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The Effects of Dixie Harrow Treatments on Greater Sage-Grouse Resource Selection

and the Nutritional Value of Sagebrush During Winter

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A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

The Effects of Dixie Harrow Treatments on Greater Sage-Grouse Resource Selection
and the Nutritional Value of Sagebrush During Winter

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Master of Science

Sagebrush (*Artemisia* spp.) is an important source of food and cover for many animals, especially during winter months. Understanding how wildlife species respond to sagebrush management actions can help improve conservation planning. Dixie harrow is a method of improving spring/summer habitat for many herbivores by reducing sagebrush cover to stimulate the growth of grasses and forbs. These treatments, however, may influence the quantity and quality of sagebrush available to greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) during winter. We evaluated the effects of Dixie harrow on sage-grouse resource selection during winter (Chapter 1) and on the nutritional value of sagebrush (Chapter 2). We were unsure what effect Dixie harrow would have on the nutritional value of sagebrush, but hypothesized that sage-grouse would select for untreated areas because they contained a higher quantity of food and cover. We captured 81 sage-grouse and fit them with GPS transmitters. Using 6,728 winter locations, we modeled third-order resource selection. Further, we collected samples of sagebrush plants that sage-grouse had eaten from (n = 54), samples of sagebrush plants passed by but not eaten from (n = 54), as well as samples from random locations inside (n = 60) and outside Dixie harrow treatments (n = 60). Contrary to our hypothesis, sage-grouse selected for Dixie harrow treatments during winter. We found that sage-grouse selectively browsed sagebrush plants with increased nutritional value, and that sage-grouse browsed plants inside treatments more frequently than outside the treatments, but Dixie harrow treatments had no measurable effect on the nutritional value of sagebrush. Based on our results, Dixie harrow treatments performed at the southern extent of the sage-grouse range will create habitat that sage-grouse prefer during winter, but we were unable to ascertain why sage-grouse select for Dixie harrow treatments during winter.

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CHAPTER 1

Greater Sage-Grouse and Dixie Harrow Treatments: Resource Selection During Winter

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ABSTRACT

Sagebrush (*Artemisia* spp.) is an important food source for many animals, particularly during the winter months. Sagebrush conservation practices can be evaluated by monitoring sagebrush-obligate species such as greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse). Dixie harrow is a method of improving spring/summer habitat for sage-grouse (and other herbivores) by reducing sagebrush cover to stimulate the growth of grasses and forbs. However, Dixie harrow could also consequentially reduce availability of sagebrush during winter. Our objective was to measure resource selection by sage-grouse during winter within a landscape where Dixie harrow treatments were prevalent (Grass Valley, Utah). We hypothesized that sage-grouse would select for untreated areas during winter because untreated areas provide sage-grouse with an increased quantity of food and increased cover for avoiding predators. Using third-order resource selection functions (RSFs), we modeled habitat use in response to Dixie harrow treatments, vegetation, topography, and anthropogenic features. Our RSF utilized a database of 6,728 GPS locations from 14 sage-grouse (6 males and 8 females) that were acquired during the winter months of 2016–2018. Contrary to our hypothesis, we found that sage-grouse selected for treatment areas ($p < 0.05$). Sage-grouse also selected for sagebrush-dominated sites, while avoiding trees ($p < 0.05$). Our results suggest that Dixie harrow treatments may provide high quality winter habitat for sage-grouse.

INTRODUCTION

Winter has a negative impact on the body condition and survival of many herbivores (Loison and Langvatn 1998, DeLgiudice et al. 2002, Hurley et al. 2014). Food sources are key to surviving winter conditions because, as the food supply becomes limited, animals deplete their fat stores and loose muscle mass (Kaji et al. 2004, Monteith et al. 2013). In general, building a reserve of fat during the fall increases the likelihood of survival for animals living in temperate regions during winter (Cook et al. 2004, Monteith et al. 2013). However, if body condition is poor entering winter, survival greatly depends on the quantity and nutritional quality of the available forage during winter months (Monteith et al. 2011).

On western rangelands, sagebrush (*Artemisia* spp.) is a source of food and cover for many herbivores during winter, when many other plants are inaccessible (e.g., covered by snow) or of low nutritional value from entering a dormant state (Wallestad and Eng 1975, Amasino 2004, Johansson et al. 2015, Smith et al. 2015). Herbivores can maintain fat during winter by consuming evergreen forage such as sagebrush, however, nearly half of the sagebrush that was present in North America before European settlement has been lost to agriculture, energy development, reservoirs, roads, fire, exotic plants, urbanization and encroachment by pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.) (Braun 1998, Schroeder et al. 2004, Kuroiwa et al. 2017). Remaining areas of sagebrush have become fragmented by either land conversion or habitat degradation, and are now often isolated (Knick et al. 2003, Connelly et al. 2004, Schroeder et al. 2004). These changes have negatively influenced many sagebrush-obligate species.

Monitoring sagebrush-obligates has become commonplace; these efforts provide information on species status and trends, but they can also be an effective means of evaluating the condition

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of sagebrush ecosystems (Rich et al. 2005, Hanser and Knick 2011, Copeland et al. 2014, Carlisle et al. 2018). Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a sagebrush-obligate species who rely heavily on sagebrush for both food and cover year-round (Connelly et al. 2000). During winter, adult sage-grouse nearly exclusively eat sagebrush (Wallestad and Eng 1975). During other times of the year, adult sage-grouse incorporate forbs and insects into their diet as they become available, though sagebrush still makes up the majority of their diet (Wallestad and Eng 1975). Sage-grouse's nearly complete reliance on sagebrush during winter makes it an ideal time to monitor sage-grouse use of sagebrush and evaluate the condition of sagebrush ecosystems, even though the energy reserves of sage-grouse during winter are relatively high (Remington and Braun 1988).

Sage-grouse habitat overlaps important habitat for other species; therefore, conserving sage-grouse habitat benefits many other species (Rich et al. 2005, Wisdom et al. 2005, Hanser and Knick 2011, Copeland et al. 2014, Carlisle et al. 2018). Conservation of sage-grouse habitat will have the greatest benefit to those species who have needs most similar to sage-grouse (Carlisle et al. 2018). Other sagebrush-obligates, such as the sagebrush sparrow (*Artemisiospiza nevadensis*), pygmy rabbit (*Brachylagus idahoensis*), and pronghorn (*Antilocapra americana*), would likely benefit from conservation of sage-grouse habitat (Rowland et al. 2006). Similarly, mule deer (*Odocoileus hemionus*) also eat sagebrush, and show a significant overlap in habitat use with sage-grouse during winter (Copeland et al. 2014). Conservation of winter habitat for sage-grouse would likely benefit all species who forage on or find cover in sagebrush during winter; however, sage-grouse habitat is not always managed in a way that preserves sagebrush.

In some areas, sagebrush cover has been reduced using Dixie harrow treatments to stimulate understory growth (Dahlgren et al. 2006, Baxter et al. 2017). By increasing understory growth of

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grasses and forbs, habitat is improved for the brood-rearing period of the sage-grouse lifecycle (Dahlgren et al. 2006, Baxter et al. 2017). However, the removal of sagebrush by Dixie harrow may have unexpected effects on winter habitat. Habitat treatments that remove sagebrush reduce the amount of available forage and cover during winter, and may also alter the nutritional value of sagebrush as it reestablishes (Wambolt 2004). Reestablishing sagebrush may differ in palatability, nutrient content, or defensive chemistry when compared to older sagebrush (Wambolt 2004, Frye et al. 2013). Further, removal treatments may alter patterns of shrub structure preferred by sage-grouse. Sage-grouse have been found to select for the edges of habitat treatments during the brood-rearing period (Baxter et al. 2017), but more research is needed to know how these treatments affect habitat selection by sage-grouse during winter.

Our objective was to analyze how Dixie harrow treatments influenced resource selection by sage-grouse in Grass Valley, Utah, during winter. We hypothesized that sage-grouse would select for untreated areas during winter because they contain relatively dense sagebrush cover, which provides sage-grouse with a higher quantity of food, more thermal cover, and more cover from predators.

METHODS

Study Area

Our study area in Grass Valley, Utah, provided us with the opportunity to study sage-grouse resource selection within a mosaic of Dixie harrow treatments; approximately 6,000 hectares of sagebrush in Grass Valley were treated using Dixie harrow between 1997 and 2008. The Bureau of Land Management (BLM) performed these treatments to stimulate the growth of grasses and forbs. A tractor was used to drag a Dixie harrow implement that removed 50% of the older

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sagebrush (age 80–100 years old) (Dahlgren et al. 2006). Young sagebrush plants now occupy treated areas with interspersed grasses and forbs. Common sagebrush species in Grass Valley include black sagebrush (*Artemisia nova*), big sagebrush (*Artemisia tridentata*), and silver sagebrush (*Artemisia cana*). Other common vegetation includes forbs such as dandelion (*Taraxacum* spp.), lupine (*Lupinus* spp.), and milkvetch (*Astragalus* spp.); grasses such as downy brome (*Bromus tectorum*), bluegrass (*Poa* spp.), blue grama (*Bouteloua gracilis.*), squirreltail (*Elymus elymoides.*), and wheatgrass (*Agropyron* spp.); and trees such as quaking aspen (*Populus tremuloides*), singleleaf pinyon (*Pinus monophylla*), and Utah juniper (*Juniperus osteosperma*). During winter most plants in our study area are senescent except sagebrush, singleleaf pinyon, and Utah juniper.

