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Long-term declines in greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') populations have captured the attention of land and wildlife managers. Fragmentation and loss of large, continuous sagebrush (*Artemisia* spp.) habitats is considered the leading cause of decreased populations of sage-grouse throughout their entire range. In response, managers in many areas have implemented small sagebrush reduction treatments to improve habitat conditions for brood-rearing sage-grouse. As such, a large body of research has focused on vegetative responses, and, to a lesser degree, wildlife-population responses to sagebrush habitat manipulations. Some research has shown potential benefits of habitat treatments to sage-grouse in mountain big sagebrush (*A. tridentata vaseyana*). Although vegetation in Wyoming big sagebrush (*A. t. wyomingensis*) responds differently than in mountain big sagebrush following reduction treatments, the response of sage-grouse to treatments in mountain or Wyoming big sagebrush communities has not been thoroughly investigated. The purpose of my thesis was to evaluate habitat selection and short-term (4 years since treatment) demographic response by sage-grouse to treatments in Wyoming big sagebrush habitats.

My study was the first to evaluate both short-term demographic responses and habitat selection of sage-grouse to mowing and tebuthiuron treatments in Wyoming big sagebrush habitats. I conducted my research by using pre- and post-treatment data from n = 512 radio-marked female sage-grouse over a 7-year period (2011–2017) within the 4,595 km^2 Jeffrey City study area in central Wyoming, USA. My study employed a Before-After Control-Impact design with 3 years of pre-treatment (2011–2013) and 4 years of post-treatment (2014–2017) data to evaluate sage-grouse responses. Mowing and tebuthiuron treatments were implemented in mosaic patterns replicated across 2 study areas each nested within our larger study area during winter and spring 2014, respectively. Mowing reduced canopy cover to ~25.4 cm and tebuthiuron treatments were applied at a rate of 0.22 kg/ha active ingredient to achieve 50% sagebrush kill. Two remaining nested study areas served as offsite untreated control areas.

Our primary objective for Chapter 2 was to identify how treatments influenced habitat selection of female sage-grouse during nesting, brood-rearing, and broodless periods. We found nesting, brood-rearing, and broodless sage-grouse selected for mowing and tebuthiuron treatment areas before and after treatment; however, a before-after treatment interaction suggested selection did not differ or was less strong after treatments. The primary objective for Chapter 3 was to assess the short-term demographic response of sage-grouse to treatments in Wyoming big sagebrush. We did not detect a before-after impact of sagebrush treatments on sage-grouse nest success, brood success, or adult female survival. The results of my thesis research suggest that treating Wyoming big sagebrush may not increase the habitat quality of Wyoming big sagebrush for sage-grouse. This suggests managers should assess the need and predicted success of sagebrush reduction treatments in Wyoming big sagebrush that are intended to enhance habitat conditions for breeding sage-grouse.

HABITAT SELECTION AND SHORT-TERM DEMOGRAPHIC RESPONSE OF GREATER SAGE-GROUSE TO HABITAT TREATMENTS IN WYOMING BIG SAGEBRUSH

By

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CHAPTER ONE

INTRODUCTION

Background

The rapid expansion of human civilization over recent centuries has resulted in drastic alteration to terrestrial and aquatic environments. For example, from 1700–1990 global agricultural and pasture lands increased approximately 5.5- and 6.5-fold, respectively (Goldewijk 2001). By comparison, the average worldwide rate of deforestation decreased from 1990–2005 because of afforestation and forest regeneration efforts; however, as of 2005, the world's forests were still diminishing at a rate of 0.18% per year (FAO 2006). Average human population growth rates in rural areas are greater near protected areas (Wittemyer et al. 2008) emphasizing the intrinsic and instrumental value placed on these regions; however, this attraction could potentially have a negative influence on species within the protected area. Moreover, habitat loss resulting from energy exploration can impact wildlife survival and behavior (Northrup and Wittemyer 2013). Habitat loss is generally accepted as the leading cause of population declines and extinction events. Current human impacts are believed to be responsible for reducing earth's biodiversity to its lowest point in the last 65 million years (Wilson 1989). Impacts of habitat destruction to wild vertebrate populations have been widely documented, with countermeasures often including establishment of conservation reserves and habitat improvement. Approximately 29% of the earth's terrestrial and marine regions are considered protected areas (UNEP-WCMC and IUCN 2016). Areas that do not fall under protection may receive special efforts to promote the establishment of higher quality habitats for targeted species of concern affected by anthropogenic change.

Conservation and restoration of high quality wildlife habitat is essential to the persistence of wildlife populations. Historically, species density was believed to be an appropriate measure of habitat quality, however habitat quality is not only a function of an animal's use of habitat, but also its ability to survive and reproduce (Van Horne 1983). An animal's ability to survive and reproduce is directly correlated to the quality of habitat that it occupies (Wilson and Nussey 2010). As such, wildlife researchers have reported the importance of demographic rates as direct measures of habitat quality (Johnson 2007). For example, Gunnarsson et al. (2005) found that Icelandic black-tailed godwit (*Limosa limosa islandica*) bred at higher densities and more successfully in coastal areas compared to inland areas, suggesting that coastal regions were of higher quality to godwit populations. Martin (1998) demonstrated that preferred habitats of nesting passerines was positively related to fitness. Understanding the relationship between species occurrence and survival across heterogeneous habitats becomes necessary when focusing conservation efforts and management of a species of interest. Habitat management practices often aim to increase habitat quality for select wildlife species. For example, Carter et al. (2002) used prescribed burning to increase forage availability for northern bobwhite (*Colinus virginianus*), but found similar short-term survival rates and nest success between treatment and control sites, suggesting that treatment areas did not increase individual bobwhite fitness. Rocky Mountain elk (*Cervus elaphus*) selected mechanically thinned and burned forest stands in the spring while selecting against treatments or using treatment areas equal to their availability during summer (Long et al. 2008). In the same study, mule deer (*Odocoileus hemionus*) either selected against treated areas or used them proportional to their availability (Long et al. 2008). A comprehensive review of herbicide applications, mechanical treatments, and prescribed fire in Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) habitats intended to enhance habitats for sagebrush-occurring wildlife suggested that relatively little benefit exists for wildlife as a result of treating this subspecies of big sagebrush; however, more experimental work was deemed necessary (Beck et al. 2012).

Over the past half century, declining trends in populations of the greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse'; Connelly et al. 2004, Schroeder et al. 2004, Nielson et al. 2015) have captured the attention of wildlife managers. The distribution of sage-grouse was believed to have declined to nearly half its presettlement range by 2000 (Schroeder et al. 2004). A recent investigation found estimated yearly population declines of 0.8−2.1% from 1965–2015 (Connelly et al. 2004, Nielson et al. 2015, WAFWA 2015) with the most alarming rates occurring after 2005 (Nielson et al. 2015). From 1999 to 2005, the United States Fish and Wildlife Service (USFWS) received 8 petitions to list sage-grouse under the U.S. Endangered Species Act of 1973, but listing was not found to be warranted or was warranted but precluded due to other species of higher conservation priority (U.S. Fish and Wildlife Service 2010). More recently, in 2015, the USFWS did not find listing the sage-grouse under the Endangered Species Act was warranted (U.S. Fish and Wildlife Service 2015). However, without continued conservation efforts to protect and improve sage-grouse habitat, the species could become listed in the future.

Declines in sage-grouse populations are attributed to anthropogenic change and degradation of sagebrush ecosystems (Connelly et al. 2004). Fragmentation in the form of energy extraction or conversion of sagebrush landscapes to agricultural fields eliminates large tracts of undisturbed sagebrush habitats, leading to declines in sage-grouse populations (Swenson et al.

1987, Braun 1998, Doherty et al. 2008, Gregory and Beck 2014, LeBeau et al. 2014). As a result, the focal point of most sage-grouse conservation in recent years has focused on mitigating the loss of, or improving, sagebrush habitats. For example, Wyoming's Core Area Policy was implemented to limit disturbance in areas of Wyoming with the highest sage-grouse breeding population densities (Doherty et al. 2011, Kiesecker et al. 2011). Habitat treatments by way of reducing sagebrush cover to increase the herbaceous understory in sagebrush communities is also a potential technique that has seen widespread implementation aimed at improving habitat quality for sage-grouse (Beck et al. 2012). However, increased quality of sagebrush habitat for sage-grouse must result from habitat manipulations for this management technique to strengthen populations.

Sage-grouse are a sagebrush obligate species due to their yearlong dependence on sagebrush communities for cover and food (Connelly et al. 2004, Crawford et al. 2004). The diet of sage-grouse consists almost exclusively of sagebrush leaves from late fall through early spring (Wallestad and Eng 1975) and sagebrush are the primary shrub used for nesting concealment (Wallestad and Pyrah 1974, Connelly et al. 1991, Sveum et al. 1998, Moynahan et al. 2007, Kolada et al. 2009), so the importance of sagebrush to the species cannot be overstated. However, all seasonal and life-stage requirements must be properly managed for the species to persist. Insects and forbs are important sage-grouse food sources during late spring and summer periods (Wallestad and Eng 1975, Dahlgren et al. 2015b). Insects are an important component of a sage-grouse chick's diet (Klebenow and Gray 1968, Peterson 1970) and greater insect consumption is correlated with increased chick growth and survival (Johnson and Boyce 1990). Insects, primarily beetles, account for over half of one-week-old chick diets (Klebenow and Gray 1968). After the first week of life, sage-grouse chick dependence on insect consumption is reduced (<25% of diet), and forbs become the major food source of 2–10 week-old chicks (Klebenow and Gray 1968). Insects form a smaller portion of adult sage-grouse foods, only comprising 3% of their annual diet (Wallestad and Eng 1975). Grasshoppers (Orthoptera) are the main insect consumed by adults, followed by relatively small amounts of ants (Hymenoptera) and beetles (Coleoptera; Wallestad and Eng 1975). While the herbaceous community is an important component to sage-grouse breeding habitat, the protein provided by invertebrates is critical for sage-grouse chicks. Furthermore, prelaying females with greater nutritional status have been found to be positively correlated to reproductive success (Dunbar et al. 2005) and re-nesting attempts (Gregg et al. 2006); therefore, treatments may be a beneficial management practice to bolster sage-grouse populations if greater nutritional quality in treated habitat is achieved. Greater plant diversity in sagebrush systems may lead to increased insect abundance and diversity early in the growing season; however, water availability may be the driving factor behind insect responses (Wenninger and Inouye 2008).

In attempts to improve sagebrush communities for sage-grouse, 3 common sagebrush reduction treatments have typically been implemented with the intent of increasing the herbaceous understory and diversifying shrub communities in sagebrush habitats, including prescribed burning, mechanical alteration, and herbicide application (Beck et al. 2012). Understanding how habitat treatments alter sagebrush ecosystems is particularly important due to slow regeneration time of sagebrush (Baker 2006, Beck et al. 2009, Hess and Beck 2012) as well as needs of wildlife species that rely on sagebrush for year round habitat. Sage-grouse habitat guidelines recommend that breeding habitats, including nesting and brood-rearing periods, should be managed for 15–25% sagebrush cover (Connelly et al. 2000b), so widespread sagebrush removal does not align well with sage-grouse life history requirements; however, if sagebrush cover falls within this threshold and improves food resources during the brood-rearing period, treatments may benefit sage-grouse populations.

Vegetation Responses to Sagebrush Treatments

By 1974, nearly 2 million ha of the sagebrush steppe on federally managed lands were estimated to have received sagebrush control (Vale 1974). Herbicide application was the most common method of sagebrush reduction through the mid-1970s with intentions to increase grassy forage species for livestock (Vale 1974) through the use of 2,4-D (2,4-dichlorophenoxyacetic acid) to kill broad-leafed plants (e.g., Mueggler and Blaisdell 1958). Treatments of 2,4-D are effective at reducing sagebrush cover and increasing grass cover (Sturges 1986). Burned sagebrush communities tend to respond similarly to sagebrush treated with 2,4-D, such that burns are generally effective at increasing herbaceous vegetation in mature stands of Wyoming big sagebrush (Davies et al. 2007). However, fires in big sagebrush communities often completely removes sagebrush within burn perimeters (Harniss and Murry 1973, Wambolt and Payne 1986), with little if any regeneration 6 (Wambolt and Payne 1986 in Wyoming big sagebrush), 12 (Harniss and Murry 1973 in mountain big sagebrush [*A. t. vaseyana*]), or 14 (Beck et al. 2009 in Wyoming big sagebrush) years after treatments. Mountain big sagebrush canopy cover may recover as quickly as 25 years after fire, whereas Wyoming big sagebrush requires at least 50–120 years for canopy cover to return to unburned conditions (Baker 2006, 2011).

Methods of sagebrush management have shifted from eliminating to reducing sagebrush cover in consideration of the dependence of sage-grouse on sagebrush. Reduction in sagebrush cover increases nutrient levels (i.e., inorganic nitrogen; Davies et al. 2011), water availability (Leaf 1975), and sunlight availability to the herbaceous understory. Mechanical treatments are implemented to selectively remove the crown of the plant or completely remove some plants to reduce shrub canopy cover and density. Mowing treatments, for example, remove the top growth of sagebrush plants while inflicting minimal disturbance to the herbaceous understory. Tebuthiuron is becoming a popular herbicide targeting only shrubs; the magnitude of dead sagebrush cover and density is related to the active ingredient application rate (Olson and Whitson 2002). At low rates (0.1–1.1 kg active ingredient [ai]/ha), tebuthiuron does not eliminate all living sagebrush cover (Whitson and Alley 1984, Johnson et al. 1996, Olson and Whitson 2002) and allows woody structure of dead shrubs to remain standing.

Davies et al. (2012b) found increases in herbaceous cover following mowing treatments in Wyoming big sagebrush were primarily from undesirable species (i.e., cheatgrass [*Bromus tectorum*] and nonnative forb species). In comparison, exotic annual grass invasion does not uniformly occur in the sagebrush steppe following burning and mowing in mountain big sagebrush communities (Davies et al. 2012a) or infrequent fires in Wyoming big sagebrush (Porensky and Blumenthal 2016). Research from north-central Wyoming found no difference in perennial grass height or cover between mowing treatments and reference sites up to 9 years after treatment in Wyoming big sagebrush (Hess and Beck 2012). Perennial forb cover did not differ between mowed, burned, and control areas up to 3 years following treatment in Wyoming big sagebrush, whereas both areas of sagebrush control displayed greater levels of annual forb cover compared to control sites (Davies et al. 2012a). One study in south-central Utah examined vegetative response to Dixie harrow and Lawson aerator mechanical treatments in mountain big sagebrush; these treatments were intended to target the removal of mature sagebrush plants without having large effects on young sagebrush and herbaceous vegetation (Dahlgren et al. 2006). Forb cover was highest in plots treated with Dixie-harrow compared to Lawson-aerator and control plots, whereas tebuthiuron plots had the greatest response in forb cover compared to mechanical treatment and control sites (Dahlgren et al. 2006). However, in Wyoming big sagebrush communities in our study area, mowing, tebuthiuron, and untreated areas did not differ in forb dry mass the first 2 years post-treatment (Smith 2016).

