.

Model number	β coefficients and 85% confidence intervals																
	Intercept	SLOPE	VRM11	ELEV	D.RI.TR	D.TREES	D.SHRUB	D.GRASS	D.SH.WA	D.ROADPAV	D.ROAD2T	D.PLINE	N.TREAT	N.TREAT2	PRE.POST	PRE.POST2	IN.OUT
47	−0.70* [−0.99; −0.42]	−0.47* [−0.65; −0.28]		0.39* [0.18; 0.59]		0.72* [0.56; 0.89]		0.13 [−0.01; 0.28]		0.59* [0.31; 0.86]	0.24* [0.07; 0.41]	0.39* [0.16; 0.62]	−2.58* [−3.28; −1.87]	1.96* [1.33; 2.59]	−2.66* [−3.52; −1.80]	1.36* [0.17; 2.56]	−0.55* [−0.98; −0.12]
51	−0.76* [−1.04; −0.47]	−0.48* [−0.66; −0.30]		0.48* [0.24; 0.73]	0.04 [−0.13; 0.20]	0.76* [0.58; 0.93]			−0.23* [−0.44; −0.03]	0.48* [0.21; 0.76]	0.23* [0.06; 0.40]	0.31* [0.08; 0.55]	−2.31* [−2.98; −1.64]	1.76* [1.17; 2.36]	−2.60* [−3.46; −1.74]	1.30* [0.04; 2.55]	
43[1]	−0.70* [−0.99; −0.42]	−0.47* [−0.65; −0.28]		0.37* [0.15; 0.59]	0.03 [−0.14; 0.19]	0.72* [0.54; 0.89]		0.13 [−0.02; 0.28]		0.59* [0.32; 0.87]	0.24* [0.07; 0.41]	0.38* [0.15; 0.62]	−2.56* [−3.27; −1.84]	1.95* [1.32; 2.58]	−2.67* [−3.53; −1.80]	1.37* [0.18; 2.56]	−0.55* [−0.99; −0.12]
53	−0.71* [−0.99; −0.43]	−0.48* [−0.67; −0.30]		0.35* [0.13; 0.58]	0.04 [−0.12; 0.20]	0.73* [0.55; 0.90]	−0.05 [−0.21; 0.10]			0.61* [0.33; 0.89]	0.24* [0.07; 0.41]	0.34* [0.11; 0.58]	−2.52* [−3.23; −1.81]	1.95* [1.32; 2.58]	−2.67* [−3.53; −1.80]	1.36* [0.17; 2.56]	−0.52* [−0.95; −0.09]
48	−0.76* [−1.04; −0.48]	−0.41* [−0.60; −0.23]	0.03 [−0.15; 0.20]	0.35* [0.15; 0.55]		0.72* [0.56; 0.88]		0.12 [−0.03; 0.26]		0.57* [0.30; 0.84]		0.52* [0.30; 0.73]	−2.30* [−2.96; −1.63]	1.70* [1.10; 2.29]	−2.66* [−3.51; −1.81]	1.37* [0.17; 2.57]	
41	−0.68* [−0.96; −0.40]	−0.48* [−0.66; −0.30]			0.16* [0.01; 0.30]	0.70* [0.53; 0.87]				0.82* [0.58; 1.06]	0.22* [0.05; 0.39]	0.16 [−0.04; 0.36]	−2.35* [−3.05; −1.65]	1.94* [1.31; 2.56]	−2.66* [−3.53; −1.80]	1.37* [0.18; 2.57]	−0.49* [−0.92; −0.07]
44	−0.77* [−1.05; −0.50]	−0.44* [−0.62; −0.26]	−0.01 [−0.19; 0.16]	0.44* [0.20; 0.69]	0.04 [−0.12; 0.20]	0.77* [0.59; 0.94]			−0.21* [−0.42; −0.01]	0.51* [0.23; 0.79]		0.42* [0.20; 0.65]	−2.27* [−2.93; −1.60]	1.69* [1.10; 2.28]	−2.72* [−3.57; −1.88]	1.43* [0.27; 2.58]	
45	−0.67* [−0.95; −0.39]	−0.48* [−0.66; −0.30]				0.75* [0.59; 0.91]				0.85* [0.61; 1.08]	0.21* [0.04; 0.38]	0.16 [−0.03; 0.36]	−2.44* [−3.14; −1.75]	1.99* [1.37; 2.62]	−2.62* [−3.48; −1.75]	1.33* [0.13; 2.53]	−0.46* [−0.88; −0.04]
54	−0.77* [−1.05; −0.48]	−0.43* [−0.61; −0.25]	0.01 [−0.17; 0.18]	0.33* [0.11; 0.55]	0.04 [−0.12; 0.20]	0.73* [0.57; 0.90]				0.58* [0.31; 0.85]		0.48* [0.27; 0.70]	−2.25* [−2.92; −1.58]	1.69* [1.09; 2.28]	−2.68* [−3.53; −1.84]	1.39* [0.19; 2.58]	
52[1]	−0.76* [−1.04; −0.48]	−0.41* [−0.60; −0.23]	0.03 [−0.14; 0.20]	0.34* [0.12; 0.55]	0.03 [−0.14; 0.19]	0.71* [0.54; 0.88]		0.11 [−0.03; 0.26]		0.58* [0.31; 0.85]		0.51* [0.29; 0.73]	−2.28* [−2.95; −1.60]	1.69* [1.09; 2.29]	−2.67* [−3.52; −1.81]	1.37* [0.18; 2.57]	
49	−0.70* [−0.99; −0.41]	−0.44* [−0.62; −0.26]				0.71* [0.55; 0.88]	−0.07 [−0.22; 0.08]			0.83* [0.59; 1.06]	0.18* [0.01; 0.35]	0.19 [−0.01; 0.38]	−2.24* [−2.90; −1.58]	1.82* [1.22; 2.42]	−2.53* [−3.41; −1.64]	1.23 [−0.06; 2.53]	
55	0.13 [−0.02; 0.28]																