The major landforms in the area are Dutton Mountain, Monroe Mountain, Otter Creek Reservoir, and Parker Mountain. Local communities include Antimony, Greenwich, and Koosharem. The elevation in our study area ranged from 1,942 to 3,421 meters. Average annual snowfall in Antimony was 53 centimeters. Winter temperatures reached an average low of -14 °C and an average high of 4 °C from 1981 to 2010 (ClimateData 2017).

Sage-grouse Monitoring

We used a spotlighting method to capture sage-grouse during March, April, May, September, and October from 2016 to 2018 (Wakkinen et al. 1992). We captured sage-grouse within Dixie harrow treatments and from surrounding leks, and fit them with GPS transmitters (22-gram rump-mounted transmitters made by GeoTrak Incorporated®) (Figure 1-1). We assigned sex to each captured sage-grouse according to their plumage and mass (Bihrle 1993, Connelly et al. 2004). GPS transmitters acquired four locations daily (01:00, 08:00, 16:00, and 21:00 GMT)

November–February, and five locations daily (07:00, 14:00, 17:00, 20:00, and 23:00 GMT) March–October. The GPS transmitters stored their locations and transmitted them to a satellite every three days. We monitored GPS-mounted sage-grouse by downloading their locations weekly to evaluate habitat use and movement patterns.

Sage-grouse Home Ranges

Using R package BBMM (Brownian Bridge Movement Model), we modeled the home range for each sage-grouse by creating a utilization distribution from all their locations from March 2016 to March 2018 (Horne et al. 2007). BBMM calculates a motion variance from spatiotemporal data, and then uses this variance to calculate a utilization distribution along the path of travel (Newton et al. 2017). We used the 95% isopleth from the utilization distribution of each sage-grouse to represent its home range. The purpose of our study was to model how sage-grouse utilized Dixie harrow habitat treatments during winter, so only those sage-grouse whose annual home ranges overlapped Dixie harrow treatments and those who transmitted winter locations were included in our models. Home ranges of individual sage-grouse that did not overlap Dixie harrow treatments were excluded from the study because we could not say with surety that those sage-grouse were aware of the presence of Dixie harrow treatments. It should be noted that the home ranges in our sample were a subset of the true population's range in Grass Valley.

Statistical Analysis

To evaluate sage-grouse habitat use during winter we used a third-order resource selection function (RSF) (Johnson 1980, Marzluff et al. 2004, Manly et al. 2007, Sawyer et al. 2009). We

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generated 40 random locations/kilometer² within each home range to represent the habitat available to each individual, and weighted random locations such that random locations would hold equal weight to use locations in our models. We confirmed that 40 random locations/km² accurately represented available habitat by testing that the true means of our covariates were within the confidence intervals of the sample means taken from our random locations (Baxter et al. 2017). Because we needed to do this for every covariate from the home range of each individual, and by chance a few individuals would have a statistical confidence interval that did not overlap the true mean, we determined to have generated enough random points once 95% of all covariates had a sample confidence interval that overlapped the true mean. We calculated true means, sample means, and their confidence intervals using ArcGIS Pro (ESRI).

We attached habitat variables to both use and random locations using ArcGIS Pro (ESRI®, Redlands, CA). The habitat variables we evaluated included a mixture of Dixie harrow treatment, vegetative, topographic, and anthropogenic covariates (Table 1-1). Specifically, we attached distance to Dixie harrow treatment edge, vegetation cover type, distance to shrubs, distance to trees, elevation, aspect, terrain ruggedness, distance to major roads, distance to minor roads, distance to agriculture, and distance to electric lines to all use and random locations. Cover types were taken from the United States Geological Survey's Landfire program (Landfire 2008), and binned into the categories of shrub, herb, tree, road, and agriculture. We used these binned cover types to calculate distances to shrubs, trees, and agriculture. To calculate distance to minor roads and major roads we imported major and minor road centerlines from Utah's State Geographic Information Database (SGID). To measure the effects of topology, we included the variables elevation, aspect, and the TRI Riley measurement of terrain ruggedness; all of which were derived from a ten-meter Digital Elevation Model. Because our study site was remote,

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anthropogenic features were few, and we limited anthropogenic-related covariates to be distance to major roads, distance to minor roads, and distance to electric lines.

To properly compare distance measurements and other continuous variables to each other, each continuous variable was scaled according to its mean. Further, the relationship between sage-grouse use and habitat variables likely decreases with distance, so non-linear methods of measuring distance needed to be evaluated. To model non-linear distance relationships, we created new variables using squared distance, and four different decay functions of distance with α = 50, 250, 500, and 1000 (Carpenter et al. 2010, Fedy et al. 2014, Baxter et al. 2017). We used logistic regression of sage-grouse use in response to distance and a random variable for bird ID to test different distance measurement methods. This model was tested with each different method of measuring distance, and we then selected the best fit measurement of distance using AIC (Akaike Information Criterion) (Carpenter et al. 2010, Lautenbach et al. 2017, Newton et al. 2017). This hierarchal selection of distance measurement units provided us with a less arbitrary method of measuring distance for each variable applied to our third-order resource selection function.

Because we averaged coefficients across all individuals, we used a single *a-priori* model for each individual, rather than using AIC to select best fit models (Marzluff et al. 2004, Sawyer et al. 2009). This allowed us to treat each individual (or each beta coefficient) as the sample unit, rather than the locations of each sage-grouse (Marzluff et al. 2004, Sawyer et al. 2009, Winder et al. 2014, Lautenbach et al. 2017). Our *a-priori* model was based on sage-grouse preference for sagebrush as food and cover (Wallestad and Eng 1975, Carpenter et al. 2010, Connelly and Knick 2011), preference for sagebrush treatment edges (Dahlgren et al. 2006, Baxter et al. 2017), avoidance of trees (Baruch-Mordo et al. 2013), and avoidance of anthropogenic features

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(Aldridge and Boyce 2007, Carpenter et al. 2010, Hess and Beck 2012). Resource selection preferences were determined by logistic regression. The resulting beta values illustrated sage-grouse preference or avoidance of habitat variables. We averaged all coefficients, and calculated variance using the formula

$$Var(\bar{\beta}_j) = \frac{1}{n^2} \sum_{i=0}^{n} SE^2 \hat{\beta}_{ij}$$

with averaged coefficients ($\bar{\beta}_j$) being equal to one divided by the number of individuals (n) squared multiplied by the sum of the standard error squared of each individual's coefficient ($\hat{\beta}_{ij}$) for that covariate (Marzluff et al. 2004). This method of calculating variance treats each individual as a sample unit, and quantifies uncertainty in the averaged coefficient (Marzluff et al. 2004). We used our averaged coefficients to create a surface of predicted sage-grouse use in Grass Valley. We then divided this surface into 7 quantiles based on relative probability of use, and categorized these quantiles as "very high", "high–very high", "high", "medium–high", "medium", "low–medium", and "low" probability of use. We validated our model by referencing the number of use locations in each quantile from a new dataset of sage-grouse locations not used in the analyses that were collected from November 2018 to March 2019.

RESULTS

Sage-grouse Monitoring

We monitored 67 total sage-grouse (31 males and 36 females) from March 2016 to March 2018. During the first year of our study, we captured 29 sage-grouse (12 males and 17 females), and during the second year we captured 38 sage-grouse (19 males and 19 females). In that time we collected 46,304 sage-grouse locations. Of the 67 sage-grouse we captured, only 15 (6 males

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and 9 females) had home ranges that overlapped our Dixie harrow treatments and transmitted locations during winter (those whose home ranges did not overlap Dixie harrow were excluded because we could not say with surety that those sage-grouse were aware of the presence of Dixie harrow treatments). Dixie harrow treatments occurred primarily on the northern portion of our study area whereas sage-grouse were captured throughout. We collected a total of 6,728 use locations from those 15 sage-grouse during winter (Figure 1-2). We defined the winter period as being November–March when sage-grouse feed almost exclusively from sagebrush plants (Wallestad and Eng 1975, Remington and Braun 1988).