Invertebrate Responses to Sagebrush Treatments

Heterogeneity of vegetation may positively correlate to insect abundance and diversity (Dennis et al. 1998, Wenninger and Inouye 2008); therefore, vegetation manipulation may influence the insect community. Relative abundance of beetles increased during the first year post-fire in mountain big sagebrush (Nelle et al. 2000), but this is not consistent with other studies in mountain big sagebrush (Pyle and Crawford 1996) or Wyoming big sagebrush (Fischer et al. 1996, Rhodes et al. 2010). Decreased ant abundance was detected during the second and third years after prescribed burns compared to reference areas in southeastern Idaho (Fischer et al. 1996). Ants positively responded to 1-year-old burns before returning to relative abundance levels consistent with unburned vegetation at 3–5 year old burn sites in mountain big sagebrush (Nelle et al. 2000). In Wyoming big sagebrush, up to 67% fewer ants were captured in burned habitats compared to control areas (Rhodes et al. 2010). No positive response in insect biomass was detected following burning treatments (Hess and Beck 2014), or between mowed, tebuthiuron, and untreated areas up to 2 years following treatment (Smith 2016) in Wyoming big sagebrush communities in Wyoming. No difference in ant and beetle counts between burned, mowed, or reference sites were detected, but greater grasshopper abundance was found in burned sites compared to reference sites in Wyoming big sagebrush in the Bighorn Basin of north-central Wyoming (Hess and Beck 2014). Similarly, increased grasshopper captures resulted in early May and June during the second and third year after prescribed fire in Wyoming big sagebrush in central Oregon (Rhodes et al. 2010). In contrast, no differences in grasshopper abundance at different aged burns (1–14 year old burns) and unburned areas were detected in mountain big sagebrush habitats (Nelle et al. 2000). Furthermore, studies that have detected differences in insect abundance following disturbances in mountain big sagebrush (e.g., Nelle et al. 2000) and Wyoming big sagebrush (e.g., Rhodes et al. 2010) indicate that these differences were not biologically significant.

Sage-grouse Responses to Sagebrush Treatments

The presence of greater grass cover and height is believed to contribute to increased survival of sage-grouse nests (Gregg et al. 1994, Sveum et al. 1998, Holloran et al. 2005, Doherty et al. 2014). However, the lack of sufficient sagebrush cover resulting from sagebrush treatments likely reduces sage-grouse habitat quality. Low sage-grouse occurrence in sagebrush strips treated with 2,4-D (Martin 1970), female avoidance of burns for nesting (Byrne 2002), and decreased male lek attendance following prescribed fire (Connelly 2000a) and 2,4-D treatments (Wallestad 1975) result from sagebrush elimination methods, suggesting negative population effects from loss of sagebrush in efforts to increase grass.

Mechanical and herbicide treatments conducted more recently indicate variable sage-grouse responses to treatment. Over a period of 25 years, Dahlgren et al. (2015a) found male lek attendance increased approximately 2-fold following the reduction of big sagebrush (i.e., Wyoming big sagebrush, mountain big sagebrush, and basin big sagebrush [*A. t. tridentata*]) canopy cover; however, in the later years of the study, male lek attendance declined as the level of treated sagebrush in their study area approached 15%. A study measuring response in annual lek counts in Wyoming, found mechanical treatments and prescribed burning were negatively associated with population growth, whereas chemical treatments did not impact sage-grouse populations until 11 years after treatment when a positive relationship was displayed (Smith and Beck 2018). Dahlgren et al. (2006) used sage-grouse pellet counts to quantify sage-grouse use of tebuthiuron, mechanical, and control plots in mountain big sagebrush and found greater use of chemical treatments. Bird-dog flushes provided further support to the initial findings of the Dahlgren et al. (2006) study as more individual and brood-rearing sage-grouse were detected in tebuthiuron treated areas compared to control. Another Utah study also evaluated the influence of mechanical treatments in mountain big sagebrush on brood-rearing sage-grouse and found broods selected for areas in and adjacent to treatments (Baxter et al. 2017). In general, population responses to sagebrush treatments are variable and may be related to the amount and type of treatment (see Dahlgren et al. 2015a, Smith and Beck 2018) and positive sage-grouse use have been detected in systems where mountain big sagebrush cover was reduced by tebuthiuron (Dahlgren et al. 2006) or mechanical treatments (Baxter et al. 2017).

Study Area

Our ~4,595 km^2 (1,135,449 ac) study area encompassed portions of Fremont and Natrona counties, Wyoming, and consisted of approximately 78% Bureau of Land Management, 8% State, and 14% privately administered lands (Fig. 1.1). Yearly average precipitation was 26 cm (10 in; PRISM Climate Group 2016) and elevation ranged from 1,594 to 2,534 m (5,230 to 8,314 ft). Important woody species forming shrub communities in the study area included Wyoming big sagebrush, mountain big sagebrush, basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), yellow rabbitbrush (*Chrysothamnus vicidiflorus*), and rubber rabbitbrush (*Ericameria nauseosa*). Major land uses during the study included livestock grazing. There is interest to resume uranium mining, once a major land use in the area.

Study Design and Objectives

To better understand declining population trends and reduced distribution of sage-grouse over the past several decades (Connelly et al. 2004, Schroeder et al. 2004, Nielson et al. 2015), it is important to understand the effects of treatment on various sagebrush habitats. Although sage-grouse are considered sagebrush obligates, they rely on a mix of herbaceous plant species for concealment cover and nutrient resources during various seasonal periods. Although the idea of treating sagebrush to benefit sage-grouse may be conceptually justified, applied research supporting sagebrush reduction practices to enhance sage-grouse habitats and populations in Wyoming big sagebrush systems are lacking from the literature and have often shown negative or insignificant impacts (see Beck et al. 2012).

The response of sage-grouse to mowing and tebuthiuron treatments in Wyoming big sagebrush utilizing pre- and post-treatment data from the same study site has not been previously investigated. The purpose of my thesis research was to evaluate whether mowing and herbicide treatments in Wyoming big sagebrush results in negative, neutral, or positive responses relative to three sage-grouse demographic parameters: 1) nest success, 2) brood success, and 3) adult female survival. Additionally, I evaluated habitat selection of nesting, brood-rearing, and broodless females in relation to mowing and tebuthiuron treatments. In total, 512 female sage-grouse were captured and collared for monitoring during our study, with only 10% (*n* = 52) of the individuals providing both pre- and post-treatment location data.

Our study was designed as a Before-After Control-Impact (BACI) study with 3 years of pre-treatment and 4 years of post-treatment data collection comparing demographic rates and habitat selection patterns of sage-grouse relative to treated Wyoming big sagebrush habitats. To address my objectives of evaluating demographic and habitat selection responses to treatments, a pre-treatment phase of the study occurred during spring and summer 2011–2013. The treatment phase was completed during winter and spring 2014 where the Bureau of Land Management (BLM) Lander-Field Office approved mowing of 4.9 km^2 (1,208 ac) across 2 study sites for mechanical treatments, reducing sagebrush to a height of 25.4 cm (10 in). In early May 2014, 6.1 km^2 (1,500 ac) were treated with tebuthiuron at a rate intended for a 50% sagebrush kill (0.22 kg active ingredient [ai]/ha) at 2 herbicide study areas. As expected, Wyoming big sagebrush cover experienced immediate and delayed reductions to mowing and tebuthiuron treatments, respectively (Table 1.1).

To identify treatment areas, a resource selection function (RSF) model was developed to assess habitat use for sage-grouse during the early brood-rearing period by using locations from radio-marked female grouse in 2011 and 2012 (Smith 2016). This model yielded 230.8 km^2 (57,040 ac) of predicted high use early brood-rearing habitat across 6 study areas for potential treatment. Treatments were randomly assigned to study areas and implemented following Wyoming Game and Fish Department protocols for treating sagebrush in Core Areas (WGFD 2011). Early brood-rearing areas were selected for treatment because nesting and early brood-rearing habitat are often considered to have similar vegetative characteristics (Connelly et al. 2000b). Therefore, the greatest sage-grouse response would be seen by treating habitats used during the early brood-rearing period, often considered the first 2 weeks post-hatch (Thompson et al. 2006). The remaining two study areas served as offsite untreated control areas. Please see Appendix A in Smith (2016) for more details about our study design.

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Table 1.1. Means, standard errors (SE), and 95% confidence intervals (LCL and UCL) of live, dead, and total Wyoming big sagebrush cover (%) relative to mowed, tebuthiuron, and respective control sites in central Wyoming, USA, 2014–2017.

		2014				2015				2016				2017			
Site	Wyoming big sagebrush cover (%)	Mean	SE	LCL	UCL	Mean	SE	LCL	UCL	Mean	SE	LCL	UCL	Mean	SE	LCL	UCL
Mowed	Live	7.8	1.0	5.8	9.8	7.6	1.2	5.2	10.0	9.7	1.1	7.5	11.9	9.7	1.5	6.8	12.6
	Dead	3.5	0.3	2.9	4.1	3.3	0.4	2.5	4.1	3.6	0.5	2.6	4.6	4.4	0.5	3.4	5.4
	Total	11.3	0.9	9.5	13.1	10.9	1.4	8.2	13.6	13.3	1.1	11.1	15.5	14.1	1.6	11.0	17.2
$\text{Mowed}_{\text{Control}}$	Live	15.7	1.4	13.0	18.4	15.7	1.7	12.4	19.0	18.5	1.6	15.4	21.6	18.5	1.5	15.6	21.4
	Dead	1.0	0.2	0.6	1.4	1.2	0.2	0.8	1.6	1.2	0.3	0.6	1.8	2.2	0.4	1.4	3.0
	Total	16.7	1.5	13.8	19.6	16.9	1.8	13.4	20.4	19.7	1.7	16.4	23.0	20.7	1.8	17.2	24.2
Tebuthiuron	Live	22.5	1.3	20.0	25.0	11.0	0.8	9.4	12.6	12.9	1.2	10.5	15.3	10.5	1.1	8.3	12.7
	Dead	1.4	0.3	0.8	2.0	12.1	0.9	10.3	13.9	10.4	0.8	8.8	12.0	11.2	1.1	9.0	13.4
	Total	23.9	1.4	21.2	26.6	23.0	1.2	20.6	25.4	23.3	1.1	21.1	25.5	21.8	1.0	19.8	23.8
$\text{Tebuthiuron}_{\text{Control}}$	Live	17.4	2.5	12.5	22.3	14.0	2.0	10.1	17.9	15.0	2.0	11.1	18.9	14.6	1.9	10.9	18.3
	Dead	1.9	0.5	0.9	2.9	4.4	1.0	2.4	6.4	4.0	0.8	2.4	5.6	5.0	1.2	2.6	7.4
	Total	19.3	2.7	14.0	24.6	18.3	2.4	13.6	23.0	19.1	2.3	14.6	23.6	19.6	2.3	15.1	24.1

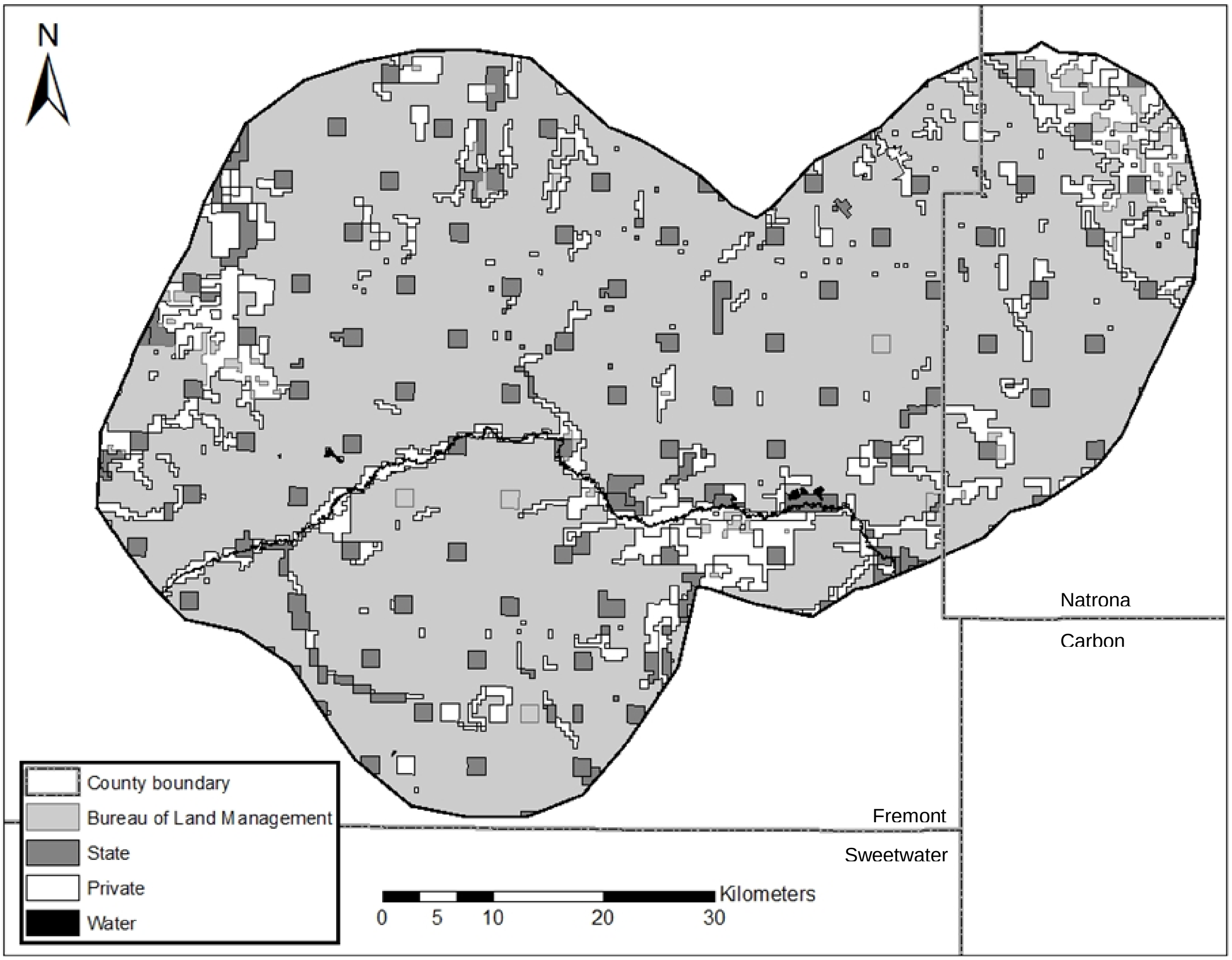

Figure 1.1. Land ownership within our study area delineated by a 99% kernel utilization distribution of sage-grouse locations during breeding and summer seasons in central Wyoming, USA, from 2011−2017.