[1] Uninformative model based on AIC_c and variables.

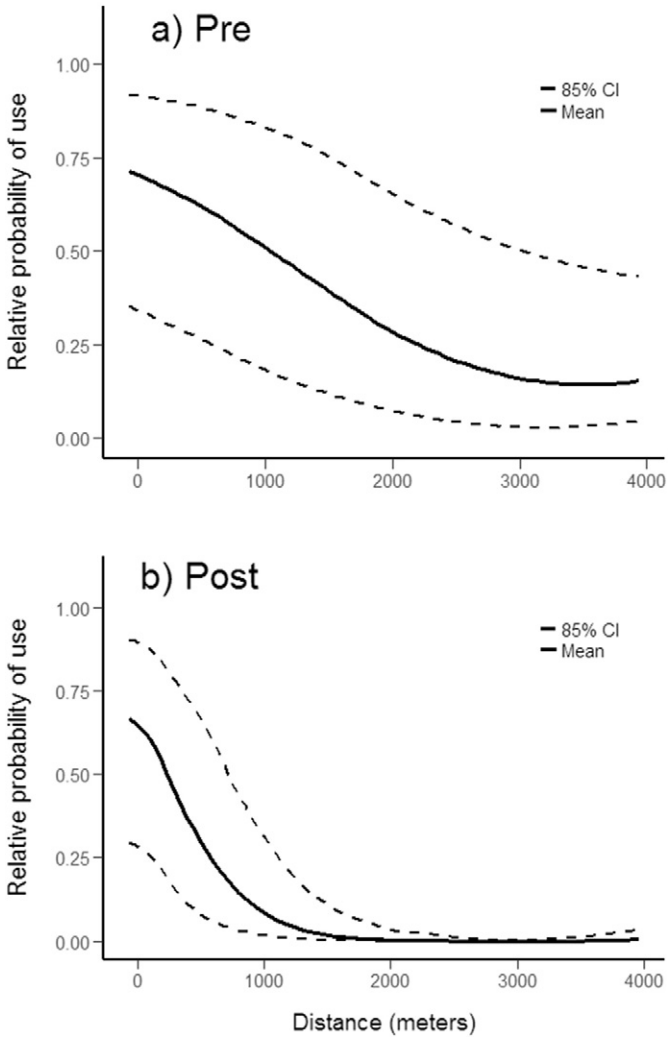


Figure 4. Resource selection functions showing relative probability of use for greater sage-grouse *(Centrocercus urophasianus)* in Strawberry Valley, Utah, United States as related to distance to edges of mechanically altered mountain big sagebrush *(Artemisia tridentata vaseyana)* a) before implementation of treatments (1998 − 2009) and b) in the years following treatment (2010 − 2016).

be found in the supplementary material (Table S1 in the online version at http://dx.doi.org/10.1016/j.rama.2017.01.007).

Models may contain uninformative variables despite having some measure of AIC_c weight (Arnold, 2010). We used AIC_c values and model composition to identify the most supported models and which variables were informative (Arnold, 2010). For example, if a model with a lower AIC_c differed by the addition of only one variable and approximately 2.0 AIC_c from a similar model ranked above it, we considered that variable uninformative and advanced the top (more parsimonious) model. In the case of multiple models with support, we did not model average β coefficients (Cade, 2015). Instead, we used the merTools package (Knowles and Frederick, 2015) in R 3.1.3 (R Core Team, 2015) to produce predicted responses with 85% confidence intervals and then averaged those values on the basis of the relative AIC_c weight of the most-supported models. We followed this procedure, first, to produce a graphical representation of the relative probability of use as a function of distance to a treatment edge. Second, we generated two predictive maps, one each for PRET and POST, by applying this procedure to each raster pixel in our study area. We then used five equal-area bins to categorize the relative probabilities of use for each pixel from low to high (Fedy et al., 2015).