Covariate Selection

To model available habitat, we generated 40 random locations/kilometer^2 in each home range. We attached the following covariates to both use and random locations: distance to Dixie harrow treatment edge, vegetation cover type, distance to shrubs, distance to trees, elevation, aspect, terrain ruggedness, distance to major roads, distance to minor roads, distance to agriculture, and distance to electric lines. The true mean of our covariates were between the confidence intervals of our sample means in 157 of 165 cases (95.15%) of individual sage-grouse and habitat variables, which qualified 40 random locations/kilometer^2 in each home range as sufficient to represent available habitat. However, several of our covariates proved to be collinear: distance to Dixie harrow treatment edge, distance to agriculture, distance to major roads, distance to electric lines, and elevation ($|r| \geq 0.65$). Our binary covariate for being inside or outside of Dixie harrow treatments was highly correlated with distance to Dixie harrow treatment edge ($|r| \geq 0.9$), and moderately correlated with distance to shrubs ($|r| \geq 0.65$). To address collinearity we simplified our model by excluding distance to agriculture, distance to

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major roads, distance to electric lines, elevation, and our binary variable for Dixie harrow treatments. Our final *a-priori* model consisted of distance and squared distance variables for distance to Dixie harrow treatment edge, distance to cover type "shrub" with a 50 meter decay, distance to cover type "tree", and distance to minor roads with a 500 meter decay.

Resource Selection

The beta coefficients from one female sage-grouse were highly inflated, (likely because she logged only 20 locations before dying midwinter) and all of her beta coefficients were removed from further analysis. The averaged beta coefficients from the remaining 14 individuals suggested that sage-grouse preferred to be near Dixie harrow treatment edges, near shrubs, and far from trees ($p < 0.05$) (Table 1-2). Individually, 8 sage-grouse selected areas near treatment edges, 4 selected areas far from treatment edges, 2 showed no preference to treatment edges, 9 selected areas near shrubs, 1 selected areas far from shrubs, 4 showed no preference to shrubs, 12 selected areas far from trees, 2 showed no preference to trees, 2 selected areas far from minor roads, 2 selected areas near minor roads, and 10 showed no preference to minor roads.

Using averaged beta coefficients we created a surface of the relative probability of use by sage-grouse in Grass Valley (Figure 1-3). We categorized the surface into seven quantiles as being "very high", "high–very high", "high", "medium–high", "medium", "low–medium", and "low" probability of use. Then, using a new dataset of sage-grouse locations collected from November 2018 to March 2019, we validated our model by evaluating the number of use locations that overlapped each quantile. Of 411 use locations the number of locations that overlapped each quantile were: 389 (94.6%) "very high", 4 (1%) "high–very high", 0 "high", 1 (0.2%) "medium–high", 0 "medium", 11 (2.7 %) "low–medium", and 6 (1.5%) "low". We found

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that our model reliably predicted resource selection by sage-grouse during winter in Grass Valley.

DISCUSSION

Contrary to our hypothesis, we found that sage-grouse preferred Dixie harrow treatments over untreated areas (Figure 1-4). The effects of Dixie harrow treatment in Grass Valley may not be applicable to such treatments in other areas; our results apply best to conditions most similar to those that existed in our study area. In our case, Dixie harrow resulted in the establishment of young sagebrush with interspersed grasses and forbs. Dixie harrow could easily result in a grass dominated treatment area, which would likely not have the same effect on resource selection by sage-grouse as it did in Grass Valley.

Our findings may also be unique, and not applicable to many other sage-grouse populations, because Grass Valley is at the southern extent of the sage-grouse range. Here, winters are relatively mild, and even the youngest sagebrush plants are rarely covered by snow for long periods of time. If our study area had been located farther north, the sagebrush plants in treatment areas likely would have been buried in snow while untreated sagebrush remained above the snow. This could shift sage-grouse preference towards untreated and older sagebrush.

It was expected that sage-grouse would avoid trees and prefer sagebrush, and this was confirmed by the beta values of individual sage-grouse for our distance measurements. However, our model results strongly suggest that sage-grouse were selecting against trees rather than for sagebrush from both our individual and averaged beta values. We suspect that this is due to the proportion of Grass Valley that is dominated by sagebrush. Within our study area, 84% of 6,728 use locations, and 73% of 29,748 random locations were 0 meters from sagebrush (at a 30 meter

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resolution). By contrast, 1.2% of use locations, and 9.4% of random locations were 0 meters from trees. Sage-grouse may have been selecting more strongly for sagebrush, but that relationship wasn't well measured by our linear model. Our results were likely affected by the homogeneity of the landscape.

Sage-grouse exhibited an unexpected preference for Dixie harrow treatments in Grass Valley during winter. The complete removal of sagebrush would have had deleterious effects, but partial removal (that consequentially stimulates the growth of young sagebrush) may in fact improve the quality of sagebrush habitat in treatment areas. Because Dixie harrow treatments reduced percent sagebrush cover, we suppose that the positive relationship between sage-grouse use and our Dixie harrow treatments could be due to improved nutritional quality of younger sagebrush plants, or increased visibility of predators (Hagen et al. 2011, Frye et al. 2013). However, these results may not apply at more northern latitudes, where deep snow would likely render young sagebrush plants unavailable. Further research is needed to understand the effects of Dixie harrow treatments on sagebrush habitat quality.