CHAPTER TWO

GREATER SAGE-GROUSE HABITAT SELECTION IN SAGEBRUSH MODIFIED BY MOWING AND TEBUTHIURON

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ABSTRACT

Global environmental and anthropogenic changes have modified ecosystems worldwide impacting many species by altering habitat quality. The greater sage-grouse (*Centrocercus urophasianus*) is experiencing population declines as a result of habitat loss and degradation. The utility of habitat restoration efforts focusing on restoring brood-rearing habitat to bolster populations is being investigated by wildlife researchers as one means to mitigate the negative impacts that diminishing and degraded sagebrush (*Artemisia* spp.) communities have on sage-grouse. Sagebrush management through shrub reduction methods to improve habitat quality has produced variable results, largely split between habitats dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*) or mountain big sagebrush (*A. t. vaseyana*). The purpose of our research was to evaluate habitat selection of nesting, brood-rearing, and non-brood rearing (i.e., broodless) female sage-grouse in relation to mowing and tebuthiuron treatments in Wyoming big sagebrush using 3 years of pre-treatment (2011–2013) and 4 years of post-treatment (2014−2017) data. Treatments occurred in 2014, where mowing treatments reduced sagebrush height to 25.4 cm over 4.9 km^2 across 2 study areas, and 2 tebuthiuron treatment areas totaling 6.1 km^2 reduced living sagebrush cover to 50% of pre-treatment cover across 2 other study areas. We found that sage-grouse selected for mowed- and tebuthiuron-treated sagebrush during nesting, brood-rearing, and broodless periods before and after treatments. However, a treatment by period (before and after) interaction suggested that selection either did not differ before and after treatment or selection for treatments was less pronounced following treatments for all life stages. Overall, our results suggested that sage-grouse did not alter their habitat selection behaviors in response to mowing and tebuthiuron treatments in Wyoming big sagebrush breeding habitats. These findings corroborate previous research that suggests treatments to reduce Wyoming big sagebrush do not increase habitat quality for sage-grouse during the breeding season. Managers should use caution when modifying remaining intact sagebrush habitats for sage-grouse and other sagebrush occurring wildlife.

KEY WORDS *Centrocerus urophasianus*, resource selection, mechanical treatment, chemical treatment, Wyoming big sagebrush.

INTRODUCTION

Habitat management and restoration is a common practice that allows land managers to achieve desired vegetation and wildlife communities across landscapes. Natural environmental disturbances are often mimicked by wildlife ecologists to achieve immediate results in specific locations. Prescribed burns, mechanical treatments, and chemical applications are common methods of manipulating vegetation to obtain preferred vegetation and wildlife species composition (Beck et al. 2012). These methods are widely implemented across various vegetation communities to reverse ecological succession through the conversion of climax communities into systems dominated by pioneer or intermediate species (Harper 2007). For example, in northwest British Columbia, mechanical thinning created forest canopy openings in mature western hemlock (*Tsuga heterophylla*) stands allowing shade intolerant plant species opportunity to colonize treated areas (Steventon et al. 1998). As a result, individual species abundance for some birds and small mammals differed between clear-cut and uncut forests (Steventon et al. 1998). Furthermore, (Reinkensmeyer et al. 2007) reported varying avian communities and densities across successional states of mountain big sagebrush (*Artemisia tridentata vaseyana*) communities in central Oregon including postburn grassland, mountain big sagebrush-Idaho fescue (*Festuca idahoensis*), mountain big sagebrush with juniper (*Juniperus* spp.) encroachment, and old-growth juniper successional stages, suggesting that habitat manipulations may favor certain avian assemblages depending on successional stage.

Not only can various habitats alter wildlife communities, but habitat treatments are also implemented with the intent of increasing habitat use for a specific species. For example, elk (*Cervus elaphus*) altered their habitat selection in response to mechanical thinning and prescribed burning of dense forest stands in northeastern Oregon depending on spatial scale and time of year (Long et al. 2008). Habitat treatments can also benefit certain species during specific seasonal periods and age classes (e.g., Bergman et al. 2014). Increased mule deer (*Odocoileus hemionus*) fawn survival resulted in winter range areas where habitat treatments reduced pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) encroachment into shrubland communities (Bergman et al. 2014). Habitat treatments have become a popular management technique to benefit greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘sage-grouse’). Sage-grouse are sagebrush-obligate species experiencing population declines (Connelly et al.

2004, Nielson et al. 2015, WAFWA 2015) and reduced range (Schroeder et al. 2004) due primarily to habitat loss and disturbance (Braun 1998, Connelly et al. 2004, Doherty et al. 2008, Gregory and Beck 2014, LeBeau et al. 2014). Prescribed burns, mechanical treatments, and chemical applications in sage-grouse breeding habitats often aim to reduce big sagebrush cover thereby increasing habitat quality for specific life-stages during the reproductive period (Beck et al. 2012, Dahlgren 2015b).

Because brood-rearing female sage-grouse generally select areas with intermediate sagebrush cover (<16.9%; Hagen et al. 2007), sagebrush management practices aimed at releasing forbs and grasses from competition with a dominant sagebrush overstory may provide an effective means to restore sage-grouse brood-rearing habitat (Connelly et al. 2000b). However, reduction in male sage-grouse lek attendance highlights the negative impact of burns on sage-grouse populations in Wyoming big sagebrush (*A. t. wyomingensis*; Connelly et al. 2000a) and in Wyoming and mountain big sagebrush communities (Coates et al. 2016). Similarly, 2,4–dichlorophenoxyacetic acid treatments in big sagebrush resulted in low occurrence within treated areas (Martin 1970) and reduced male lek attendance (Wallestad 1975) further suggesting large sagebrush removals do not benefit sage-grouse. In contrast, areas receiving mechanical and carefully applied chemical treatments that reduce, but do not eliminate, sagebrush canopy cover have shown increased selection by sage-grouse (Dahlgren et al. 2006, Baxter et al. 2017).

Literature focusing on sagebrush habitat management for sage-grouse implies treatments may be more effective at improving brood-rearing conditions in mountain big sagebrush than in Wyoming big sagebrush (Beck et al. 2012). Sage-grouse broods selected for areas that were near chain harrow and mowing treatment edges in mountain big sagebrush (Baxter et al. 2017).

Greater adult and brood use at tebuthiuron treatment sites compared to both mechanical (Lawson-aerator and Dixie-harrow) and control areas provides additional support for sagebrush reduction treatments in mountain big sagebrush brood-rearing habitats (Dahlgren et al. 2006). Although not significant, increased sage-grouse use of mechanical treatments compared to control areas was found in the same study (Dahlgren et al. 2006). Sagebrush cover reduced by a pasture aerator resulted in increased sage-grouse use in Wyoming big sagebrush dominated communities at low elevations (1950–2110 m) compared to low elevation control areas; however, sage-grouse did not select treated areas at higher elevations (2120–2250 m) with greater shrub diversity in northeastern Utah (Stringham 2010). At a different location in northeastern Utah, pellet density as an index for sage-grouse abundance, did not differ between aerated and control sites comprised of all 3 big sagebrush subspecies 1 and 2 years after treatment (Stringham 2010). Another study in Utah found twice the number of males occupying leks following sagebrush canopy reduction (Dahlgren et al. 2015b). Small mowing, herbicide, and prescribed burning treatments in a mosaic may increase sage-grouse abundance; however, a potential threshold for reducing sagebrush cover may have been detected as declines resulted after 15% of the landscape received treatment (Dahlgren et al. 2015b).

Some herbicide and mechanical treatments in mountain big sagebrush systems have resulted in positive sage-grouse responses; however, sage-grouse responses to sagebrush reduction methods in Wyoming big sagebrush communities are less studied and may suggest differing results between vegetation types. Our study was designed to evaluate how habitat selection of nesting, brood-rearing, and broodless sage-grouse could potentially be altered in response to mechanical and chemical treatments in Wyoming big sagebrush habitats during the breeding season. Mowing and tebuthiuron treatments are 2 common methods to reduce sagebrush cover and density to increase habitat quality for sage-grouse. We used 7 years (2011–2017) of data collected during 3 years pre-treatment (2011–2013) and 4 years post-treatment (2014–2017) to evaluate how sage-grouse responded to 2 mowing and 2 tebuthiuron treatment areas in central Wyoming, USA. Specifically, we evaluated how the amount of treatment and distance to nearest treatment influenced habitat selection by nesting, brood-rearing, and broodless sage-grouse before and after treatment implementation. Managers must understand the response of sage-grouse in all regions of their range as variations in vegetation type and sagebrush reduction methods may contribute to the overall effectiveness of habitat treatments for sage-grouse.

STUDY AREA

Our study was located near Jeffrey City, Wyoming, USA (42.49'N, -107.83'W) and encompassed ~4,595 km^2 across Fremont and Natrona counties. We used a 99% kernel utilization distribution generated from breeding and summer season locations of female sage-grouse collected from 2011–2017 to delineate the overall study area boundary (Figure 2.1). Elevation ranged from 1,594 to 2,534 m and yearly average precipitation was 26 cm (PRISM Climate Group 2016). Approximately 78% of the lands were federally managed by the Bureau of Land Management, 14% privately owned, and 8% under state ownership. Wyoming big sagebrush was the dominant shrub typifying our study area; mountain big sagebrush, basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), yellow rabbitbrush (*Chrysothamnus vicidiflorus*), and rubber rabbitbrush (*Ericameria nauseosa*) were also present. The predominant land use across the study area was livestock grazing.

METHODS

Study Design

We implemented a before-after study to evaluate sage-grouse habitat selection during critical life stages, and thereby evaluated the practicality of mowing and tebuthiuron treatments in Wyoming big sagebrush. Our study investigated breeding and summer season responses of nesting, brood-rearing, and broodless female sage-grouse to treatments by comparing 3 years of pre-treatment data (2011–2013) to 4 years of post-treatment data (2014–2017). Mowing and tebuthiuron treatments occurred in winter and spring 2014, respectively. We implemented treatments in areas that were predicated to be high probability of use during the early brood-rearing period (i.e., first two weeks post hatch). Probability of use was modeled across our study area using early brood-rearing locations from radio-marked sage-grouse during 2011 and 2012 (Smith 2016). Mowing treatments were implemented during January and February 2014 and totaled 4.9 km^2 across 2 areas reducing sagebrush height to approximately 25.4 cm. Tebuthiuron (1.12 kg/ha [0.22kg/ha active ingredient]) was aerially applied to 6.1 km^2 of sagebrush habitat across 2 additional areas in early May 2014. The application rate of tebuthiuron was expected to result in a 50% reduction in shrub cover. Live Wyoming big sagebrush cover was 25.18 ± 3.62 % (SE) and 13.63 ± 6.79 % less in mowed and tebuthiuron treated areas, respectively, compared to paired untreated areas during 2017. Mowing and tebuthiuron treatments were applied in mosaic patterns where no point within a treatment was more than 60 m from undisturbed sagebrush habitats (*sensu* Dahlgren et al. 2006; see Figure 2.2). All treatments adhered to Wyoming Game and Fish Department protocols for treating sagebrush in Core Areas (WGFD 2011). Additionally, we refrained from treating sagebrush in areas where shrub cover was less than 2 standard deviations of the mean grouse use location (7.9%; Homer et al. 2012), within 100 m from water, and slopes exceeded

15%. Smith (2016) provides supplementary information regarding treatment design and implementation.

Capture and Monitoring

Female sage-grouse were captured by hoop netting and spotlighting (Giesen et al. 1982, Wakkinen et al. 1992) during March, April, or August each year to avoid disturbing nesting and early brood-rearing sage-grouse. During late winter and early spring, we focused captures in areas surrounding known leks, and used radio-marked individuals to locate roosting female groups in summer to increase our sample size going into the following year. We deployed 3 different transmitter types weighing 22 g to monitor female sage-grouse; PVC-covered wire necklace Model A4060 (hereafter, very high frequency or 'VHF;' Advanced Telemetry Systems Incorporated, Isanti, MN), PVC-covered wire necklace G10 UltraLITE GPS Logger with built in VHF transmitter (Advanced Telemetry Systems Incorporated, Isanti, MN), or rump-mounted Global Positioning System (GPS) backpack transmitter (PTT-100 Solar Argos/GPS PTT, Microwave Telemetry, Columbia, MD, USA). From 15 March through 30 April, GPS transmitters were set to collect female locations at 5 fixed periods (0700, 1000, 1300, 1600, 2400). After 30 April, GPS transmitters were programmed to obtain 6 locations per day through late August (0600, 0900, 1200, 1500, 1800, 2400) with the Argos system (CLS America, Largo, MD, USA). Radio-marked females were located weekly from mid-April through mid-August each year with R-1000 hand-held receivers and 3-element Yagi antennas (Communication Specialists, Orange, CA). When necessary, we used telemetry equipment onboard a fixed-wing aircraft to locate VHF radio-marked females that could not be located on the ground. To be consistent with weekly monitoring patterns of VHF-marked individuals, location data from GPS equipped females were rarified by randomly selecting one midday location for each individual per week. Sage-grouse were captured, marked, and monitored in adherence to University of Wyoming Institutional Animal Care and Use Committee protocols (03132011 and 20140128JB0059) and Wyoming Game and Fish Department Chapter 33 scientific research permit 801.

Nesting grouse were located by circling the female's transmitting signal until a visual of an incubating female was obtained. Subsequent nest checks occurred by triangulation and maintaining a distance of at least 30 m from the nest to avoid human-induced nest depredation or abandonment (e.g., Kirol et al. 2012). Brood-rearing sage-grouse were characterized as such after obtaining a visual of at least one chick or visualizing brood-rearing behavior by the female (i.e., broken wing display, vocalizations, etc.) during telemetry visits following nest completion. When we could not obtain brood status during daytime telemetry visits, we confirmed observations with nighttime spotlight visits. Regardless of reproductive status, all females were monitored weekly during the breeding and summer seasons.

Analysis

Defining availability in treated study areas.—Characterizing population level habitat availability for brood-rearing and broodless females becomes difficult as they traverse the landscape. Moreover, animals may modify their selection of habitats in altered landscapes (e.g., Harju et al. 2011), therefore we aimed to ensure that treated areas were actually available to individuals used in subsequent modelling efforts. That is, assessing availability at the level of the entire study area (e.g., an MCP surround all locations of individuals throughout the study) may be misleading; treated areas may not actually be available to every radio-marked individual in our study. This is exacerbated by the high fidelity of sage-grouse to seasonal habitats (e.g., Holloran and Anderson 2005), suggesting that grouse are unlikely to make large-scale movements to novel areas once they have established seasonal ranges. Therefore, we defined the extent of available habitats within each of the 4 treated areas based on individual nesting locations in relation to treatment areas. To determine an appropriate distance in which nesting females were considered to have treatments available to them, we used locations collected from females equipped with GPS transmitters that nested in a given year to determine the distance between the location of each nest and all locations of that individual collected over the 3 weeks prior to nest initiation. This time period is when females are bred and begin seeking nest locations (Schroeder et al. 1999). We then placed a circular analysis region around nests documented with all transmitter types based on this distance (median value = 3.47 km, from 47 individual-years) and considered treatments available to a nesting female if her nest was within 3.47 km of a treatment. Those individuals were then assigned to the treatment type and study area they were spatially associated with. Females that nested farther than 3.47 km from a treatment were not used to delineate the extent of available habitats further. We pooled all summer locations of individuals that had treatment areas available to them and generated 80% Kernel Utilization Distributions (KUD; default bivariate; Worton 1989) to determine available habitats for each of the 4 treatment areas (Figure 2.3). We then excluded nest, brood-rearing, and broodless female locations from all locations collected over the duration of the study that were outside of each availability extent for each treatment study area. Remaining locations were assigned to treatment study area and available locations (n = 40 per use location) were generated separately for nest, brood-rearing, and broodless female locations within each treatment study area.