To help assess final models, we used variance inflation factors (VIF) to further test for multicollinearity among variables. We considered VIF > 10 to indicate evidence of multicollinearity (Aldridge and Boyce, 2007; O'Brien, 2007; Coates and Delehanty, 2010; Holloran et al., 2015). To assess predictive ability of our final models, we performed a *k*-folds cross validation with $k = 5$ (Long et al., 2009). We randomly sorted observations into 5 partitions, with an approximately equal number of locations in each partition. During each iteration of this procedure, we used four partitions (80% of the data) as the training set to estimate model coefficients and the remaining partition (20% of the data) to test model predictions. We repeated this procedure until all observations were used as both the test set and part of the training set.

Results

Vegetation Response

Mechanical treatments significantly reduced crown area, shrub height, and shrub cover in POST vs PRET samples (Table 2). Mean percent shrub cover at POST sites was roughly half (0.16 ± 0.01) that of PRET (0.32 ± 0.01) sites (Fig. 2). Percent grass cover was higher POST (0.31 ± 0.02) compared with PRET (0.12 ± 0.01). Statistically, grass richness (mean number of species per site detected in 0.25 m^2 quadrats) POST (1.73 ± 0.09) was higher than PRET (1.40 ± 0.04), although the effect size was relatively small (estimated difference of 0.33). Forb richness (1.51 ± 0.06 PRET, 1.31 ± 0.11 POST) and percent forb cover (0.12 ± 0.01 PRET, 0.13 ± 0.01 POST) were not different between POST and PRET periods.

Sage-Grouse Response

We used 418 locations from 72 sage-grouse (mean, 5.8 ± 0.7 locations per individual; range, 1 − 28) to build models in our mixed-effects logistic regression analysis. Of the 418 locations, 333 were from 61 PRET sage-grouse and 85 were from 11 POST sage-grouse. We compared these use locations to 918 random locations (453 locations PRET, 461 locations POST). Mean distance (± SE) of brood locations to future treatment edge was 823.9 ± 66.6 m PRET, while POST mean distance to those same edges after treatment was 208.2 ± 46.2 m. Only 37.2% (124 of 333) of PRET brood locations were within 90 m of a future treatment edge. Conversely, 75.3% (64 of 85) of POST brood locations were ≤90 m from a treatment edge (Fig. 3). Seventy-five percent of PRET locations were within 955.4 m of the future treatment edges, while 75% of POST locations were within 84.5 m of treatment edges after mechanical treatment.