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Figure 1-1: Photo of a female greater sage-grouse (*Centrocercus urophasianus*) fit with a rump-mounted GPS harness. Greater sage-grouse were captured and fit with GPS harnesses in Grass Valley, Utah, during March, April, May, September, and October from 2016 to 2018.
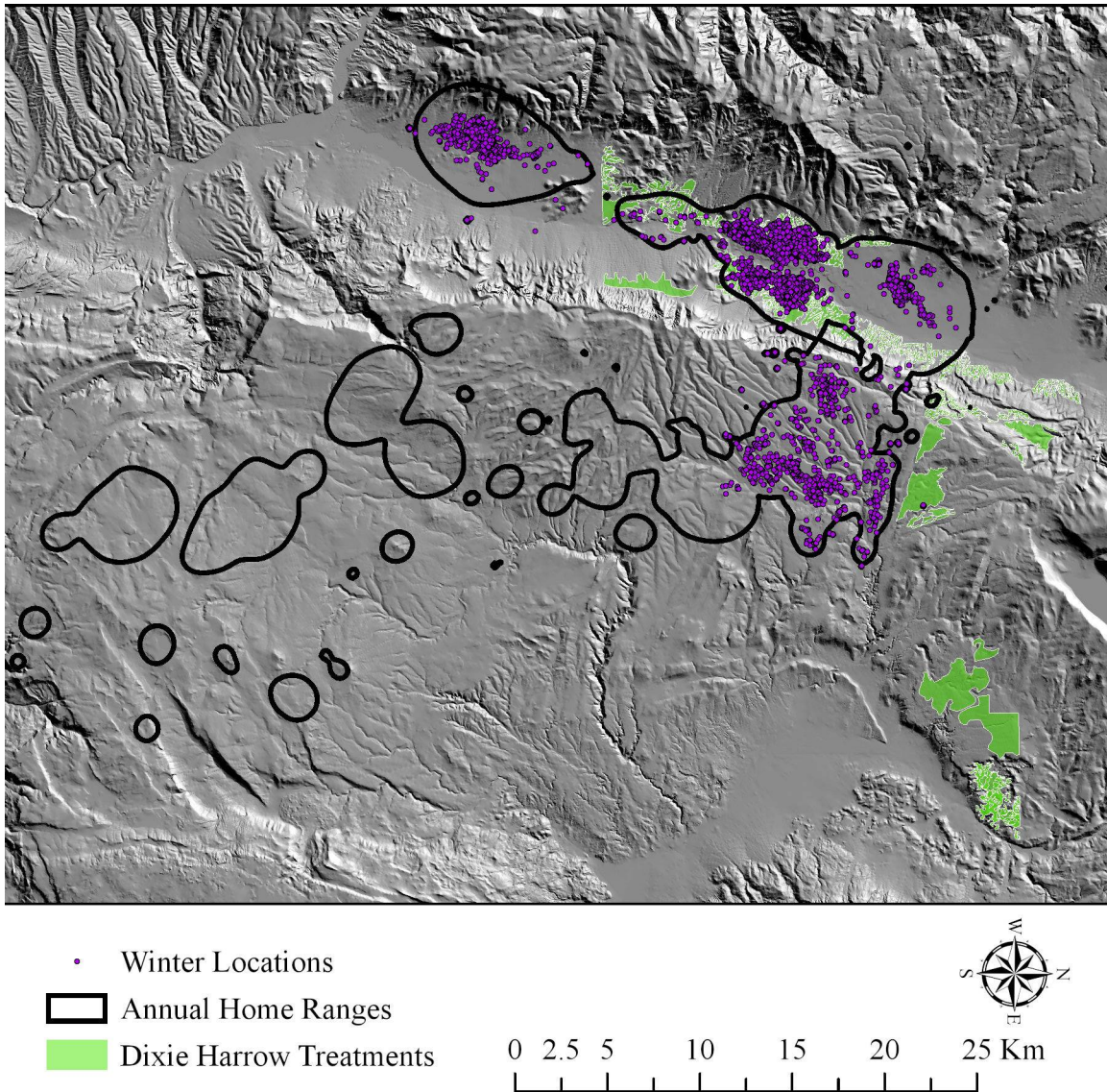
Figure 1-2: Map of greater sage-grouse (*Centrocercus urophasianus*) use within Grass Valley, Utah. The annual home ranges (black outline) were created by combining the 95% isoclines from the utilization distributions of 15 greater sage-grouse, which were created using Brownian bridge movement models. Greater sage-grouse locations (purple points) were collected from November 2015 to March 2016 and from November 2017 to March 2018.
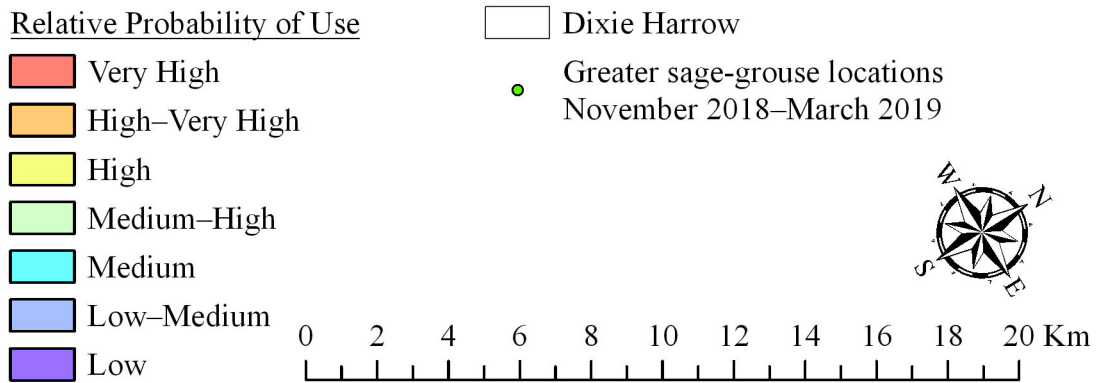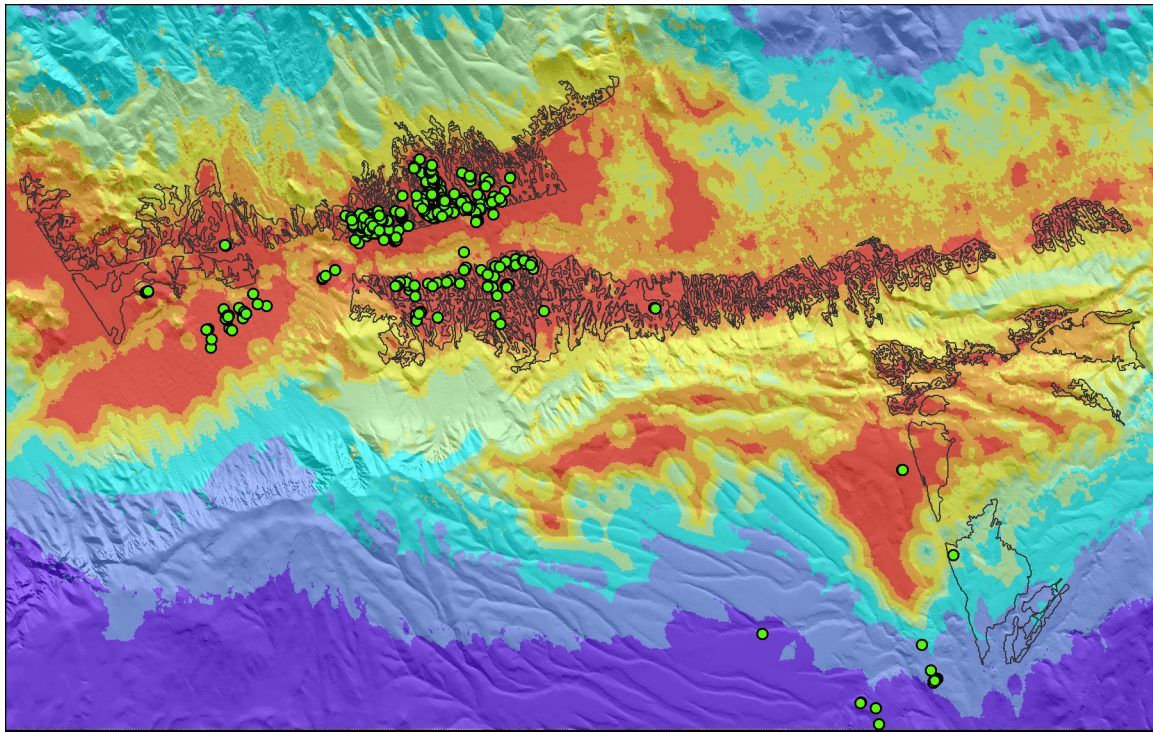
Figure 1-3: Map of the relative probability of use by greater sage-grouse (*Centrocercus urophasianus*) within Grass Valley, Utah, during winter. Dixie harrow treatments are outlined in black. Locations of sage-grouse that were used to validate our model (green points) were collected from November 2018 to March 2019 (after the study period).
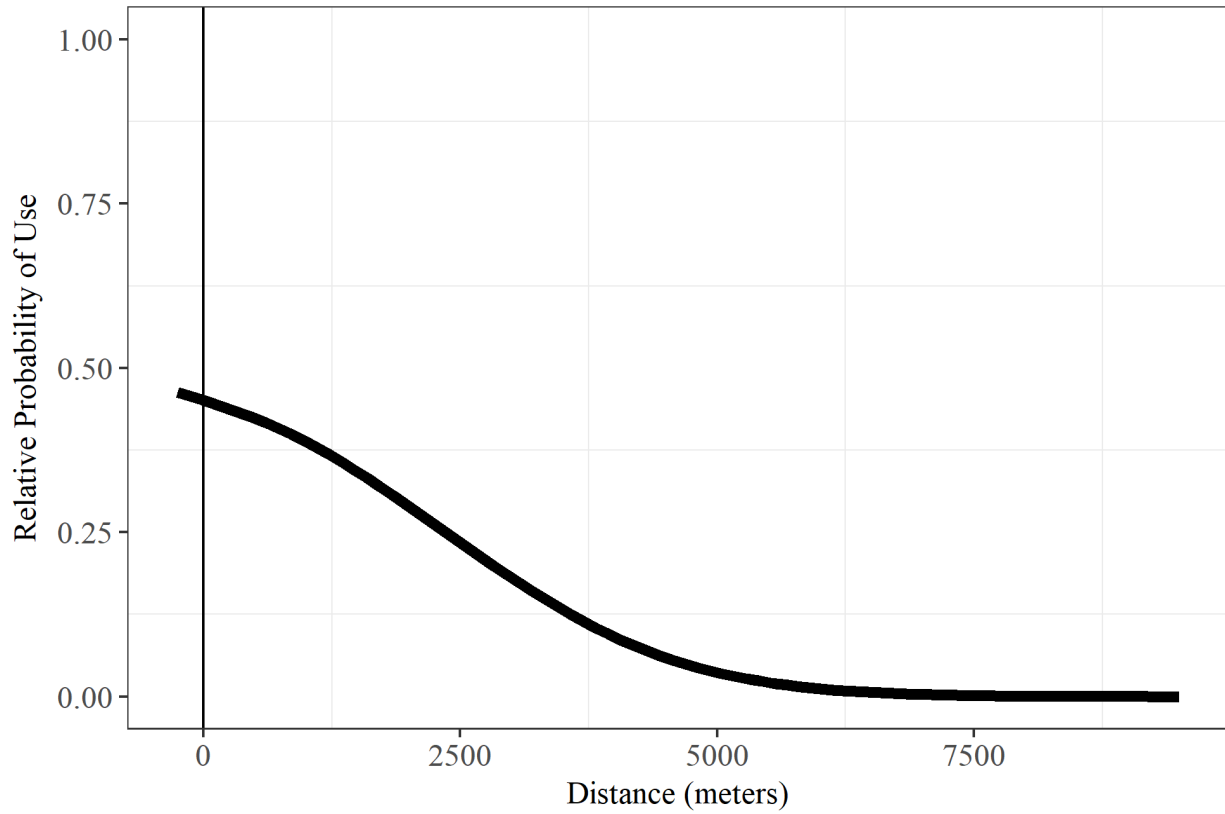
Figure 1-4: Plot of relative probability of use by greater sage-grouse (*Centrocercus urophasianus*) in relation to Dixie harrow treatment edges in Grass Valley, Utah, from November 2015 to March 2016 and November 2017 to March 2018. Negative distances represent locations that are within Dixie harrow treatments.

TABLES

Table 1-1: List of predictor variables included in our modeling process. Distance variables were first compared using a hierarchal modeling process. Distance variables which fit best were advanced to be used in *a-priori* model for resource selection by greater sage-grouse (*Centrocercus urophasianus*) during winter in response to Dixie harrow treatments in Grass Valley, Utah.