Predictor variables.—We evaluated the influence of remotely sensed predictor variables at the raster cell (30 m) and within 4 circular analysis regions: 0.335-km radii (0.35 km^2), 0.564-

km radii (1 km^2), 0.930-km radii (2.7 km^2), and 1.6-km radii (8.0 km^2; Table 2.1). We chose these analysis regions based on sage-grouse biology (Holloran and Anderson 2005, Aldridge and Boyce 2007, Fedy et al. 2014, Kirol et al. 2015) and federal management directives (Bureau of Land Management 2015). We used a 30-m digital elevation map (DEM; U.S. Geological Survey 2011) to calculate slope (%). Remotely sensed vegetation layers were derived from the National Land Cover Database Shrubland Products (Xian et al. 2015). We calculated an Integrated Normalized Difference in Vegetation Index (INDVI) from 8-NDVI data (LP DAAC 2017) by summing NDVI values from 1 May–15 August. We quantified surface disturbance (areas of bare ground resulting from removal of vegetation) following the Wyoming Density Disturbance Calculation Tool protocol (Wyoming Geographic Information Science Center 2016). Treatment variables were derived from a shapefile that was created by marking the perimeter of each treatment with a handheld GPS (Garmin GPSmap 62s, Garmin, Olath, Kansas, USA).

Statistical analysis.—To assess the potential influence of treatments on sage-grouse resource selection during the breeding season, we developed 6 binomial generalized mixed models with package 'lme4' (Bates et al. 2015) to individually evaluate nesting, brood-rearing, and broodless female sage-grouse habitat selection. We subset data by used and available locations within mowing and tebuthiuron treated areas to generate separate models for each life stage (nesting, brood-rearing, broodless) and treatment type (mowing and tebuthiuron). All models contained the random effects of treatment area and individual (nested within each year). For each model, we first evaluated the influence of all variables except those related to treatments on full data sets. This approach allowed us to develop a 'base' model that accounted for environmental and anthropogenic features that may influence selection. We determined the most predictive of each analysis region in a single variable framework and retained the most supported variable based on Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). For example, we only retained one variable that represented big sagebrush cover. In addition, we only retained the most predictive variable describing shrub cover (big sagebrush cover, sagebrush cover, or shrub cover) and shrub height (sagebrush height or shrub height). We ensured remaining predictors were not correlated ($|r|$ >0.6; Allison 2009) and retained the most predictive of each correlated variable based on AICc. We then employed a manual backward variable selection procedure by removing the least significant variable (based on *P*-value) until we reached a model with 5 variables. We continued removing variables if models with fewer than 5 variables had lower AICc values. We then compared the base model to treatment models containing variables in the base model with the addition of an individual treatment variable, plus the treatment × period interaction term. The treatment variables we assessed included distance to treatment, plus the amount of treatment (ha) within each of the 4 analysis regions. Each treatment model also contained a treatment × period (before and after) interaction term. We selected the most supported treatment model based on the lowest AICc value and compared that to the base model. A significant interaction between treatment and period would indicate a change in resource selection following treatment implementation.

RESULTS

We captured and radio-marked 512 female sage-grouse from spring 2011–2017. Use locations evaluated in our nest, brood, and broodless female habitat selection analyses were 282, 560, and 1,639, respectively (Table 2.2). Sage-grouse continued to use treated areas post-treatment, with the exception that no grouse nests were located within mowed areas after treatment (Table 2.3).

Nest Habitat Selection

The most supported nest habitat selection model in mowed areas included $Bsage_{930}$, $Herb_{1600}$, Litter, $Slope_{564}$, and $Treatment_{335}$ × Period (Tables 2.3 and 2.4). Regardless of period, females selected for mowed treatment areas for nesting at the 0.335 km circular analysis region scale (β = 0.148, 95% CI = 0.091 to 0.205); however, the significant treatment × period interaction term suggested that selection for mowed areas was not as strong following treatments (β = −0.165, 95% CI = −0.261 to −0.070; Table 2.4 and Fig. 2.3).

The most supported nest habitat selection model in tebuthiuron areas included Sage, $Bare_{564}$, $Slope_{930sd}$, $SDist_{335}$, and EucTreatment × Period (Tables 2.3 and 2.4). In tebuthiuron treatment areas, nests occurred closer to treatments both before and after herbicide application (β = −0.780, 95% CI = −1.309 to −0.251; Table 2.4 and Fig. 2.3). We did not detect a significant before-after treatment interaction at tebuthiuron treatment areas (β = 0.421, 95% CI = −0.151 to 0.994; Table 2.4 and Fig. 2.3), suggesting there was no change in selection following tebuthiuron treatments.

Brood Habitat Selection

The most supported brood habitat selection model in mowed areas included $Shrub_{1600sd}$, $ShrubHeight_{564sd}$, INDVI, Bare, $SDist_{564}$, and EucTreatment × Period (Tables 2.3 and 2.5). The most supported brood habitat selection model in tebuthiuron areas included $ShrubHeight_{335sd}$, INDVI, $Herb_{335}$, Bare, $SDist_{1600}$, and EucTreatment × Period (Tables 2.3 and 2.5). Females with broods used areas closer to mowed (β = –0.191, 95% CI = −0.305 to –0.077; Table 2.5 and Fig. 2.4) and tebuthiuron treatment areas (β = –0.412, 95% CI = −0.612 to –0.212; Table 2.5 and Fig. 2.4), but we did not detect a pre- or post-treatment change in brood-rearing habitat selection at either mowed (β = 0.080, 95% CI = −0.051 to 0.210; Table 2.5 and Fig. 2.4) or tebuthiuron treatment areas (β = 0.080, 95% CI = −0.166 to 0.327; Table 2.5 and Fig. 2.4).

Broodless Female Habitat Selection

The most supported broodless female habitat selection model in mowed areas included $Shrub_{930sd}$, INDVI, Litter, $Slope_{335}$, EucSDist, and EucTreatment × Period (Tables 2.3 and 2.6). Broodless females used areas closer to mowed sagebrush (β = –0.092, 95% CI = −0.142 to –0.041; Table 2.6 and Fig. 2.5); although females still selected for mowing treatments after sagebrush reduction, selection was not as strong compared to pre-treatment occurrence (β = 0.056, 95% CI = 0.006 to 0.106; Table 2.6 and Fig. 2.5).

The most supported broodless female habitat selection model in tebuthiuron areas included $Shrub_{335sd}$, Bare, Slope1600, $SDist_{1600}$, and EucTreatment × Period (Tables 2.3 and 2.6). Broodless females used areas closer to tebuthiuron treatments (β = –0.458, 95% CI = −0.609 to –0.307; Table 2.6, Fig. 2.5) before and after treatment implementation. We did not detect a pre- or post-treatment interaction at tebuthiuron treatment areas (β = 0.129, 95% CI = −0.038 to 0.295; Table 2.6, Fig. 2.5) indicating no change in selection following tebuthiuron application.

DISCUSSION

Our study is the first to evaluate habitat selection of nesting, brood-rearing, and broodless female sage-grouse in relation to mechanical and tebuthiuron treatments in Wyoming big sagebrush landscapes utilizing pre- and post-treatment radio-marked female location data. Our robust study design utilizing 3 years of pre-treatment and 4 years of post-treatment data across replicated treatment sites strengthens conclusions drawn from our research. Overall, our results suggest that sage-grouse did not select habitats based on mowing and tebuthiuron treatments. Results from each of our 6 models suggested that grouse were selecting areas closer to treatments before they were implemented, confirming that we treated high use areas. This increased the likelihood of detecting a change in habitat selection following treatments. Our results also demonstrated that nesting, brood-rearing, and broodless females used areas near treatments after treatments were implemented. However, we only detected a significant treatment × period interaction in 2 instances to suggest that selection differed before and after treatments. Nesting female sage-grouse selected nest locations in areas with more mowing treatments during before and after periods, but the strength of selection was less post-treatment. Similarly, broodless females selected for areas closer to mowing treatments, but selection was not as strong following treatments. We did not detect a difference in habitat selection before or after treatment for nesting and broodless females in tebuthiuron treatment areas or for brood-rearing females in both mowing and tebuthiuron treated areas. Our results provide no evidence that mowing and tebuthiuron treatments encourage habitat use by sage-grouse in breeding habitats dominated by Wyoming big sagebrush. The removal of undesirable vegetation types can benefit selected species; however, reducing sagebrush density and cover to benefit a sagebrush-obligate species begs the question of there being more effective management approaches.

Our results provide additional evidence that treatments intended to improve conditions for wildlife should be carefully considered. Other bird species have shown varying responses to habitat manipulations. Increased use of burned and mowed sites by capercaillie (*Tetrao urogallus*) in Britain was attributed to increased bilberry (*Vaccinium myrtillus*) cover that resulted from treatments (Handcock et al. 2011). Northern bobwhite quail (*Colinus virginianus*) selected for disked and herbicide treated areas on a reclaimed surface mine in western Kentucky (Brooke et al. 2015). Grassland specialist bird species experiencing population declines in the Chihuahuan Desert responded positively to shrub removal with herbicides and occurred at greater abundances in treatments compared to untreated areas at the expense of reducing habitat quality for other shrub-land species (Coffman et al. 2014). Habitat improvement practices must be carefully evaluated to ensure habitat alterations are not detrimental to non-target species, especially on specialist species (Fulbright et al. 2018).

Seasonal habitats outside of breeding and summer habitats (i.e., wintering areas) should be avoided for sagebrush reduction treatments (Connelly et al. 2000b) because sage-grouse rely on sagebrush for dietary needs (Wallestad and Eng 1975, Dahlgren et al. 2015a) and tall sagebrush stands (≥20 cm above snow) are selected for winter use sites (Beck 1977). Treatments may result in increased crude protein of Wyoming big sagebrush leaves for at least 6 years post treatment; however, this is unlikely a biologically significant tradeoff with the reduction of sagebrush height and cover resulting from treatments (Davies et al. 2009, Smith et al. 2018). Sage-grouse habitat management should not focus on one seasonal period and respective sage-grouse requirements. In addition to habitat improvement techniques to mitigate declining sage-grouse populations, areas of known importance to the species can be protected. Wyoming's Sage-Grouse Executive Order (State of Wyoming 2011) is a conservation policy designed to protect and improve sage-grouse breeding habitats based on population density estimates from lek data. The policy limits anthropogenic change that causes surface disturbance in sage-grouse Core Areas (State of Wyoming 2011). Although protecting sage-grouse Core Areas during the breeding season does not necessarily protect sage-grouse requirements during other times of the year (i.e., winter; Smith et al. 2016), other sagebrush-occurring species could potentially benefit from the protection of sagebrush landscapes from disturbance. For example, mule deer have been found to avoid areas of natural gas exploration (Sawyer et al. 2006), but in areas where development and disturbance are limited by Core Area regulations, mule deer recruitment may increase (≥70% Core Area overlap; Gamo and Beck 2017). If guidelines for treating sagebrush within Core Areas are adhered, sage-grouse habitat management can occur at finer scales, but may not benefit other sagebrush-associated bird species (Carlisle et al. 2018). Neutral or negative impacts of mowing treatments in our study area on Brewer's sparrow (*Spizella breweri*) and sage thrasher (*Oreoscoptes montanus*) suggests treatments designed to improve habitat quality for sage-grouse may not benefit co-occurring sagebrush-obligate bird species (Carlisle et al. 2018). No nesting attempts were detected within mowed habitats for 3 sagebrush-obligate species (sage-grouse [this study], Brewer's sparrow, and sage thrasher [Carlisle et al. 2018]) suggesting complete loss of nesting habitat within mowed sagebrush habitat post-treatment. In contrast, sagebrush-generalist species (i.e., Vesper Sparrow, *Pooecetes gramineus*) may have positive or neutral responses to fine-scale mowing treatments (Carlisle et al. 2018).

Combinations of chemical, mechanical, and prescribed burns in small mosaic patterns within mixed big sagebrush systems (i.e., Wyoming big sagebrush, mountain big sagebrush, and basin big sagebrush [*A. t. tridentata*]) may benefit sage-grouse populations at low treatment levels (i.e., <15% treated landscape; Dahlgren et al. 2015b). Additionally, potential benefit of chemical treatments at the population level was detected in Wyoming, but only 10 years after treatment (Smith and Beck 2018). In contrast, burns and mechanical treatments in landscapes primarily dominated be Wyoming big sagebrush showed no benefit to sage-grouse populations at 1, 3, 5, and 10-year lag intervals (Smith and Beck 2018). Our findings further support that treatments do not benefit sage-grouse in Wyoming big sagebrush communities, especially during reproductive life stages. However, some mechanical (Baxter et al. 2017) and chemical treatments (Dahlgren et al. 2006) in mountain big sagebrush display positive sage-grouse use responses. If our mowing and tebuthiuron treatments occurred in Wyoming big sagebrush habitats of lower quality, the potential of detecting a sage-grouse response may have increased; however, our treatments were implemented in areas with the greatest expected vegetation response. Conversely, treating areas of predictably lower vegetation response could also have further lowered their suitability as sage-grouse habitat. Dahlgren et al. (2006) attributed increased sage-grouse use of tebuthiuron treated areas to increased forb cover following treatments. Wyoming big sagebrush communities are likely to respond differently to sagebrush reduction and forbs are generally similar in treated and control areas following treatment (Fischer et al. 1996, Davies et al. 2012, Hess and Beck 2014). In our same study area, both mowed and tebuthiuron treatment areas had similar forb dry mass compared to untreated areas, further suggesting correlation between sage-grouse and forb responses. Supplemental seeding of forbs may increase the amount of forbs available in treated areas (Stringham 2010, Dahlgren et al. 2015b) and increase likelihood of sage-grouse use following sagebrush treatments; however, restoration practices in early brood-rearing habitat in our study did not include seeding of herbaceous species.

MANAGEMENT IMPLICATIONS

Our findings support conclusions from Beck et al. (2012) that sage-grouse in Wyoming big sagebrush may not respond positively to habitat treatments and managers should carefully evaluate objectives for the landscape prior to implementing sagebrush treatments. A developing literature base highlighting variable and often undesirable invertebrate and herbaceous responses to sagebrush reduction methods suggests treatments may not improve sage-grouse populations over the short-term in Wyoming big sagebrush habitats (Fischer et al. 1996, Hess and Beck 2014). We do not recommend large-scale habitat manipulations in Wyoming big sagebrush communities to provide uplift to sage-grouse populations. Current management should instead focus on protecting large undisturbed sagebrush landscapes.

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Table 2.1. Variables used to evaluate greater sage-grouse nest, brood, and broodless female habitat selection relative to mowing and tebuthiuron treatments in Wyoming big sagebrush, central Wyoming, USA, 2011–2017.

Variable name	Description
Bare[1]	Bare ground (%; Xian et al. 2015)
Bsage[1,2]	Big sagebrush (*Artemisia tridentata*) cover (%; Xian et al. 2015)
EucSDist	Euclidean distance to nearest surface disturbance (km)
EucTreatment	Euclidean distance to Treatment (km)
Herb[1]	Herbaceous (%; Xian et al. 2015)
INDVI	Integrated Normalized Difference in Vegetation Index calculated by summing 8-day NDVI data from 1 May–15 August each year (LP DAAC 2017)
Litter[1]	Litter (%; Xian et al. 2015)
Period	Pre- or post-treatment
Sage[1,2]	Sagebrush (all *Artemisia* spp.) cover (%; Xian et al. 2015)
SageHeight[1,2]	Sagebrush height (cm; Xian et al. 2015)
SDist[1]	Surface disturbance ha (bare ground resulting from vegetation removal)
Shrub[1,2]	Shrub cover (%; Xian et al. 2015)
ShrubHeight[1,2]	Shrub height (cm; Xian et al. 2015)
Slope[1,2]	Slope (%) derived from 30-m digital elevation map (DEM; USGS 2011)
Treatment[1]	Treatment (ha)

[1]Mean assessed within 0.335, 0.564, 0.930, and 1.6-km radii circular analysis regions.
[2]Standard deviation assessed within 0.335, 0.564, 0.930, and 1.6-km radii circular analysis regions.