Overall, greater sage-grouse selected areas that were 1) far from trees, paved roads, and powerlines; 2) high in elevation; 3) near treatment edges; and 4) consisting of gentle slopes (Tables 3 and 4). Post-treatment sage-grouse showed stronger selection for areas near treatments than did pretreatment sage-grouse (Fig. 4). All models with ≤ 2 ΔAIC_c contained slope (negative), elevation (positive), distance to trees (positive), distance to paved roads (positive), distance to powerlines (positive), distance to treatment (negative), squared distance to treatment (positive), interaction term of distance to treatment and binary PRET/POST variable (negative), and squared interaction term of squared distance to treatment and binary PRET/POST variable (positive). The interaction term and distance to treatment edge had the greatest and second greatest influences, respectively, on habitat selection in our sample (see Table 4).

We disregarded one of the three models with $\Delta AIC_c \leq 2$ due to an uninformative parameter (Arnold, 2010) (see Table 3). The third-ranked model was 2 AIC_c higher than the top-ranked model, with the addition of only one variable. Distance to an edge consisting of riparian and trees was uninformative, with confidence intervals overlapping zero ($\beta = 0.03$, [−0.20; 0.25]; see Table 4). Using coefficients from the two informative models with $\Delta AIC_c < 2$, we projected relative probability of use

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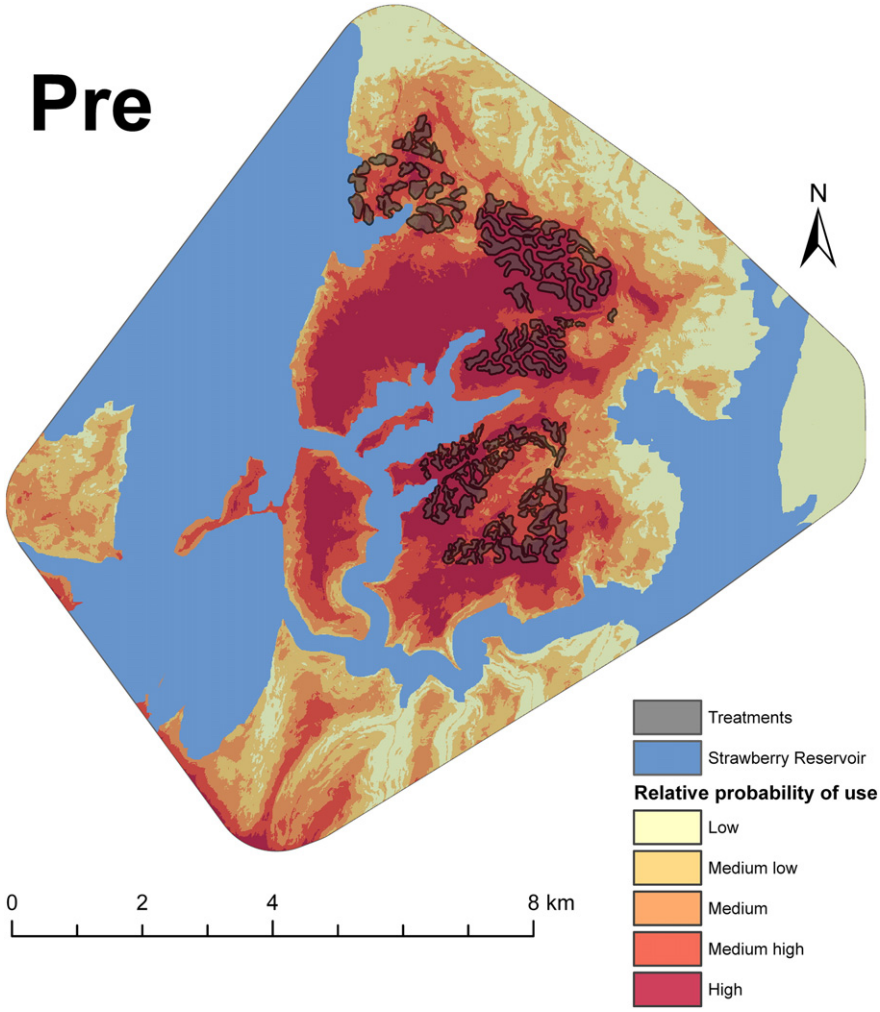