Variable Name	Description
Topographic	
Elev	Elevation in meters
Aspect	The four cardinal directions of aspect
Slope	Slope in degrees
TRI	Terrain Ruggedness Index (continous/unbinned)
TRIClass	Terrain Ruggedness Index (binned)
Anthropogenic	
DistMinorRd	Distance to minor roads
DistMinorRdSquared	Distance to minor roads squared
DistMajorRd	Distance to major roads
DistMajorRdSquared	Distance to major roads squared
DistAg	Distance to agriculture
DistAgSquared	Distance to agriculture squared
DistElecLine	Distance to electric lines
DistElecLineSquared	Distance to electric lines squared
Vegetation	
Veg	Vegetation cover type (binned)
DistShrub	Distance to shrubs
DistShrubSquared	Distance to shrubs squared
DistTree	Distance to trees
DistTreeSquared	Distance to trees squared
Treatment	
TREAT	Binary variable for being inside or outside Dixie harrow treatment
DistEdge	Distance to Dixie harrow treatment edges
DistEdgeSquared	Distance to Dixie harrow treatment edges squared

Table 1-2: Mean coefficient values ($\bar{\beta}$), standard errors (SE), and 95% confidence intervals (CI) for relative probability of use by greater sage-grouse (*Centrocercus urophasianus*) from November 2015 to March 2016 and from November 2017 to March 2018 in Grass Valley, Utah. Greater sage-grouse selected for Dixie harrow treatments, shrub-dominated areas, and locations relatively further from trees. The number of individuals that selected for (+) or against (-) each variable is also given.

Predictive Variable	$\bar{\beta}$	SE	95% CI	Number of sage-grouse with use significantly associated with predictive variable	
				+	-
Distance to Dixie Harrow Treatment Edge	-0.58	0.29	(-1.14 , -0.01)	4	8
Distance to Dixie Harrow Treatment Edge ²	-2.60	3.6	(-9.67 , 4.47)	4	4
Distance to Habitat Type Shrub (50 Decay)	-0.33	0.08	(-0.48 , -0.17)	1	9
Distance to Habitat Type Tree	0.66	0.06	(0.54 , 0.79)	12	
Distance to a Minor Road (500 Decay)	0.03	0.03	(-0.03, 0.09)	2	2

CHAPTER 2

Greater Sage-Grouse and Dixie Harrow Treatments: Nutritional Value of Sagebrush

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ABSTRACT

Herbivores generally consume plants that provide them with nutrients requisite to maintain and improve body condition while avoiding plants with relatively high concentrations of defensive compounds. The nutritional value of sagebrush (*Artemisia* spp.) differs significantly by species, subspecies, and plant. Habitat treatments such as Dixie harrow (which potentially result in the establishment of younger sagebrush) may also influence the nutritional value of sagebrush. Monitoring greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) use of habitat treatments is an effective method for modeling the effects of habitat treatments on herbivore foraging decisions. GPS tracking of a sage-grouse population in Grass Valley, Utah, suggests that sage-grouse spend a significant amount of time in Dixie harrow treatments during winter, when sagebrush constitutes more than 99% of their diet. This observation provides an opportunity to evaluate selection of forage by sage-grouse in relation to Dixie harrow treatments, as well as to evaluate any differences in the nutritional composition between sagebrush plants inside and outside Dixie harrow treatments. We predicted that (1) sage-grouse would select sagebrush plants that maximize primary metabolite consumption and minimize intake of secondary metabolites, (2) sage-grouse would browse sagebrush plants located within Dixie harrow treatments more frequently than in untreated areas, and (3) sagebrush within Dixie harrow treatments would differ in nutritional value from sagebrush in untreated areas because the sagebrush plants inside Dixie harrow treatments are generally younger. We based our predictions on previous observations of heavy use of Dixie harrow treatments by sage-grouse during winter

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(Chapter 1). We found that sage-grouse avoided secondary metabolites when foraging and also browsed plants inside Dixie harrow treatments more often than statistically expected. However, sagebrush plants inside Dixie harrow treatments did not differ from plants outside Dixie harrow treatments in their concentrations of primary or secondary metabolites; we therefore were unable to ascertain why sage-grouse selectively foraged inside Dixie harrow treatments.

INTRODUCTION

Herbivores optimize their diet by eating plants that provide the highest nutritional value (Timothy et al. 1987, McArt et al. 2009, Frye et al. 2013). Different species of plants, different individual plants of the same species, different parts of the same plant, and even the same parts of a plant during different seasons of the year all differ in nutritional value (Kelsey et al. 1982, Remington and Braun 1985, Timothy et al. 1987, Frye et al. 2013). Nutritional value is measured by the concentration of nutrients and plant secondary metabolites (PSMs). Nutrients such as protein and fiber promote plant growth, and are known as primary metabolites. PSMs are derived from primary metabolites and can also promote plant growth, but are mostly thought to discourage herbivory (Verma and Shukla 2015). PSMs act as toxins and inhibit digestion of nutrients by binding themselves to primary metabolites (Kohl et al. 2015, Verma and Shukla 2015).

On western rangelands, sagebrush (*Artemisia* spp.) is an important source of food for many herbivores (Wallestad and Eng 1975, Amasino 2004, Johansson et al. 2015, Smith et al. 2015). The nutritional value of sagebrush differs by species, subspecies, plant, and season (Timothy et al. 1987, Frye et al. 2013, Jaeger et al. 2016). To maximize their fitness while consuming sagebrush, herbivores eat from plants high in primary metabolites while avoiding plants high in

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secondary metabolites (Timothy et al. 1987, Frye et al. 2013). However, finding balance between consuming plants high in primary metabolites while avoiding those high in secondary metabolites can be complex. For example, when compared to black sagebrush (*Artemisia nova*), Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) has a 10% higher concentration of crude protein and a 32% higher concentration of monoterpenes (Frye et al. 2013). When greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are given a choice between Wyoming big sagebrush and black sagebrush, they select to forage on black sagebrush more frequently, even though Wyoming big sagebrush is higher in protein (Frye et al. 2013). This suggests that the nutritional value of black sagebrush is comparatively higher to sage-grouse because it has a relatively low concentration of monoterpenes. The potential detriment of consuming a higher concentration of PSMs outweighs the benefit of a potentially increased intake of protein. Thus we see that foraging decisions are finely balanced between the relative concentrations of nutrients and PSMs.

Sage-grouse are a sagebrush-obligate species, and have therefore adapted to mitigate the effects of consuming PSMs by producing enzymes that resist secondary metabolite inhibition during digestion (Kohl et al. 2015). However, despite these specialized enzymes, sage-grouse still minimize their intake of PSMs when selecting sagebrush that is high in primary metabolites (Remington and Braun 1985, Sauls 2006, Frye et al. 2013). Sage-grouse selectively browse sagebrush that is low in decadence (Remington and Braun 1985). If sage-grouse select for less decadent sagebrush (which are likely younger plants), young sagebrush plants may also be higher in primary metabolites and/or lower in secondary metabolites.

Young and vigorous sagebrush plants are often found in sites treated by Dixie harrow. Dixie harrow treatments involve either partial or complete removal of sagebrush to promote grass and

forb diversity. Forbs are a staple in the diet of young sage-grouse broods (Drut et al. 1994, Dahlgren et al. 2006). However, while forbs are important for the brood-rearing period, sagebrush constitutes the vast majority of sage-grouse diet during adulthood, reaching 100% of their diet during winter (Wallestad and Eng 1975). Dixie harrow treatments reduce the amount of sagebrush available to sage-grouse during winter, but may increase the nutritional value of sagebrush by promoting the growth of young and vigorous sagebrush plants.

Our objective was to evaluate selection of forage by sage-grouse in relation to Dixie harrow treatments, as well as evaluate any differences in the nutritional composition of plants inside and outside Dixie harrow treatments. We predicted that (1) sage-grouse would select sagebrush plants that maximize primary metabolite consumption and minimize intake of secondary metabolites, (2) sage-grouse would browse sagebrush plants located within Dixie harrow treatments more frequently than in untreated areas, and (3) sagebrush within Dixie harrow treatments would differ in nutritional value from sagebrush in untreated areas because the sagebrush plants are generally younger.

METHODS

Study Area

Our study area in Grass Valley, Utah, provided us with the opportunity to study sage-grouse habitat selection and foraging preferences within a mosaic of Dixie harrow treatments; approximately 6,000 hectares of sagebrush in Grass Valley were treated using Dixie harrow between 1997 and 2008. The Bureau of Land Management (BLM) performed these treatments to stimulate the growth of grasses and forbs during spring and summer. A tractor was used to drag a Dixie harrow implement that removed 50% of the older sagebrush (age 80–100 years old)

(Dahlgren et al. 2006). Young sagebrush plants now occupy treated areas with interspersed grasses and forbs. Common sagebrush species in Grass Valley include black sagebrush (*Artemisia nova*), big sagebrush (*Artemisia tridentata*), and silver sagebrush (*Artemisia cana*). Other common vegetation includes forbs such as dandelion (*Taraxacum* spp.), lupine (*Lupinus* spp.), and milkvetch (*Astragalus* spp.); grasses such as downy brome (*Bromus tectorum*), bluegrass (*Poa* spp.), blue grama (*Bouteloua gracilis*.), squirreltail (*Elymus elymoides*.), and wheatgrass (*Agropyron* spp.); and trees such as quaking aspen (*Populus tremuloides*), singleleaf pinyon (*Pinus monophylla*), and Utah juniper (*Juniperus osteosperma*). During winter most plants in our study area are senescent except sagebrush, singleleaf pinyon, and Utah juniper.