Table 2.2. Number of use locations in nest, brood, and broodless female habitat selection analyses at mowing and tebuthiuron treatment areas pre- and post-treatment in Wyoming big sagebrush, central Wyoming, USA, 2011–2017.

	Nesting		**Brood-rearing**		**Broodless**	
	Before	After	Before	After	Before	After
Mow	58	113	99	201	377	582
Tebuthiuron	22	89	102	158	198	482

Table 2.3. Proportion of nest, brood, and broodless female locations within future mowed and tebuthiuron treatment areas (pre-treatment) and following treatment implementation (post-treatment) in Wyoming big sagebrush, central Wyoming, USA, 2011–2017. No greater sage-grouse location data (N/A) were collected for nests in 2011, broods in 2011, or broodless females in 2017 within tebuthiuron treatment study areas.

	Pre-treatment locations			Post-treatment locations			
	2011	2012	2013	2014	2015	2016	2017
Nests							
Mowed	0.13	0.16	0.08	0.00	0.00	0.00	0.00
Tebuthiuron	N/A	0.22	0.08	0.05	0.18	0.19	0.05
Broods							
Mowed	0.00	0.00	0.00	0.02	0.00	0.03	0.02
Tebuthiuron	N/A	0.23	0.11	0.00	0.12	0.03	0.11
Broodless							
Mowed	0.04	0.04	0.03	0.02	0.01	0.00	0.00
Tebuthiuron	0.00	0.10	0.04	0.09	0.10	0.11	N/A

Table 2.4. Top and competitive models explaining greater sage-grouse nest, brood, and broodless female habitat selection relative to mowing and tebuthiuron treatments in Wyoming big sagebrush, central Wyoming, USA, 2011–2017. Number of parameters (K), change in Akaike's Information Criterion score from the top model (ΔAICc), and Akaike weights (w_i) to evaluate model fit for sage-grouse habitat selection.

Model	K	ΔAICc	w_i
Nest			
Mow (Base Model: $Bsage_{930}$ + $Herb_{1600}$ + Litter + $Slope_{564}$)			
Base Model + $Treatment_{335}$ × Period	10	0.00	0.45
Base Model + EucTreatment × Period	10	1.42	0.22
Base Model + $Treatment_{564}$ × Period	10	1.95	0.17
Base Model + $Treatment_{930}$ × Period	10	3.01	0.10
Base Model + $Treatment_{1600}$ × Period	10	4.20	0.06
Base Model	7	12.32	0.00
Null (Individual + Location)	3	163.78	0.00
Tebuthiuron[a] (Base Model: Sage + $Bare_{564}$ + $Slope_{930sd}$ + $SDist_{335}$)			
Base Model + EucTreatment × Period	10	0.00	1.00
Base Model + $Treatment_{930}$ × Period	10	14.59	0.00
Base Model + $Treatment_{564}$ × Period	10	15.72	0.00
Base Model	7	16.06	0.00
Base Model + $Treatment_{335}$ × Period	10	17.10	0.00
Null (Individual + Location)	3	28.15	0.00
Brood			
Mow[a] (Base Model: $Shrub_{1600sd}$ + $ShrubHeight_{564sd}$ + INDVI + Bare + $SDist_{564}$)			
Base Model + EucTreatment × Period	11	0.00	0.86
Base Model + $Treatment_{335}$ × Period	11	5.29	0.06
Base Model + $Treatment_{930}$ × Period	11	5.87	0.05
Base Model + $Treatment_{546}$ × Period	11	6.33	0.04
Base Model	8	12.65	0.00
Null (Individual + Location)	3	253.78	0.00
Tebuthiuron[a] (Base Model: $ShrubHeight_{335sd}$ + INDVI + $Herb_{335}$ + Bare + $SDist_{1600}$)			
Base Model + EucTreatment × Period	11	0.00	1.00
Base Model + $Treatment_{930}$ × Period	11	22.52	0.00
Base Model + $Treatment_{564}$ × Period	11	23.52	0.00
Base Model + $Treatment_{335}$ × Period	11	23.91	0.00
Base Model	8	28.17	0.00
Null (Individual + Location)	3	254.61	0.00

Broodless Female

Mow[a] (Base Model: $Shrub_{930sd}$ + INDVI + Litter + $Slope_{335}$ + EucSDist)			
Base Model + EucTreatment × Period	11	0.00	0.94
Base Model	8	7.13	0.03
Base Model + $Treatment_{930}$ × Period	11	8.20	0.02
Base Model + $Treatment_{335}$ × Period	11	9.51	0.01
Base Model + $Treatment_{564}$ × Period	11	9.52	0.01
Null (Individual + Location)	3	619.98	0.00
Tebuthiuron[a,b] (Base Model: $Shrub_{335sd}$ + Bare + $Slope_{1600}$ +$SDist_{1600}$)			
Base Model + EucTreatment × Period	10	0.00	1.00
Base Model	7	69.22	0.00
Base Model + $Treatment_{564}$ × Period	10	69.90	0.00
Base Model + $Treatment_{335}$ × Period	10	70.28	0.00
Null (Individual + Location)	3	452.85	0.00

[a]Model containing $Treatment_{1600}$ × Period failed to converge.

[b]Model containing $Treatment_{930}$ × Period failed to converge.

Table 2.5. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) from models evaluating environmental and treatment variables on greater sage-grouse nest habitat selection relative to mowing and tebuthiuron treatments in Wyoming big sagebrush, central Wyoming, USA, 2011–2017.

Parameter	Estimate	SE	LCL	UCL
Mow				
Intercept	-4.602	0.215	--	--
$Bsage_{930}$	0.985	0.160	0.672	1.298
$Herb_{1600}$	-0.540	0.131	-0.798	-0.282
Litter	0.523	0.108	0.311	0.734
$Slope_{564}$	0.261	0.131	0.003	0.518
$Treatment_{335}$	0.148	0.029	0.091	0.205
Period	0.286	0.178	-0.064	0.636
$Treatment_{335}$ × Period	-0.165	0.049	-0.261	-0.070
Tebuthiuron				
Intercept	-3.165	0.275	--	--
Sage	0.263	0.093	0.080	0.446
$Bare_{564}$	0.212	0.108	0.000	0.423
$Slope_{930sd}$	0.114	0.103	-0.087	0.316
$SDist_{335}$	-1.476	0.648	-2.746	-0.207
EucTreatment	-0.780	0.270	-1.309	-0.251
Period	-0.357	0.301	-0.948	0.234
EucTreatment × Period	0.421	0.292	-0.151	0.994

Table 2.6. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) from models evaluating environmental and treatment variables on greater sage-grouse brood habitat selection relative to mowing and tebuthiuron treatments in Wyoming big sagebrush, central Wyoming, USA, 2011–2017.

Parameter	Estimate	SE	LCL	UCL
Mow				
Intercept	-3.649	0.158	--	--
$Shrub_{1600sd}$	0.352	0.075	0.205	0.500
$ShrubHeight_{1600sd}$	-0.336	0.072	-0.476	-0.195
INDVI	-0.185	0.079	-0.340	-0.030
Bare	-0.734	0.056	-0.844	-0.624
$SDist_{564}$	0.136	0.045	0.048	0.224
EucTreatment	-0.191	0.058	-0.305	-0.077
Period	-0.155	0.179	-0.506	0.196
EucTreatment × Period	0.080	0.067	-0.051	0.210
Tebuthiuron				
Intercept	-3.60	0.334	--	--
$ShrubHeight_{335sd}$	0.223	0.070	0.086	0.360
INDVI	-0.100	0.074	-0.245	0.045
$Herb_{335}$	0.394	0.080	0.238	0.551
Bare	-0.704	0.072	-0.846	-0.563
$SDist_{1600}$	-0.426	0.168	-0.755	-0.097
EucTreatment	-0.412	0.102	-0.612	-0.212
Period	-0.068	0.184	-0.430	0.293
EucTreatment × Period	0.080	0.126	-0.166	0.327

Table 2.7. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) from models evaluating environmental and treatment variables on broodless female greater sage-grouse habitat selection relative to mowing and tebuthiuron treatments in Wyoming big sagebrush, central Wyoming, USA, 2011–2017.

Parameter	Estimate	SE	LCL	UCL
Mow				
Intercept	-3.800	0.090	--	--
$Shrub_{930sd}$	0.604	0.037	0.532	0.676
INDVI	-0.169	0.045	-0.258	-0.081
Litter	0.423	0.038	0.347	0.498
$Slope_{335}$	-0.730	0.061	-0.849	-0.611
EucSDist	-0.118	0.039	-0.195	-0.041
EucTreatment	-0.092	0.026	-0.142	-0.041
Period	-0.166	0.099	-0.360	0.028
EucTreatment × Period	0.056	0.025	0.006	0.106
Tebuthiuron				
Intercept	-3.602	0.325	--	--
$Shrub_{335sd}$	0.399	0.041	0.317	0.480
Bare	-0.436	0.037	-0.508	-0.364
$Slope_{1600}$	-0.736	0.059	-0.852	-0.620
$SDist_{1600}$	-0.730	0.178	-1.079	-0.381
EucTreatment	-0.458	0.077	-0.609	-0.307
Period	-0.131	0.132	-0.391	0.128
EucTreatment × Period	0.129	0.085	-0.038	0.295

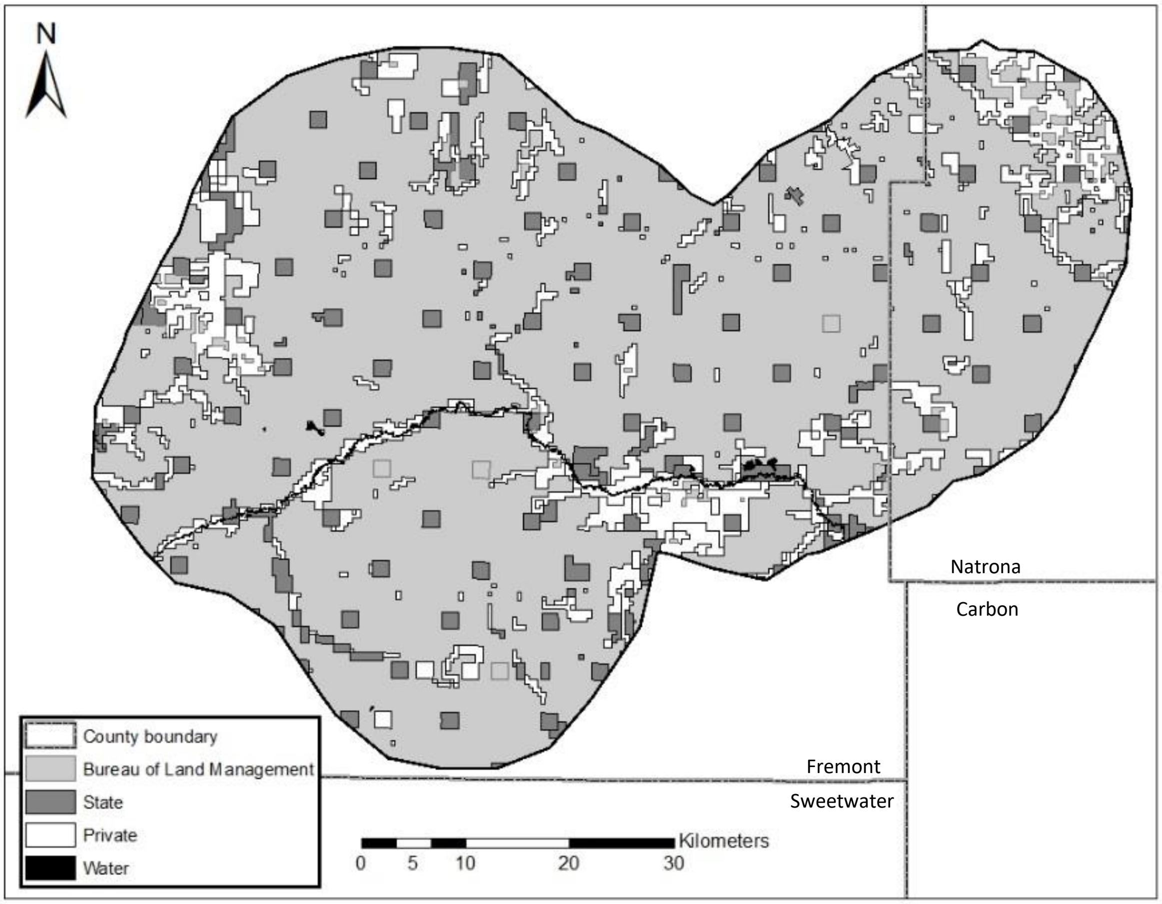

Figure 2.1. Study area defined by a 99% kernel utilization distribution of sage-grouse nesting, brood-rearing, and broodless female use locations encompassing ~4,595 km^2 in central Wyoming, USA, 2011−2017.