Figure 5. Relative probabilities of selection by greater sage-grouse *(Centrocercus urophasianus)* with broods in Strawberry Valley, Utah, United States based on mixed-effects logistic regression models. The figure shows the study area before (1998 – 2009) mechanical treatment of sagebrush *(Artemisia tridentata vaseyana)*. Relative probability of use was binned into five categories, from low (yellow) to high (red).

across the landscape within the study area for PRET (Fig. 5) and POST (Fig. 6). Mean predictive ability of the top performing models from the fivefold cross validation was high (Spearman $\rho = 0.95$; $P < 0.05$). We found no evidence for collinearity among predictor variables in any of our final models (VIF < 5), with the exception of distance to treatment and distance to treatment squared, which was expected.

Discussion

Our study provides before-and-after evidence that habitat selection by sage-grouse in Strawberry Valley changed in response to mechanical treatments of sagebrush. Distance to treatment edges had the greatest influence on overall habitat selection, while the negative, significant interaction term indicated POST females with broods selected for areas nearer to treatment edges than did PRET females with broods. A significant increase in use in and near treated areas by sage-grouse with broods provides managers some measure of validation for electing to use mechanical alterations for improving brood-rearing habitat in mountain big sagebrush. Linking use of treated areas with brood survival would provide additional justification for using mechanical treatments in areas dominated by mountain big sagebrush.

Use of treated areas by sage-grouse broods has been documented in other areas (Klebenow, 1970; Dahlgren et al., 2006; Thacker, 2010; Dahlgren et al., 2015). Moreover, similar preferences for treatment edges were observed in other studies performed in mountain big sagebrush in northern and southern Utah (Dahlgren et al., 2006; Dahlgren et al., 2015). In northern Utah, 80% of sage-grouse were found within 60 m of a treatment edge (Dahlgren et al., 2015). On Parker Mountain in southern Utah, analysis from sage-grouse pellet surveys showed a dramatic decline in number of pellets between 20 and 30 m from Dixie-harrow treatments (Dahlgren et al., 2006). Our results support findings from previous studies while adding a valuable GIS component that allowed us to determine the influence of sagebrush removal relative to other potential factors influencing brood habitat selection.

Nontreatment variables in our top models and their effect sizes were generally consistent with sage-grouse brooding ecology. Sage-grouse broods exhibited avoidance of trees (Casazza et al., 2011; Wisdom et al., 2011; Baruch-Mordo et al., 2013; Knick et al., 2013); powerlines and paved roads (Lyon and Anderson, 2003; Holloran et al., 2005; Doherty et al., 2008; Wisdom et al., 2011); and slopes > 20° (Atamian et al., 2010; Knick et al., 2013). Sage-grouse also tended to select areas with high elevations in our study area. Sage-grouse broods are often associated with riparian areas and wet meadows, which are generally situated in valley bottoms (Klebenow, 1970; Drut et al., 1994; Connelly et al., 2000; Crawford et al., 2004). One potential explanation for sage-grouse not selecting for valley bottoms in our study area may be due to the mesic nature of Strawberry Valley, where forbs and grasses retain succulence late into the summer even at high elevations. Another explanation may be associated with the fragmentation of sagebrush caused