The major landforms in the area are Dutton Mountain, Monroe Mountain, Otter Creek Reservoir, and Parker Mountain. Local communities include Antimony, Greenwich, and Koosharem. The elevation in our study area ranged from 1,942 to 3,421 meters. Average annual snowfall in Antimony was 53 centimeters. Winter temperatures reached an average low of -14 °C and an average high of 4 °C from 1981 to 2010 (ClimateData 2017).

Sage-grouse Monitoring

We used a spotlighting method to capture sage-grouse during March, April, May, September, and October from 2016 to 2018 (Wakkinen et al. 1992). We captured sage-grouse within Dixie harrow treatments and from surrounding leks, and fit them with GPS transmitters (22g rump-mounted transmitters made by GeoTrak Incorporated®). We assigned sex to each captured sage-grouse according to plumage and mass (Bihrle 1993, Connelly et al. 2004). GPS transmitters acquired four locations daily (01:00, 08:00, 16:00, and 21:00 GMT) November–February, and five locations daily (07:00, 14:00, 17:00, 20:00, and 23:00 GMT) March–October. The GPS

transmitters stored their locations and transmitted them to a satellite every three days. We monitored GPS-mounted sage-grouse by downloading their locations weekly and evaluating habitat use and movement patterns.

Sagebrush Sampling

To assess the nutritional value of sagebrush, we sampled browsed, non-browsed, and random leaves from sagebrush plants December 2017–February 2018 in treated and untreated areas. We approached areas frequented by GPS-mounted sage-grouse to locate browsed and non-browsed plants, or walked parallel transects spaced 30 meters apart until we flushed or found sign of sage-grouse. If we found sage-grouse footprints or scat within 0.5 meters of a sagebrush plant, we inspected that plant to determine if it had been browsed (Figure 2-1). Plants were determined "browsed" if we found a minimum of 10 sage-grouse bite marks, and "non-browsed" if there were no bite marks (Frye et al. 2013). Fresh sage-grouse bite marks can easily be recognized by a contrast in color between the light green exterior and dark green interior of recently nipped leaves (Welch et al. 1988, Sauls 2006, Frye et al. 2013). We limited collection of sagebrush samples at each sage-grouse sighting or "patch" to three browsed and three non-browsed samples (Welch et al. 1988, Frye et al. 2013). Because sage-grouse footprints were only recognizable in snow, warm temperatures limited our sampling period for browsed and non-browsed samples to be the few days post-snowfall (before snow melted) from December 2017 to February 2018.

Using ArcGIS Pro (ESRI®, Redlands, CA), we generated random coordinates for collecting random samples inside and outside Dixie harrow treatments. We collected samples from the three nearest plants to ten random coordinates inside a 2005 treatment, ten random coordinates outside a 2005 treatment, ten random coordinates inside a 2008 treatment, and ten random

coordinates outside a 2008 treatment. Collection of random samples did not require any tracking of sage-grouse, and was completed on non-snow days from December 2017 to February 2018. We collected random samples with no regard to the presence or absence of sage-grouse tracks or bite marks (Sauls 2006, Frye et al. 2013). For consistency during modeling, we limited collection of clippings to a single sagebrush sub-species (*A.t. wyomingensis*) at each sampling location, whether it was a browsed, non-browsed or a random location. Because the chemistry of *A.t. tridentata* and *A.t. vaseyana* differs from that of *A.t. wyomingensis* (Jaeger et al. 2016), we only collected samples from *A.t. wyomingensis*. Thus any differences in chemistry between subspecies did not influence our results when comparing sagebrush inside and outside Dixie harrow treatments.

We collected measurements of shrub canopy cover, shrub width, shrub height, basal circumference, aspect, and slope from sampled plants. To measure canopy cover, we used a line intercept method along four 25 meter transects, originating from the approximate center of the collection site. We also made a visual approximation of percent decadence for each plant. Because deep snow may render small shrubs unavailable to sage-grouse, we measured snow depth and classified snow as either hard-packed or powder. However, snow depth never exceeded 9 centimeters within our study years.

Chemical Assays

We performed lab analyses of sagebrush samples to measure the concentrations of primary and secondary metabolites (Welch et al. 1988, Sauls 2006, Frye et al. 2013). We measured water content by drying a subsample of each sagebrush sample by baking for 48 hours at 60 °C (Welch et al. 1988, Sauls 2006). After drying, we ground this subsample in a Wiley Mill prior to being

measured for fiber and protein content (Sauls 2006). We measured fiber content using an ANKOM 200 fiber analyzer. We calculated percent crude protein by measuring percent nitrogen via a LECO TruSpec CN, and multiplied percent nitrogen by 6.25 to get percent crude protein. We kept a second subsample of fresh material from each plant frozen to prevent the loss of volatile compounds through evaporation. We ground this second subsample of fresh material in liquid nitrogen using a mortar and pestle. Using a portion of the fresh subsample we measured several individual monoterpenes by headspace gas chromatography (Frye et al. 2013). We sent another portion of the fresh subsample to Boise State University to have total phenolic and coumarin concentrations measured by liquid extraction and spectrophotometry (Frye et al. 2013).

Statistical Analysis

To evaluate chemical differences in browsed and non-browsed plants, we evaluated browsing as a response to physical (shrub height, shrub crown area, shrub surface area, percent decadence, base circumference, slope, aspect, and percent cover) and nutritional (water, protein, neutral detergent fiber, acid detergent fiber, hemicellulose, total coumarin, total phenolics, and various individual monoterpenes) factors (Table 2-1). Browsed samples were compared to our non-browsed samples using logistic regression. Independent factors that were correlated with $|r| > 0.6$ were excluded from our *a-priori* models. Because multiple sagebrush samples were collected at each location (three from each random location, and six from each foraging location) we included a random variable "Patch" to account for any spatial auto-correlation. *A-priori* models were evaluated using an AICc goodness-of-fit test (Arnold 2010). Because our non-browsed samples were spatially correlated with our browsed samples, this allowed us to evaluate our

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hypothesis that sage-grouse were maximizing their consumption of primary metabolites and minimizing intake of secondary metabolites.

We used a likelihood ratio test (*G*-test) to evaluate sage-grouse preference for or against Dixie harrow treated sagebrush for food. To obtain the expected ratio of browsed plants in Dixie harrow treatments, we first created a model of the winter use area of sage-grouse by combining the individual winter use areas for birds with GPS transmitters. We created winter use areas of individual sage-grouse using R package BBMM (Horne et al. 2007). A Brownian bridge movement model, or BBMM, was used to create utilization distributions (Newton et al. 2017). When our BBMMs resulted in a use area consisting of multiple polygons, only those polygons that overlapped our Dixie harrow treatment areas were used in creating the population-level use area. Including large portions of use areas at neighboring leks that had no Dixie harrow treatments would have biased the expected ratio towards untreated habitat. By maximizing the amount of treated area in our use area we created a conservative model which allowed a greater number of expected browsing locations inside Dixie harrow treatments. We obtained the expected ratio of plants eaten within Dixie harrow treatments to those eaten in untreated areas using the ratio of Dixie harrow treatment area to untreated area within the use area.

We used our samples of sagebrush leaves that were collected from random locations inside and outside Dixie harrow treatments to evaluate differences in nutritional value between treated and untreated plants. We created *a-priori* models and used logistic regression with treatment by Dixie harrow as a response to physical and nutritional factors, as well as the random variable "Patch" to account for spatial auto-correlation. Independent factors that were correlated with |r| > 0.6 were excluded from our a-*priori* models. To evaluate our *a-priori* models we used an AICc goodness-of-fit test (Arnold 2010).

RESULTS

Sage-grouse Monitoring

During the first year of our study we captured 29 sage-grouse (12 males and 17 females), and during the second year we captured 38 sage-grouse (19 males and 19 females). We monitored 67 total sage-grouse (31 males and 36 females) from March 2016 to March 2018. In that time we collected 46,304 sage-grouse locations. Of the 67 sage-grouse we captured, only 36 survived for any portion of either winter period, and only 12 (4 males and 8 females) had winter use areas that overlapped our Dixie harrow treatment areas. Using the most recent location data from those 12 sage-grouse, we located sagebrush plants that had been browsed or not browsed by sage-grouse.

Sagebrush Collection

We collected a total of 228 sagebrush samples from December 2017 - February 2018 (Figure 2-2). Of the 228 sagebrush samples, 54 were browsed, 54 were non-browsed, and 120 were from plants at random points. Browsed and non-browsed samples were collected from plants at 18 sites and random plants were collected from 40 sites (20 inside and 20 outside Dixie harrow treatments). We collected 48 browsed samples from 16 sites within Dixie harrow treatments, and 6 browsed samples from 2 sites outside Dixie harrow treatments. All samples collected (browsed, non-browsed, and random) were from the subspecies *A. tridentata wyomingensis*, except 1 browsed sample, 3 non-browsed samples, and 4 random samples that were misclassified in the field. We confirmed subspecies of sagebrush by chemical profile, and didn't progress the misclassified samples into our modeling process (Timothy et al. 1987, Jaeger et al. 2016).