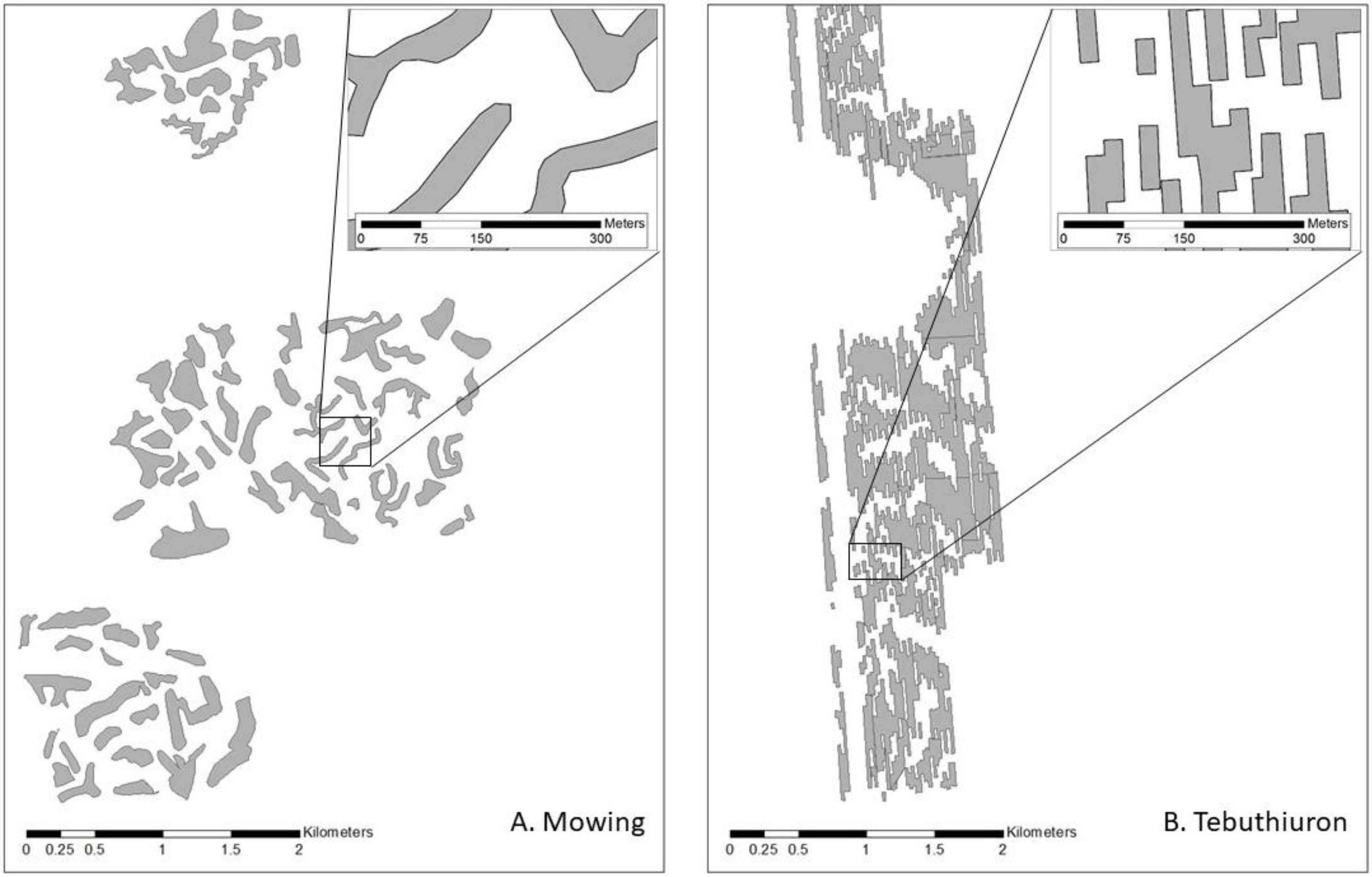

Figure 2.2. Configuration of mowing (A) and tebuthiuron (B) treatments (shaded polygons) implemented in 2014 surrounded by non-treated Wyoming big sagebrush (white) in central Wyoming, USA.

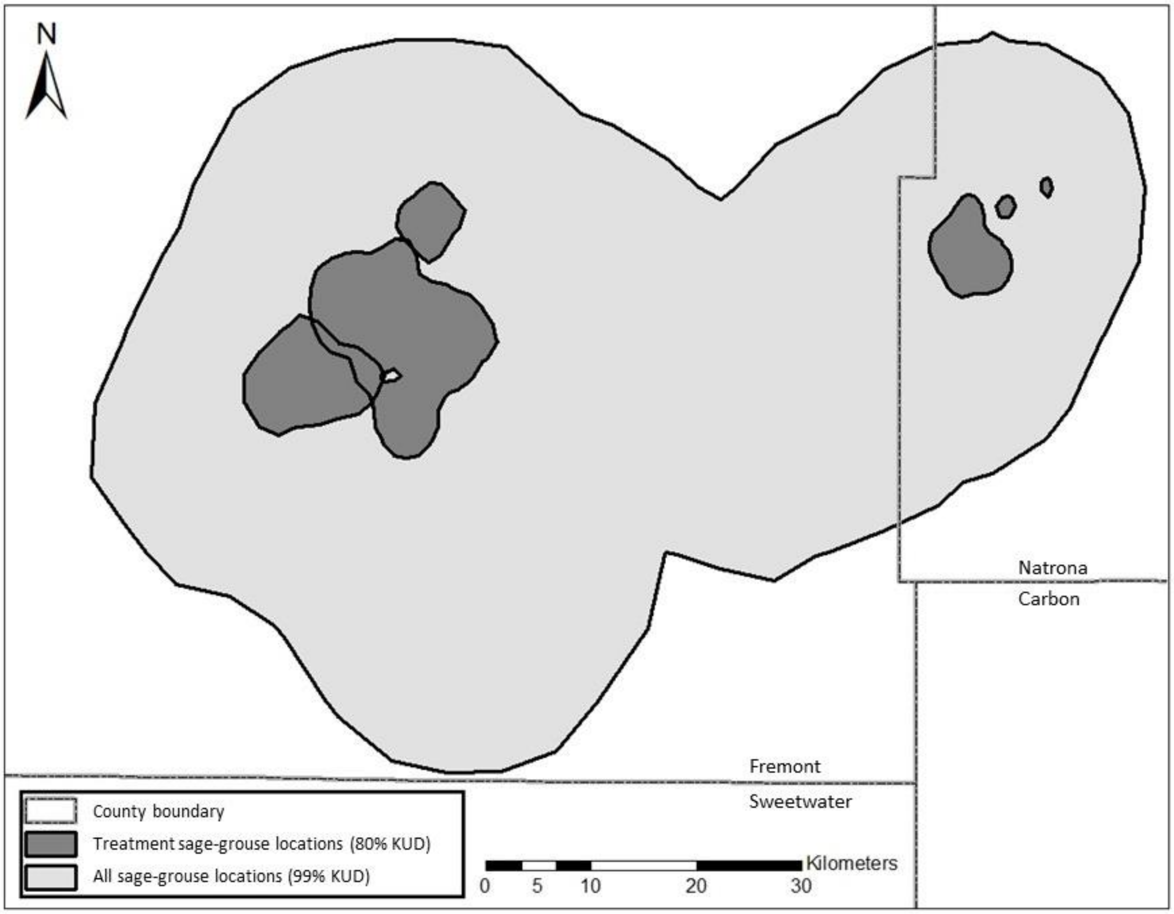

Figure 2.3. Available habitats within each of the 4 treatment areas delineated by 80% kernel utilization distributions (KUD) in central Wyoming, USA, 2011−2017.

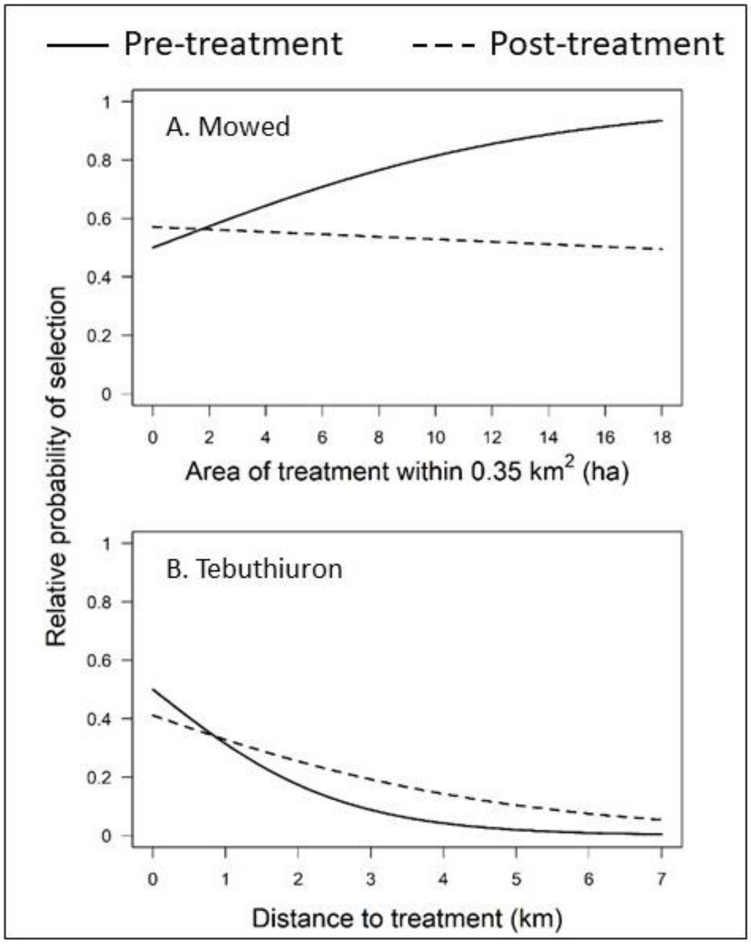

Figure 2.4. Relative probability of greater sage-grouse nest habitat selection during pre-treatment (2011–2013; solid lines) and post-treatment (2014–2017; hashed lines) time periods in relation to mowed (A) or tebuthiuron (B) treatment, central Wyoming, USA, 2011–2017.

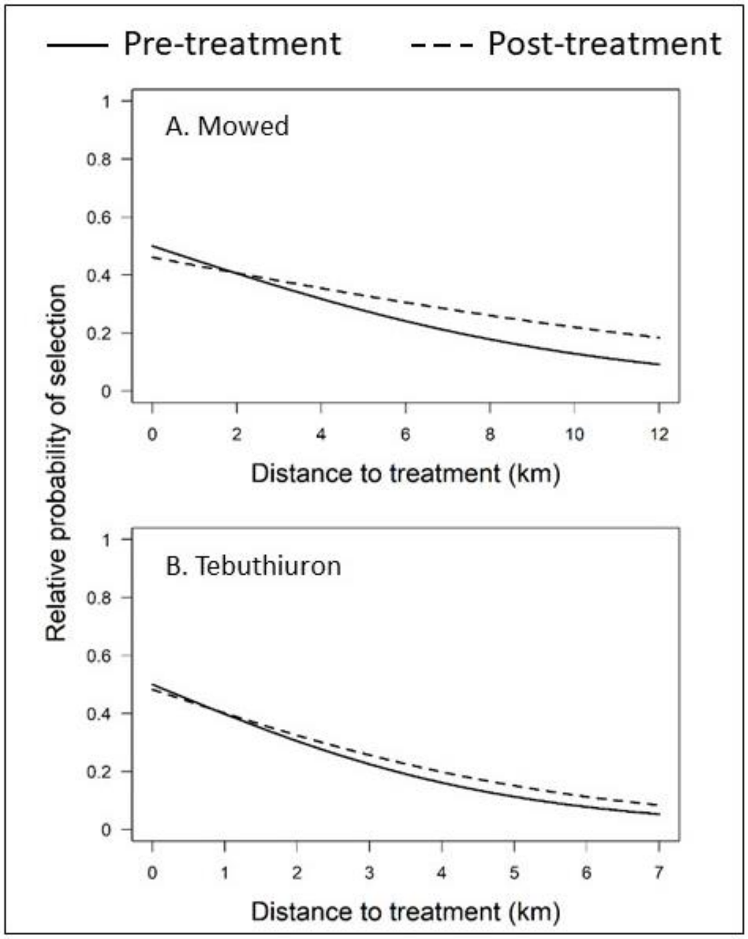

Figure 2.5. Relative probability of greater sage-grouse brood habitat selection during pre-treatment (2011–2013; solid lines) and post-treatment (2014–2017; hashed lines) time periods in relation to mowed (A) or tebuthiuron (B) treatment, central Wyoming, USA, 2011–2017.

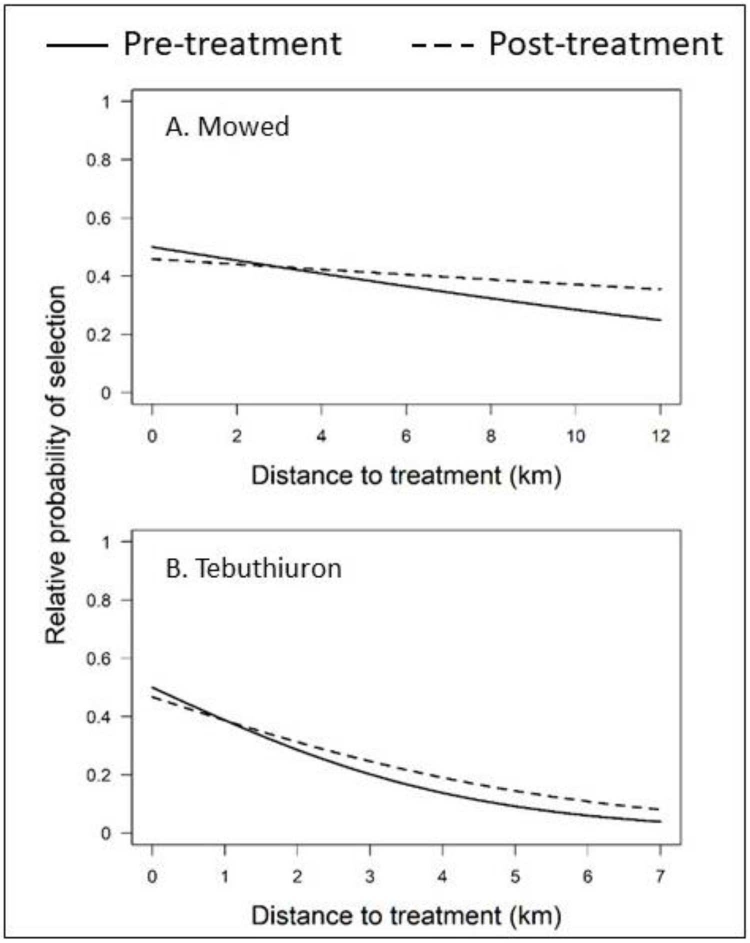

Figure 2.6. Relative probability of broodless female greater sage-grouse habitat selection during pre-treatment (2011–2013; solid lines) and post-treatment (2014–2017; hashed lines) time periods in relation to mowed (A) or tebuthiuron (B) treatment, central Wyoming, USA, 2011–2017.

CHAPTER THREE

GREATER SAGE-GROUSE DEMOGRAPHIC RESPONSE TO MOWING AND TEBUTHIURON TREATMENTS

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In the format of manuscripts submitted to *The Journal of Wildlife Management*

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ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) populations have declined range-wide largely in response to loss, fragmentation, and degradation of remaining sagebrush (*Artemisia* spp.) habitats. Wildlife practitioners have in turn responded to these declines through unparalleled conservation efforts. Treatments to reduce shrub overstory, thereby releasing herbaceous understory are one means managers have increasingly attempted to improve habitat quality for breeding sage-grouse by enhancing food and cover resources for nesting and brood-rearing. Some studies have examined sage-grouse use of treated areas; however, use alone may be a misleading indicator of treatment success as habitat quality is a function of use and an individual's ability to survive and reproduce. Research examining demographic response to treated areas is sparse, but is necessary to assess the effectiveness of sagebrush habitat treatments for sage-grouse. Our objective was to evaluate demographic response of sage-grouse to mowing and tebuthiuron (Spike® 20P) treatments in Wyoming big sagebrush (*A. tridentata wyomingensis*). Our Before-After Control-Impact study in central Wyoming, USA included 2 untreated control, 2 mechanically mowed, and 2 tebuthiuron treated study areas. We collected pre-treatment (2011–2013) and post-treatment (2014–2017) data on nest, brood, and adult female survival from 444 radio-marked female sage-grouse. In 2014, we implemented mowing and aerial-broadcast tebuthiuron treatments totaling 4.9 and 6.1 km^2, respectively. Treatment prescriptions followed Wyoming Game and Fish Department guidelines for sage-grouse core areas, which restrict surface disturbance to no more than 5%. We found no differences in nest survival between mowed and tebuthiuron treatments or between treatment and control study areas. Brood and adult female survival were not influenced by distance to mowed or tebuthiuron treatments. Our results demonstrate that fine-scale mowing and tebuthiuron treatments applied in a mosaic pattern do not generate positive or negative impacts on sage-grouse nest, brood, or adult female survival in Wyoming big sagebrush habitats.