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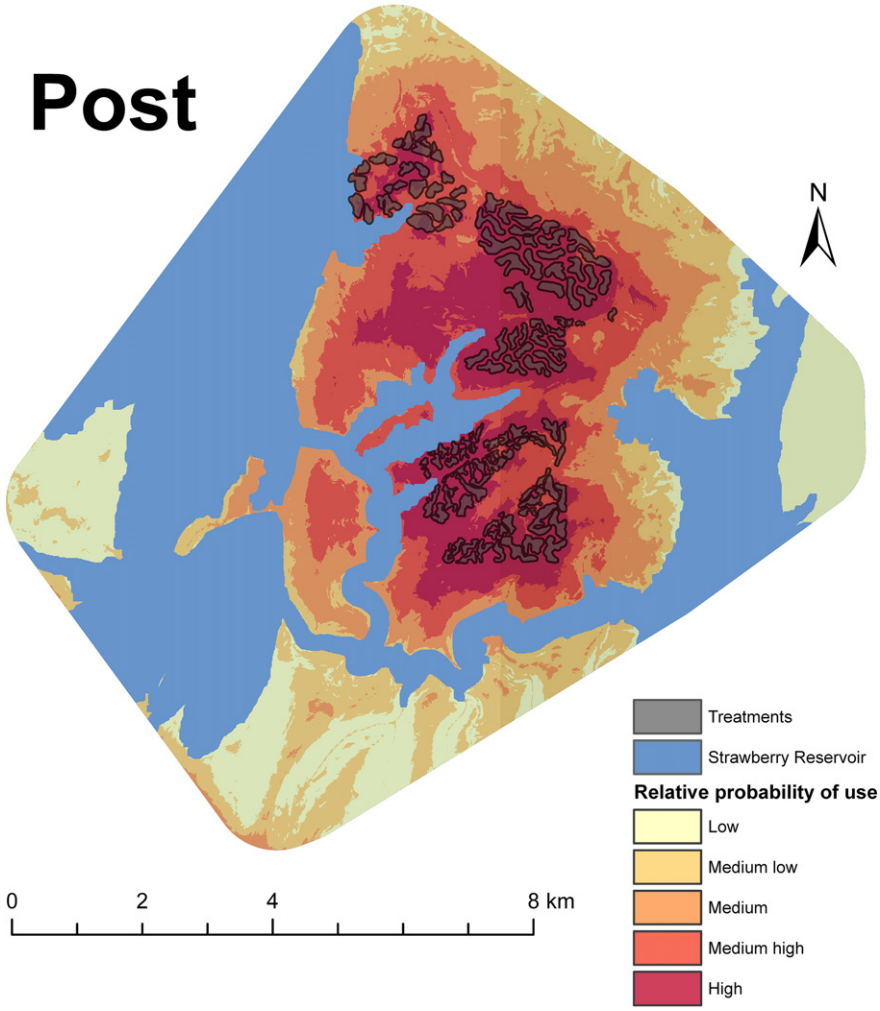


Figure 6. Relative probabilities of selection by greater sage-grouse *(Centrocercus urophasianus)* with broods in Strawberry Valley, Utah, United States based on mixed-effects logistic regression models. The figure shows the study area in the years following (2010—2016) mechanical alteration of sagebrush *(Artemisia tridentata vaseyana)*. Relative probability of use was binned into five categories, from low (yellow) to high (red).

by Strawberry Reservoir. As the reservoir filled, it created islands and small peninsulas with gentle slopes on top (preferred by female sage-grouse with broods), but it also left steep (>50-degree slope) terrain along the perimeter of the reservoir where sage-grouse broods were unlikely to be found. Consequently, tops of islands and peninsulas that were higher in elevation had greater probability of use than areas of lower elevation.