Statistical Analysis

We found nutritional differences between browsed and non-browsed plants. Model selection using an AICc selection criterion resulted in four models with a model weight ≥ 0.01 (Table 2-2). We determined that one of our four top models included an uninformative parameter based on an ΔAICc of 2.34 with only a single additional covariate from our top model and no change to log likelihood (Arnold 2010). Our top three remaining models showed significant (85% confidence intervals not overlapping zero) negative relationships to phenolic and coumarin concentrations while showing a positive relationship to the individual monoterpene camphor (Table 2-3). Percent crude protein and percent water content were nearly significant (85% confidence intervals [-0.05; 0.74] and [-0.06; 0.69] respectively) with positive relationships (Figure 2-3). None of our models with weights ≥ 0.01 included any covariates related to physical attributes, treatments, or treatment year.

Using a *G*-test for goodness-of-fit we found that sage-grouse eat from plants within Dixie harrow treatments more than statistically expected. We batched our browsed samples into the 18 sites they were collected from. Using our expected ratio of 0.34 treated to 0.66 untreated locations (15.47 km² of Dixie harrow treated habitat to 29.57 km² of untreated habitat), we calculated that the number of browsing sites found within Dixie harrow treatments should be 6. However, 16 of our 18 browsing sites were found in Dixie harrow treatments. This resulted in a *G*-value of 21.40 and a p-value < 0.05, meaning there were far more browsing sites inside Dixie harrow treatments than would have been statistically expected.

When selecting models for evaluating differences in random sagebrush samples inside and outside Dixie harrow treatments, we had two models with a model weight ≥ 0.01 (Table 2-4). Our top models included independent factors for percent cover, shrub height, and shrub

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decadence. However, only percent cover had 85% confidence intervals that did not overlap zero (Table 2-5). Neither of our top models included any covariates related to the nutritional value of sagebrush. Our best model that contained chemical covariates included variables for percent shrub cover, shrub height, shrub decadence, percent water content, percent crude protein, percent neutral detergent fiber, phenolic concentration, and coumarin concentration, but resulted an AIC weight lower than the weight of our null model.

DISCUSSION

While sage-grouse selected sagebrush to browse according to each plant's nutritional value in Grass Valley, we found no difference in nutritional value between sagebrush treated by Dixie harrow and sagebrush that hadn't been treated. Sage-grouse selected plants that were relatively low in total phenolic and coumarin concentrations, and relatively high in camphor concentration. Camphor is typically a deterrent to herbivores, but sage-grouse have adapted to minimize enzyme inhibition from camphor (Kohl et al. 2015). It should be noted that compared to other subspecies of *Artemisia tridentata*, *Artemisia tridentata wyomingensis* is known to produce very low concentrations of coumarin (Jaeger et al. 2016). Sage-grouse avoidance of PSMs in Grass Valley was generally consistent with previous studies of sage-grouse foraging habits (Welch et al. 1988, Frye et al. 2013).

We also found that sage-grouse selected for increased crude protein and water content. Percent crude protein has previously been found to be a reliable predictor of sage-grouse selection (Sauls 2006, Frye et al. 2013). Crude protein was a variable in two of our top three models, and coefficients were positive, but had an 85% confidence interval that slightly overlapped zero (Table 2-3). Percent water content was also a variable in two of our top three

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models, and had a positive coefficient, but had an 85% confidence interval that slightly overlapped zero (Table 2-3). Selection for water content has not been previously supported in literature.

Even though sage-grouse selected plants according to their nutritional value, and sage-grouse browsed plants inside Dixie harrow treatments more frequently than expected, sagebrush inside Dixie harrow treatments did not differ from untreated sagebrush in its nutritional value. We therefore were unable to ascertain why sage-grouse selected so strongly for plants within Dixie harrow treatments during winter. Sage-grouse in Grass Valley may be foraging in Dixie harrow treatments for reasons besides nutritional value. On average, Dixie harrow treatments in Grass Valley reduced percent shrub cover from 15.94% to 9.64%, reduced plant height from 47.07 cm to 26.62 cm, and reduced percent decadence from 31.3% to 12.13%. Although nutrition played a significant role when choosing plants to browse at the plant scale; visibility may be a more important factor when selecting a foraging site at the patch scale during winter (Wambolt 2004). A reduction in percent cover and plant height inside Dixie harrow treatments would potentially increase visibility. Other studies have also found that sage-grouse forage during winter in areas of increased visibility (Hagen et al. 2011, Frye et al. 2013). Further research may find sagebrush structure and cover to influence sage-grouse selection of winter forage more strongly than the nutritional quality of sagebrush at the patch scale. Further research may also find other compounds that influence sage-grouse selection of winter forage more strongly than the compounds we measured.

Our results apply best to conditions most similar to those that exist in our study area, and the effects of Dixie harrow treatment in Grass Valley may not be applicable to Dixie harrow treatments in other areas. In our case, Dixie harrow treatments resulted in the establishment of

young sagebrush with interspersed grasses and forbs. Dixie harrow could easily result in a grass-dominated treatment area, which would likely not have the same effect on sage-grouse foraging decisions as it did in Grass Valley. If sagebrush failed to reestablish there would likely be no food or cover in treated areas for sage-grouse during winter.

Our findings may also be unique, and not applicable to many other sage-grouse populations, because Grass Valley is at the southern extent of the sage-grouse range. Here, winters are relatively mild, and even the youngest sagebrush plants are rarely covered by snow for long periods of time. If our study area had been located farther north, the sagebrush plants in treatment areas likely would have been buried in snow while untreated sagebrush remained above the snow. When looking for food, sage-grouse would only find sagebrush outside Dixie harrow treatments, and a lack of above-snow sagebrush in Dixie harrow treatments may alter sage-grouse preference in favor of untreated areas.

In conclusion, sage-grouse in Grass Valley browsed from plants lower in total phenolics and coumarins, but higher in camphor, crude protein, and water content. Sage-grouse foraged for food in Dixie harrow treatments more often than was expected, but Dixie harrow treatments had no effect on the nutritional value of sagebrush. Future research may find that sage-grouse preference for Dixie harrow treatments is related to the nutritional value of sagebrush, but that relationship was not found in the compounds that we measured. Plant vigor and percent cover may be more influential than the nutritional value of sagebrush when sage-grouse are selecting areas to forage in at the patch scale.

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Figure 2-1: Photo of sagebrush plants (*Artemisia tridentata*) that greater sage-grouse (*Centrocercus urophasianus*) passed by. Greater sage-grouse footprints are recognizable in the snow. From December 2017 to February 2018, we collected samples of sagebrush that greater sage-grouse passed by in Grass Valley, Utah. Presence of footprints (or other greater sage-grouse sign) within 0.5 meters of a sagebrush plant qualified that plant for inspection of browsing activity.
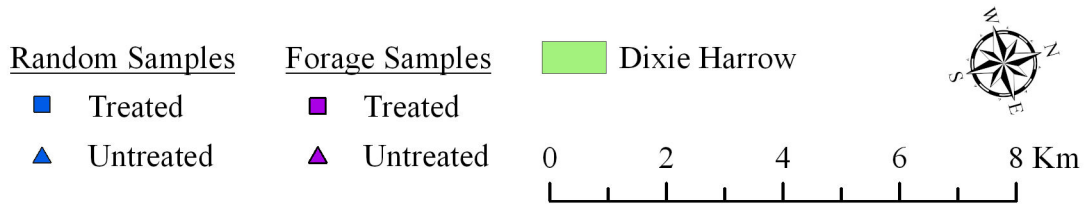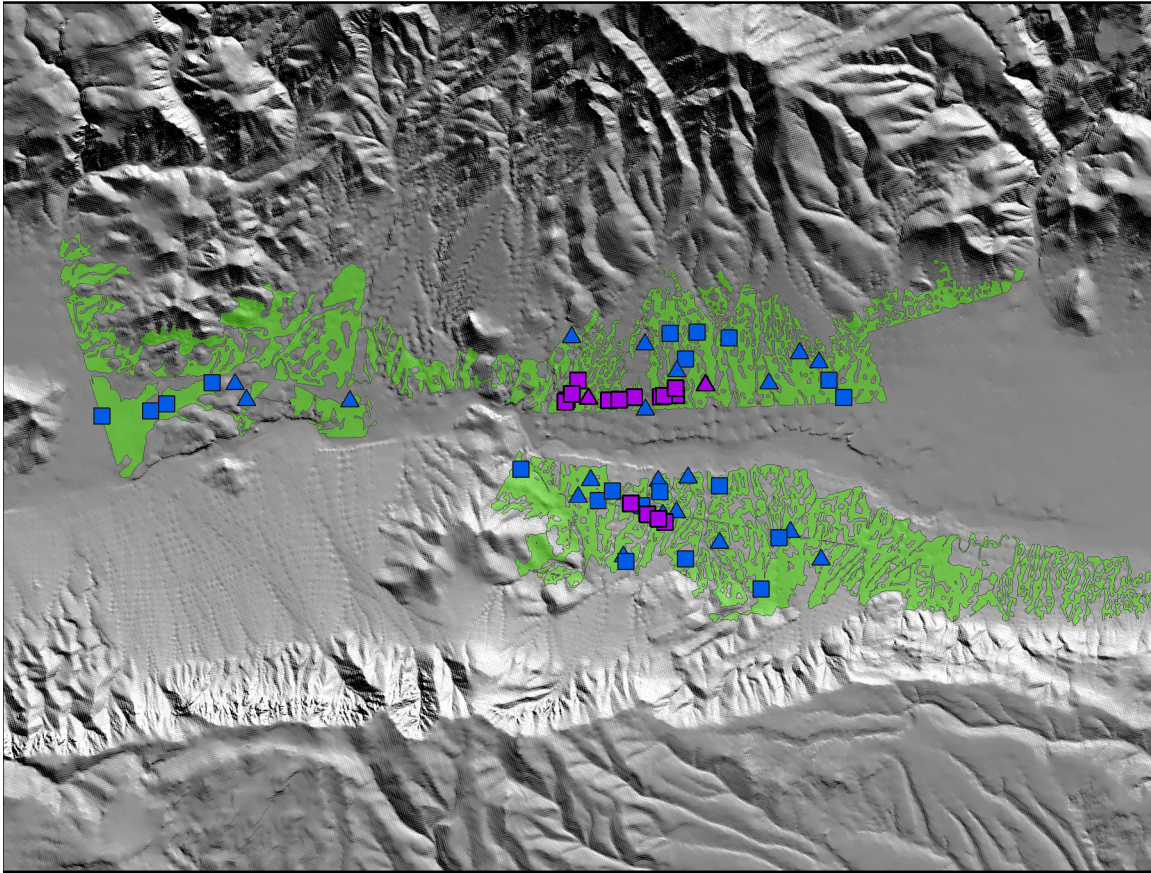
Figure 2-2: Locations of sagebrush (*Artemisia tridentata*) samples taken in Grass Valley, Utah, from December 2017 to February 2018. Samples taken from plants that greater sage-grouse (*Centrocercus urophasianus*) had either eaten from or passed by are marked by purple points. Samples collected from random locations inside and outside Dixie harrow treatments for measuring the effects of Dixie harrow treatments on the nutritional value of sagebrush are marked by blue points.