KEY WORDS *Centrocercus urophasianus*, demographic rates, mechanical treatment, chemical treatment, Wyoming big sagebrush.

INTRODUCTION

Conservation and restoration of wildlife habitats is a critical avenue of wildlife management and research, particularly in the face of drastic changes in terrestrial land use that have occurred since the mid-1800s (see Goldewijk 2001). Restoration and manipulation of habitats are often implemented to enhance conditions for wildlife populations (e.g., Hancock et al. 2011, Bergman et al. 2014). Habitat treatments typically aim to alter habitat quality for targeted species and have seen widespread implementation across both aquatic (Gowan and Fausch 1996, Eggleston et al. 1998, Syms and Jones 2000, Sass et al. 2006, Olsson and Nyström 2009) and terrestrial taxa

(Sullivan and Moses 1986, Lochmiller et al. 1991, Hagar et al. 2004, Greenberg and Waldrop 2008, Long et al. 2008). The alteration of vegetation structure and composition through treating vegetation may modify species diversity and composition by enhancing habitat conditions for the targeted species.

In the western United States, treatments have been implemented in big sagebrush (*Artemisia tridentata* spp.) communities to increase herbaceous production for domestic livestock and wildlife (Davies et al. 2009, Beck et al. 2012). The sagebrush ecosystem covers approximately 431,000 km^2 of rangelands in the western United States, providing habitat for >350 sagebrush-associated species of conservation concern (Wisdom et al. 2005). Over the past century however, fragmentation from fire and invasive species (Davies et al. 2011b, Chambers et al. 2017), and anthropogenic activities including agriculture and energy development (Leu et al. 2008) have drastically reduced the amount and composition of sagebrush habitats (Knick et al. 2003, Davies et al. 2011a). This has been associated with the declines of many sagebrush-associated species including pygmy rabbit (*Brachylagus idahoensis*; Germaine et al. 2017), sagebrush sparrow (*Artemisiospiza nevadensis*; Gilbert and Chalfoun 2011), and greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse'; Walker et al. 2007, Gregory and Beck 2014, Smith et al. 2016, Green et al. 2017). Therefore, it is imperative to understand how treatments may influence this declining ecosystem and the species that inhabit it.

By 2000, the distribution of sage-grouse had contracted to approximately 56% of its pre-1800 range (Schroeder et al. 2004). Male sage-grouse attending leks, the primary means to index sage-grouse populations, was estimated to have declined between 0.8−2.1% per year since 1965 (Connelly et al. 2004, Nielson et al. 2015, WAFWA 2015) with the most severe declines occurring over the past decade (Nielson et al. 2015). Dramatic sage-grouse population declines have led to 8 petitions to list the species under the Endangered Species Act of 1973 (USFWS 2015). Potential for listing has encouraged large-scale management efforts to conserve sage-grouse populations (State of Wyoming 2011, USFWS 2013).

Altering sagebrush communities through sagebrush removal is one potential method employed to increase the quality of sagebrush brood-rearing habitats for sage-grouse (Davies et al. 2009, Beck et al. 2012). Traditional methods of sagebrush removal including applications of 2,4-D (2,4-dichlorophenoxyacetic acid) and prescribed burning showed little benefit for sage-grouse. Klebenow (1970) reported that sage-grouse nesting in 2,4-D treated strips of sagebrush was uncommon when live sagebrush cover was 5% or less. Beck (1977) found that wintering sage-grouse used 2,4-D and other treatment sites less than their availability across the landscape. Other studies also concluded that large areas of 2,4-D treated sagebrush were not beneficial to sage-grouse populations (Peterson 1970, Wallestad and Eng 1975). Similarly, researchers reported undesirable effects on sage-grouse nesting and brood-rearing habitat in burned areas (Beck et al. 2009, 2011) and decreased male lek attendance (Connelly et al. 2000a) following burning. A recent retrospective study that accounted for wildfire, climate, and anthropogenic factors in the Wyoming Basins of central and western Wyoming found change in annual male sage-grouse lek attendance from 1994 to 2012 was negatively associated with prescribed burning and mechanical treatments as much as 11 years after treatment (Smith and Beck 2018). Only chemical treatments showed a positive relationship to annual change in male lek attendance, but only 11 years after treatments occurred (Smith and Beck 2018).

Sagebrush management practices have more recently shifted towards reducing, but not eliminating sagebrush cover with chemical and mechanical treatments. Reduction in sagebrush cover with tebuthiuron is related to the rate of application of active ingredient (Olson and

Whitson 2002), which does not eliminate all living sagebrush cover, and woody structure of dead plants remains standing. Mechanical treatments are implemented to selectively remove the crown or kill some sagebrush to reduce shrub canopy cover and density to liberate resources for herbaceous plants and young sagebrush plants. Research has demonstrated that forb abundance increases in mountain big sagebrush (*A. t. vaseyana*) following mechanical and chemical treatments, potentially explaining an increased use of treated areas by sage-grouse (Dahlgren et al. 2006, Davies et al. 2012b). Dahlgren et al. (2006) evaluated sage-grouse use of treated mountain big sagebrush with pellet counts and flush surveys and found that sage-grouse used tebuthiuron treatment areas more than mechanical and control areas. Stringham (2010) did not detect a difference in sage-grouse pellet density between aerated and control sites one and two years after treatment, but detected greater pellet densities in aerated sites that were supplemented with grass and forb seeding compared to untreated areas in northeastern Utah. Furthermore, brood-rearing sage-grouse selected areas closer to mechanically thinned mountain big sagebrush stands in Strawberry Valley, Utah (Baxter et al. 2017). Dahlgren et al. (2015) also found a positive sage-grouse response following sagebrush canopy control in Utah where the number of males occupying leks doubled following treatments. The implementation of small treatments (generally <200 ha) in a mosaic may increase sage-grouse abundance, particularly in mountain big sagebrush; however, grouse declines have been reported after treating approximately 15% of sagebrush habitat suggesting a potential threshold for treatments (Dahlgren et al. 2015).

The more widely distributed Wyoming big sagebrush (*A. t. wyomingensis*; Knick et al. 2003), typically responds differently to treatments compared to mountain big sagebrush. Specifically, forb abundance does not increase over the short-term following treatments in Wyoming big sagebrush (Davies et al. 2012a, Hess and Beck 2014). In north-central Wyoming, mechanically treated Wyoming big sagebrush sites did not meet minimum guidelines for nesting and early brood-rearing sage-grouse habitats as much as 9 years after mowing (Hess and Beck 2012). For these reasons, it is imperative to understand how sage-grouse respond to treatments across these different sagebrush communities (Fulbright et al. 2018). Although studies have assessed the effect of sagebrush treatments on sage-grouse habitat use and selection (Klebenow 1970, Dahlgren et al. 2006, Baxter et al. 2017) in mountain big sagebrush communities, it is critically important to evaluate survival and reproduction to understand how manipulated habitats may influence habitat quality (Van Horne 1983, Boyce and McDonald 1999) and to determine the success of these management practices for species such as sage-grouse (Block et al. 2001, Johnson 2007).

We evaluated how mowing and herbicide treatments in Wyoming big sagebrush influenced sage-grouse nest survival, brood survival, and adult female survival during the breeding season using pre- and post-treatment data collected from 2011–2017 in central, Wyoming, USA. Studies have evaluated overall population change (Dahlgren et al. 2015, Smith and Beck 2018) in treated mountain and Wyoming big sagebrush communities; yet we lack more fine-scale information about how individual sage-grouse vital rates may be influenced by these sagebrush treatments. To better understand potential methods to enhance habitat for declining sage-grouse populations (Connelly et al. 2004, Schroeder et al. 2004, Nielson et al. 2015), managers must understand how commonly applied habitat treatments influence sage-grouse populations. Although sage-grouse are considered sagebrush obligates, they rely on a mix of herbaceous plant species for concealment cover and nutritional resources during nesting and brood-rearing periods (Wallestad and Eng 1975, Johnson and Boyce 1990). Therefore, if treatments improve the herbaceous component of treated sagebrush habitats, treatments may improve habitat quality for sage-grouse (Hess and Beck 2012, Smith 2016, Smith and Beck 2018). Our analysis is critically important to assess the effectiveness of these two popular sagebrush treatments on the quality of sage-grouse breeding habitats.

STUDY AREA

Our study area encompassed approximately 4,595 km^2 in central Wyoming, USA in portions of Fremont and Natrona counties (Fig. 3.1). Elevation ranged from 1,594 to 2,534 m with an average annual 30-year normal precipitation and temperature of 26 cm and 6.1 °C, respectively (PRISM Climate Group 2016). The majority of lands were federally managed (78%) primarily by the Bureau of Land Management, intermixed with state (8%) and privately (14%) administered parcels. Dominant shrub species included Wyoming big sagebrush; however, mountain big sagebrush, basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), yellow rabbitbrush (*Chrysothamnus vicidiflorus*), and rubber rabbitbrush (*Ericameria nauseosa*) were prevalent at suitable sites throughout the area. Cattle grazing was the major land use during the study.

METHODS

Study Design

We used a Before-After Control-Impact design to evaluate the influence of two common sagebrush treatments on demographic rates and survival of female sage-grouse from 2011–2017. Pre-treatment data on nest, brood, and adult female survival were collected during spring and summer 2011–2013 across the entire study area. We used brood-rearing locations collected during 2011 and 2012 to identify important brood-rearing habitats (Smith 2016). Briefly, we used binomial generalized linear models to develop a resource selection function (RSF) with remotely sensed predictors to develop an RSF surface of relative probability of early brood-rearing selection across the study area. We retained the highest predicted relative probability bins and overlaid clusters of early brood-rearing locations to identify 6 spatially isolated treatment areas (2 mowed, 2 tebuthiuron, and 2 reference sites).

We followed State of Wyoming Executive Order 2011−5 guidelines detailing sage-grouse Core Area protection within Core Areas to calculate the maximum allowable disturbance by means of the Density and Disturbance Calculation Tool (DDCT) for the proposed treatment project areas (State of Wyoming 2011). We used GIS predictor variables from models used to generate the RSF (described above) to further delineate suitable treatment locations. We removed locations available for treatment when shrub cover was less than 2 standard deviations of the mean grouse use location (7.9%; Homer et al. 2012) to avoid treating areas containing sparse shrub cover, removed locations less than 100 m from water, and areas with greater than 15% slope.

Mowing and tebuthiuron treatments were implemented during winter and spring 2014. Shrub height was reduced to 25.4 cm across 2 mowing treatment study areas with mechanical mowing. Mowed habitat manipulation occurred across 2.2 km^2 and 2.7 km^2 of mowing study areas, respectively. Aerial broadcast tebuthiuron treatments (Spike® 20P, Dow AgroSciences, Indianapolis, IN, applied at 0.22 kg/ha active ingredient by Ag Flyers, Inc., Torrington, WY) were applied in early May 2014 with the intent of a 50% sagebrush kill rate. Tebuthiuron treatments occurred across 2.8 km^2 and 3.4 km^2 tebuthiuron study areas, respectively. Mechanical and herbicide treatments were applied in a mosaic pattern (see Fig. 3.1); individual treatment polygons averaged 3.3 ha in mowing and 2.8 ha in tebuthiuron treated areas. Treatments followed Wyoming Game and Fish Department Protocols for Treating Sagebrush to be Consistent with Wyoming Executive Order 2011–5; Greater Sage-Grouse Core Area

Protection (WGFD 2011). Specifically, no treatments occurred within 1.0-km of an occupied lek, surface disturbance did not exceed 5%, and treatments were configured such that all treated habitats were within 60 m of sagebrush habitats (*sensu* Dahlgren et al. 2006). Two remaining areas with marked females (described below) served as offsite untreated control study areas encompassing 16.6 km^2 and 61.1 km^2.

Capture and Monitoring

Female sage-grouse were captured with hoop nets and spotlights (Giesen et al. 1982, Wakkinen et al. 1992) during spring and summer each year. In March and April, capture efforts were focused near leks, and nighttime roost locations of radio-marked females were used to capture additional females in August. We affixed either 22 g PVC-covered wire necklace transmitters (Model A4060 [hereafter, very high frequency or VHF]) or G10 UltraLITE GPS Logger (Advanced Telemetry Systems Incorporated, Isanti, MN) or rump-mounted Global Positioning System (GPS) backpacks (22 g PTT-100 Solar Argos/GPS PTT, Microwave Telemetry, Columbia, MD, USA). GPS transmitters were programed to collect 5 locations per day from 15 March to 30 April (at 0700, 1000, 1300, 1600, 2400) and 6 locations per day from 1 May to 24 August (at 0600, 0900, 1200, 1500, 1800, 2400) with the Argos system (CLS America, Largo, MD, USA). We rarified locations collected from GPS marked individuals by randomly selecting only one location per week to be consistent with tracking intervals of VHF-marked individuals. Marked individuals were located weekly from late April through mid-August each year with R-1000 hand-held receivers and 3-element Yagi antennas (Communication Specialists, Orange, CA). We employed a fixed-wing aircraft to locate marked females that we were unable to locate with ground based telemetry. All sage-grouse were captured, radio-marked, and monitored following approved University of Wyoming Institutional Animal Care and Use Committee protocols (03132011 and 20140128JB0059) and Wyoming Game and Fish Department Chapter 33 scientific research permit 801.

We located nests of radio-collared females by homing in on the female's signal until we visually observed them incubating. We triangulated nest locations during subsequent visits to determine nesting status and maintained a distance of ≥30 m to avoid accidental flushing and potential nest abandonment. For GPS-marked individuals, we used satellite downloaded locations to identify dates of nest initiation and fate. We visually inspected potential nests after females left the location to determine nest fate. We defined nest success when at least 1 egg hatched (Rotella et al. 2004). When a female successfully hatched a nest, we determined brood fate by visually observing the female with at least one chick or the female exhibited brooding behavior during telemetry visits (Kirol et al. 2012). When brood failure was determined, we estimated the date of brood loss at the midpoint between visits when brood loss occurred if no brooding behavior was detected during successive visits. We confirmed brood status with night-time spotlight counts at approximately 35 days post-hatch (Walker 2008, Kirol et al. 2015) and considered a female to have successfully reared a brood when at least one chick was present with the female during night-time counts. We continually monitored females irrespective of nest or brood fate throughout the study period to assess adult survival.

Analysis

We evaluated sage-grouse demographic response to treatments using mixed Cox proportional hazards models (Cox 1972) for all vital rates. We assessed nest success using time to event models over a 27 d incubation period. We used a 27 d incubation period because on average, GPS equipped females (n = 30) incubated for 27 d. We used the interval counting process to assess weekly brood and adult female survival (Anderson and Gill 1982), where brood survival was assessed from hatch to 5 weeks (35 d) and adult female survival was assessed across an approximate 15-week survival period from 1 May through 15 August during each year. We allowed individuals to enter and leave the study with left and right censoring (Winterstein et al. 2001). Nest failure and brood and adult mortality dates were estimated as the mid-point between monitoring intervals when nest failure, brood loss, or mortality of adults occurred. We explored the possibility of transmitter types influencing demographic rates and included a variable for transmitter in all models if demographic rates differed between transmitter types.