Vegetation response to mechanical treatment was similar to data from other studies in mountain big sagebrush but not Wyoming big sagebrush. In mountain big sagebrush communities, when shrub cover was reduced, grass cover increased (Dahlgren et al., 2006; Davies et al., 2012c). Forb cover did not increase in association with sagebrush removal in our area as we predicted, and neither did it decrease (Davis and Crawford, 2015). This result differs from other studies where forb cover increased 2—3% in the years immediately following treatment (Dahlgren et al., 2006; Davies et al., 2012a). This difference may be due to a slight decrease in annual precipitation in 2013 and 2014 (when vegetation measurements were taken) compared with historic mean precipitation, increased resource competition between grasses and forbs, or a potential lag effect in establishment of forbs following treatment (Sturges, 1993). Vegetation response to mechanical treatment in Wyoming big sagebrush communities has been neutral at best and is often associated with negative responses (e.g., increases in annual grass cover) highlighting a potential difference between these two sagebrush communities in response to mechanical treatments (Davies et al., 2011; Beck et al., 2012; Davies et al., 2012b; Hess and Beck, 2012).

Our results demonstrated selection for mechanically altered habitat by sage-grouse during the brooding period similar to other studies (Dahlgren et al., 2006; Thacker, 2010; Dahlgren et al., 2015), while adding important empirical evidence from spatial modeling with an interactive term that captured differences between pretreatment and post-treatment. Although additional sites, years, and sage-grouse locations post treatment would certainly strengthen this analysis, our *k*-folds cross validation suggests that the altered pattern in habitat selection by sage-grouse we observed was a real effect and not overly influenced by modest sample sizes.

Sage-grouse showed a dramatic increase in selection for areas in and near the 2009 treatment, in particular. The percent area inside or within 90 m of 2009 treatment polygons that was in the medium-high category for relative probability of use decreased from 44.5% to 15.9%, while the percent area in the high category increased from 49.5% before treatment to 83.9% following mechanical alteration. The area treated in 2011 followed a similar pattern, although not as strong a contrast between PRET and POST (medium-high, 21.4%—13.0%; high, 72.1%—86.9%). The 2014 treatment held a slightly different pattern, with the percent area in the medium-high and high categories both increasing PRET to POST, from 56.8% to 61.6% and 6.9% to 38.0%, respectively. Habitat selection is a function of availability, and the 2009 treatment may have influenced sage-grouse selection for the later treatments by increasing

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availability of brood-rearing habitat and reducing selection for the 2011 and 2014 treatments, although such an effect is confounded with year. Nonetheless, an overall increase in the quantity of predicted habitat in and near treatment plots suggests that vegetation treatments improved brood-rearing habitat in our study area.

Management Implications

Our results highlight the use of mechanical treatments of sagebrush as a method for managers to increase the amount of brood habitat. Greater sage-grouse with broods selected for areas in and near mechanical treatment plots, where shrub cover was dramatically reduced and graminoid cover increased following implementation of sagebrush treatments. We suggest that mechanical treatment of mountain big sagebrush may be an appropriate method to enhance sage-grouse brood habitat when treatments target specific locales of dense (>40%) sagebrush, avoid crucial nesting or winter habitat, and leave a mosaic of sagebrush and herbaceous cover. In areas where brood-rearing habitat is not limiting or vegetation is unlikely to respond favorably, sagebrush treatments are not recommended for conservation of sage-grouse and other species such as mule deer (Fischer et al., 1996; Beck et al., 2009; Davies et al., 2009; Beck et al., 2012; Davies et al., 2012b). These concerns, however, are generally not as applicable to treatments performed in mountain big sagebrush (Dahlgren et al., 2006; Davies et al., 2012c; Davis and Crawford, 2015; this study). Additional research is needed to address the relationship between use of treatments by sage-grouse and population vital rates.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rama.2017.01.007.

Acknowledgments

We thankfully acknowledge Dr. Jerran Flinders for his foresight and involvement in the establishment of this long-term study. We thank Dr. Lance McNew, Dr. Erik Blomberg, and one anonymous reviewer for their comments that greatly improved this manuscript. We also appreciate the numerous volunteers and technicians, especially Scott Larsen, Jacob Fullmer, and Josh Nix, who helped collect data over the many years of this project.

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