TABLES

Table 2-1: List of predictor variables when modeling greater sage-grouse (*Centrocercus urophasianus*) selection of forage and differences between sagebrush (*Artemisia tridentata*) inside and outside Dixie harrow treatments in Grass Valley, Utah.

Variable Name	Description
Sampling Site	
Patch	Sampling patch site ID
In.Out	Binomial for being inside or outside Dixie harrow treatments
PercentCover	Percent shrub cover measured along 2 perpendicular 25 meter transects
Slope	Visually estimated slope at the collection site
Aspect	Visually estimated aspect at the collection site
SnowDepth	Greatest depth of snow at the collection site
Physical	
ShrubHeight	Plant height
CrownArea	Crown's longest width/2 * crown's perpendicular width/2 * π
ShrubVolume	Crown's longest width * crown's perpendicular width * plant height
Decadence	Visual estimation of the percent decadence of the sagebrush plant sampled
BaseCirc	Circumference of plant measured at ground level from the largest stem
Nutritional	
Water	Percent water
Protein	Percent crude protein
NDF	Percent NDF
ADF	Percent ADF
Hemicellulose	Percent hemicellulose
Phenolics	Concentration of total phenolics
Coumarin	Concentration of coumarin
APin	Concentration of the individual monoterpene α-pinene
BPin	Concentration of the individual monoterpene *β*-pinene
PCym	Concentration of the individual monoterpene p-cymene
Cin	Concentration of the individual monoterpene 1,8-cineole
AThu	Concentration of the individual monoterpene *α*-thujone
Cam	Concentration of the individual monoterpene camphor

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Table 2-2: Model results (model weight ≥ 0.01) from our Akaike's Information Criterion (AIC) table when evaluating sagebrush (*Artemisia tridentata wyomingensis*) that greater sage-grouse (*Centrocercus urophasianus*) had eaten from or passed by in response to physical and nutritional covariates. Table displays model structure, number of parameters (K), corrected AIC (AICc), change in AICc from the top model (ΔAICc), model weight (Wt), and log likelihood (LL).

Model Number	Model Structure	K	AICc	ΔAICc	Wt	LL
9	(1|Patch)+Water+Protein+NDF+Phenolics+Coumarin	7	137.63	0.00	0.63	-61.23
8[1]	(1|Patch)+In.Out+Water+Protein+NDF+Phenolics+Coumarin	8	139.97	2.34	0.20	-61.23
10	(1|Patch)+Phenolics+Coumarin+Cam+Cin+Athu+Bpin	8	140.83	3.20	0.13	-61.66
7	(1|Patch)+Water+Protein+NDF+Phenolics+Coumarin+Cam+Cin+Athu+Bpin	11	143.55	5.91	0.03	-59.34
12	(1|Patch)	2	148.25	10.62	0.00	-72.07

[1] Uninformative model based on AICc and variables.

Table 2-3: Coefficient values (*β*) from our top models (model weight ≥ 0.01) evaluating sagebrush (*Artemisia tridentata wyomingensis*) that greater sage-grouse (*Centrocercus urophasianus*) had eaten from or passed by in response to physical and nutritional covariates. Table displays model numbers from Table 2-2, and *β* coefficients of covariates with 85% confidence intervals. *β* coefficients with an asterisk (*) had an 85% confidence interval that did not overlap zero. Covariates match those listed in Table 2-1.

Model Number	*β* coefficients and 85% confidence intervals										
	(Intercept)	In.Out	Water	Protein	NDF	Phenolics	Coumarin	Cam	Cin	AThu	BPin
9	0.04		0.32	0.28	0.1	-0.65*	-0.50*				
	[-0.28; 0.36]		[-0.06; 0.69]	[-0.10; 0.66]	[-0.23; 0.44]	[-1.01; -0.28]	[-0.86; -0.15]				
8[1]	0.05	-0.06	0.32	0.28	0.1	-0.65*	-0.50*				
	[-0.29; 0.38]	[-1.13; 1.00]	[-0.06; 0.69]	[-0.10; 0.67]	[-0.23; 0.44]	[-1.02; -0.28]	[-0.86; -0.15]				
10	0.02					-0.76*	-0.41*	0.41*	-0.15	0.14	-0.13
	[-0.29; 0.34]					[-1.15; -0.37]	[-0.74; -0.08]	[0.02; 0.80]	[-0.58; 0.29]	[-0.21; 0.49]	[-0.50; 0.24]
7	0.03		0.3	0.34	0.1	-0.72*	-0.45*	0.44*	-0.1	0.1	-0.19
	[-0.29; 0.36]		[-0.10; 0.70]	[-0.05; 0.74]	[-0.25; 0.45]	[-1.12; -0.32]	[-0.80; -0.09]	[0.03; 0.85]	[-0.57; 0.37]	[-0.24; 0.45]	[-0.58; 0.21]
12	0.04										
	[-0.24; 0.32]										

[1] Uninformative model based on AICc and variables.

Table 2-4: Model results (model weight ≥ 0.01) from our Akaike's Information Criterion (AIC) table when evaluating sagebrush (*Artemisia tridentata wyomingensis*) that had been treated by Dixie harrow in response to physical and nutritional covariates. Table displays model structure, number of parameters (K), corrected AIC (AICc), change in AICc from the top model (ΔAICc), model weight (Wt), and log likelihood (LL).

Model Number	Model Structure	K	AICc	ΔAICc	Wt	LL
2	(1|Patch)+PercentCover	3	48.50	0.00	0.83	-21.15
3	(1|Patch)+PercentCover+ShrubHeight+Decadence	5	51.72	3.21	0.17	-20.59
10	(1|Patch)	2	58.38	9.87	0.01	-27.14

Table 2-5: Coefficient values (*β*) from our top models (model weight ≥ 0.01) evaluating sagebrush (*Artemisia tridentata wyomingensis*) that had been treated by Dixie harrow in response to physical and nutritional covariates. Table displays model numbers from Table 2-4, and *β* coefficients of covariates with 85% confidence intervals. *β* coefficients with an asterisk (*) had an 85% confidence interval that did not overlap zero. Covariates match those listed in Table 2-1.

Model Number	*β* coefficients and 85% confidence intervals			
	(Intercept)	PercentCover	ShrubHeight	Decadence
2	-5.74	-25.35*		
	[-17.33; 5.85]	[-45.27; -5.43]		
3	-7.8	-22.39*	-4.78	-2.92
	[-16.07; 0.46]	[-43.30; -1.48]	[-17.07; 7.51]	[-7.87; 2.02]
10	-12.03*			
	[-15.41; -8.64]			