Prior to evaluating the influence of habitat treatments on demographic parameters, we built environmental models for each demographic rate to account for potential variation in survival across different environmental features that individuals were exposed to. Big sagebrush communities with rich herbaceous understories are critical for sage-grouse breeding life history (Hagen et al. 2007). The Normalized Difference Vegetation Index (NDVI) indexes net plant primary production (Pettorelli et al. 2011) and has been positively correlated with sage-grouse habitat selection (Dinkins et al. 2014), population growth, and recruitment (Blomberg et al. 2012). Precipitation positively influences sage-grouse population growth and individual vital rates (Blomberg et al. 2012, Guttery et al. 2013), but precipitation timing could negatively influence nest and chick survival (Hannon and Martin 2006, Moynahan et al. 2007). For those reasons, we included estimates of remotely sensed big sagebrush percent canopy cover (Homer et al. 2012), normalized difference vegetation index (NDVI; 250 m resolution; LP DAAC 2017), and precipitation (nest and brood models only; PRISM Climate Group 2016) to account for the potential variation in how these factors influence demographic rates. NDVI estimates were available every 8 d, so we matched the nearest NDVI value to the date of estimated nest initiation, or date of locating a brood or adult. We summed precipitation data over 1, 3, and 5 days prior to estimated nest fate and before each brood location was recorded. Sage-grouse nest survival is lower 1 day after significant precipitation events (Moynahan et al. 2007, Webb et al. 2012), thus we expected precipitation events could negatively influence nest fate or brood survival over a short time interval; however, we did not expect this to be the case for adult survival. Therefore, we did not include precipitation in adult survival models. Nonetheless, annual precipitation has been shown to explain recruitment and survival in sage-grouse (Blomberg et al. 2012, 2013), so we included a random effect of year in all adult survival models to account for potential yearly variation in precipitation.

For our nest survival analysis, we used a binary classification to differentiate between control and treatment individuals. We used all locations collected from females equipped with GPS transmitters to determine the distance between the location of the nest, and all other locations collected up to 3 weeks prior to nest initiation as this is the period when females are bred and begin seeking nest locations (Schroeder et al. 1999). We placed a circular analysis region around each nest based on this distance (median value = 3.47 km, from n = 47 individual-years). If a nest encircled by 3.47 km overlapped with a treatment, we designated that individual as a treatment bird. This designation made the assumption that habitats within 3.47 km of an individual were available to that individual during the period leading up to nest initiation. Nests within a treatment study area, but having a circular analysis region that did not overlap with a treated area were considered control individuals. Control nests and nests in reference study areas were pooled for analysis if no difference in survival was detected between the two control types. Only first nests were used in our analysis because renesting events are generally less common and often experience increased survival compared to first nests (Moynahan et al. 2007).

For brood and adult survival models, classifying individuals as either treatment or control was confounded by potential carry-over effects as they moved between relocations. That is, it became difficult to classify individuals to treatment types as they navigated the landscape. Instead of a categorical treatment predictor, we assessed the influence of treatments based on the distance of an individual to the nearest treatment during each relocation event. Influence of treatments was estimated by the distance to nearest treatment.

To evaluate the influence of treatments on individual demographic rates, we followed a sequential modelling approach (Arnold 2010). We first determined the most supported random factor or combination of random factors compared to null models. For nesting models we assessed random factors that included study area, year, and individual. For brood and adult models, we evaluated year and individual as random factors, but used year as a random factor in all adult models (described above). Once the most supported random effects only models were obtained for each demographic model, we ran univariate models to select the precipitation variable (nest and brood only) that was most supported based on Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). We then explored all combinations of uncorrelated ($|r| < 0.7$; Allison 2009) variables in each environmental model to assess model improvement. We considered environmental models to be competitive with null models when the most supported base model was within 4 AICc of the null model. If environmental models showed improvement over null models, we included variables in the most supported environmental models in subsequent analyses. Variables used to assess the influence of treatments included treatment type (nest models) or distance to treatment (brood and adult models), time (pre- or post-treatment), and the treatment × time interaction in each model. A significant interaction between treatment and time would indicate a change in the measured demographic parameter following treatments. Statistical significance was set at alpha = 0.05.

RESULTS

From spring 2011–2017, we captured and radio-marked 512 female sage-grouse providing 485 nest, 1,174 brood-rearing, and 5,659 adult female locations for analysis (Table 3.1). We found no difference in survival between GPS or VHF transmitter types for our nest and brood analysis ($P \geq 0.24$). However, adult females equipped with GPS backpack transmitters had lower survival compared to other collar types ($\beta = 1.072$, 95% CI = 0.625 to 1.520), so we included transmitter type in subsequent adult survival models. In general, combined nest survival rates were higher before treatments (2011–2013; $\beta = 0.485$, 95% CI = 0.414 to 0.568) compared to after treatments (2014–2017; $\beta = 0.417$, 95% CI = 0.367 to 0.473). Likewise, overall brood survival across pre-treatment years was greater ($\beta = 0.740$, 95% CI = 0.648 to 0.844) than across post-treatment years ($\beta = 0.674$, 95% CI = 0.600 to 0.757). Average female survival was lower on the landscape before treatments ($\beta = 0.751$, 95% CI = 0.686 to 0.822) compared to after treatment implementation ($\beta = 0.810$, 95% CI = 0.764 to 0.858). However, these pre- and post-treatment survival estimates do not incorporate treatment influence and contain overlapping 95% confidence intervals for each respective demographic rate across the entire study area.

Nest Survival

The most supported nest survival model included study area as a random factor, precipitation 1 day prior to nest fate, and the treatment × period interaction term (Table 3.2). Precipitation 1 day prior to nest fate was negatively related to nest survival ($\beta = 0.036$, 95% CI = 0.013 to 0.059; Table 3.3). However, we did not detect a difference in nest survival before or after treatments between mowed and control individuals ($\beta = -0.130$, 95% CI = -0.731 to 0.471; Table 3.3, Fig.

3.2), tebuthiuron and control individuals (β = 0.841, 95% CI = −0.080 to 1.763; Table 3.3, Fig. 3.2) or between mowed and tebuthiuron treatment individuals (β = -0.946, 95% CI = −1.937 to 0.045; Table 3.4, Fig. 3.2).

Brood Survival

No models containing only environmental covariates were more supported than the null model. Therefore, we only considered the treatment × period interaction term with year as a random factor. We did not detect a difference in distance to any treatment (β = 0.026, 95% CI = −0.034 to 0.087) on brood survival following treatment implementation (Table 3.3). In addition, distance to mowed (β = 0.048, 95% CI = −0.027 to 0.123) or tebuthiuron (β = −0.007, 95% CI = −0.123 to 0.109) treatment did not influence brood survival following treatments (Table 3.5, Fig. 3.3).

Adult Female Survival

No models containing environmental covariates were more supported than a null model; our final model included a random effect of year, collar type, and the treatment × period interaction term (Table 3.2). We found no difference in distance to any treatment (β = −0.013, 95% CI = −0.056 to 0.029) on adult female survival following treatments (Table 3.3). Distance to mowed (β = −0.004, 95% CI = −0.053 to 0.046) or tebuthiuron treatments (β = −0.034, 95% CI = −0.127 to 0.058) did not influence adult female survival following treatments (Table 3.6, Fig. 3.4).

DISCUSSION

The purpose of our research was to investigate the demographic response of sage-grouse to habitat treatments, and is the first to evaluate nest, brood, and adult female survival to mowing and tebuthiuron treatments in Wyoming big sagebrush using multiple years of pre- and post-treatment data. Our study comprised of a statistically powerful Before-After Control-Impact experimental design, believed to be the ideal approach for environmental monitoring

(Underwood 1991), provides a substantial level of certainty in our results highlighting sage-grouse demographic responses to habitat treatments. We did not detect any relationships between measured demographic rates and mowing or tebuthiuron treatments suggesting that treatments in our study did not enhance or reduce sage-grouse populations. Current understanding of sagebrush habitat manipulation with the intent of improving conditions for sage-grouse is generally scant and has been limited to studies aimed at understanding how sage-grouse utilize treated areas, but not how treatments may influence important vital rates. Furthermore, current literature is largely divided between studies in Wyoming and mountain big sagebrush where herbaceous vegetation responds differently and likely facilitates differing sage-grouse responses (Beck et al. 2012, Fulbright et al. 2018).

Other ground nesting bird species exhibited neutral demographic responses to vegetation treatments. Carter et al. (2002) found similar nest success and survival of northern bobwhite (*Colinus virginianus*) between sites treated with prescribed fire and untreated areas. Treatments may provide both desired and undesired demographic responses as found by Peters et al. (2015) in quail. Northern bobwhite survival varied seasonally with greater survival in summer and lower survival in winter at treatment compared to control sites (Peters et al. 2015). Differences in survival rates across seasons in treated areas may be an important consideration for sage-grouse. Though we found evidence for a neutral demographic response to mowing and tebuthiuron treatments during the breeding season, sage-grouse rely on sagebrush for food and cover during winter (Wallestad and Eng 1975); reduction in cover and subtle changes in the nutritional quality of sagebrush could negatively influence the value of winter habitat for sage-grouse (Davies et al. 2009, Smith et al. 2018).

Treatments have been implemented to reduce sagebrush cover while simultaneously increasing important foraging resources for sage-grouse (Beck et al. 2012). Guidelines suggest 10–20% sagebrush cover for late brood-rearing sage-grouse and 15–25% cover for nesting (Connelly et al. 2000b). Females may select nesting locations based on quality of surrounding brood-rearing habitat (Gibson et al. 2016), which consists of intermediate sagebrush cover with an herbaceous understory (Drut et al. 1994, Hagen et al. 2007). During spring growth, forbs have greater nutritional quality than sagebrush leaves and have been found to contribute up to 50% of pre-laying sage-grouse diets (Barnett and Crawford 1994). The nutritional status of females is important for egg development and quality; any herbaceous response resulting from sagebrush treatments would likely explain an increase in nest survival as treatments generally reduce sagebrush heights to levels that females will not use for nesting. Greater forb availability at local scale nest sites (Gibson et al. 2016) and between study areas (Drut et al. 1994) has been found to positively influence reproductive success for sage-grouse. Accessibility to nutrient rich food sources during the prelaying, nesting, and brood-rearing periods are important for sage-grouse recruitment. If increased forb and insect production does not result from treatment implementation (see Hess and Beck 2014), increased reproductive success may not result from habitat manipulations. Insect and forb dry mass within our study did not differ between treatment types or between treated and untreated areas up to two growing seasons after treatments occurred (Smith 2016), which may have influenced our observed neutral demographic responses. Furthermore, forb mass was less than or equal to paired reference areas up to 4 years following both treatment types (Smith et al. unpublished data). Sage-grouse did select for mechanically thinned mountain big sagebrush stands in Utah that experienced increased grass cover but no difference in forb cover following treatments (Baxter et al. 2017), suggesting that other factors, such as increased grass cover might influence sage-grouse selection of treatments. Further research is necessary to evaluate this relationship.

Our study investigated short-term local-scale demographic response to treatments; however, landscape-scale research occurring over greater time periods also support our conclusion that treatments may not positively influence sage-grouse populations. Smith and Beck (2018) found mechanical treatments were predictive of sage-grouse population declines in Wyoming up to 11 years after treatment. However, chemical treatments >10 years old were positively associated with male lek attendance (Smith and Beck 2018), suggesting that there may be a delayed population response to some types of sagebrush treatment. Another study investigating older stands of treated sagebrush found that artificial sage-grouse nests had greater rates of predation in untreated areas compared to 25-year old areas treated by disking and spraying followed by supplemental crested wheatgrass (*Agropyron desertorum*) seeding (Ritchie et al. 1994). Although Ritchie et al. (1994) suggested that given time to recover, treated sagebrush stands can positively influence nest survival, artificial nests may not accurately represent real nest predation rates of ground nesting birds (Storaas 1988, Wilson et al. 1998) and decreased shrub cover has been associated with sage-grouse nest failure (Coates and Delehanty 2010, Webb et al. 2012, Lockyer et al. 2015).

While we did not detect an influence of treatments on sage-grouse demographic rates, we acknowledge that our study was conducted over a small temporal period and that treatments were small relative to historical sagebrush treatments in Wyoming (Johnston et al. 2018, Smith and Beck 2018). The size of treatments was restricted by current guidelines for treating sage-grouse habitats in Wyoming (WGDF 2011). Nonetheless, managers should use caution when altering intact Wyoming big sagebrush. Managing sagebrush habitat for one life stage of a particular species may be detrimental to the species as a whole and to other sagebrush dependent and associated species (Fulbright et al. 2018). Given the long-term recovery rates of Wyoming big sagebrush following treatments (Watts and Wambolt 1996, Beck et al. 2009), it is possible that treatments could provide some long-term benefit to sage-grouse populations. However, this information currently does not exist and practitioners must determine if treatments are acceptable without long term data.

MANAGEMENT IMPLICATIONS

Our results support the developing paradigm that habitat treatments are less beneficial (or a negative factor) to sage-grouse in Wyoming big sagebrush communities compared to mountain big sagebrush habitats, at least over the short term (Beck et al. 2012, Smith and Beck 2018). We recommend future research investigate the response of other sagebrush-dependent species, in addition to sage-grouse, to habitat manipulations intended to benefit sage-grouse. In the absence of long-term data on sage-grouse demographic responses to treatments, managing large intact sagebrush landscapes appears to be more beneficial to sage-grouse populations than reducing sagebrush cover, particularly if the intended results (i.e., increased food resources) are not achieved.

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Table 3.1. Number of locations used to evaluate the influence of mowing and tebuthiuron treatments on greater sage-grouse demographic rates, central Wyoming, USA, 2011–2017.

	Pre-treatment (2010–2013)			Post-treatment (2014–2017)		
	Mow	Tebuthiuron	Control	Mow	Tebuthiuron	Control
Nests	45	28	86	87	91	148
Broods	245	195	--	404	330	--
Adults	1,381	763	--	1,840	1,675	--

Table 3.2. Top and competitive models explaining variability of greater sage-grouse demographic rates in central Wyoming, USA, 2011–2017. Number of parameters (K), change in Akaike's Information Criterion score from the top model (ΔAICc), and Akaike weights (w_i) to evaluate model fit for sage-grouse demographic rates.

Model	K	ΔAICc	w_i
Nest			
Treatment (Treatment × Time + Precipitation$_{1\ d}$ + Study Area)	7	0.00	0.98
Environmental (Precipitation$_{1\ d}$ + Study Area)	2	8.09	0.02
Null (Study Area)	1	14.61	0.00
Brood			
Null (Year)	1	0.00	0.91
Treatment (Distance × Time + Year)	4	4.59	0.09
Adult			
Null (Transmitter Type + Year)	2	0.00	0.82
Treatment (Distance × Time + Transmitter Type + Year)	5	3.02	0.18

Table 3.3. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) from models evaluating environmental and treatment variables on greater sage-grouse nest, brood, and adult female survival in central Wyoming, USA, 2011–2017.

	Nest				**Brood**				**Adult Female**			
Parameter	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**
Environmental												
Precipitation (1 d)	0.036	0.012	0.013	0.059	--	--	--	--	--	--	--	--
Transmitter Type[a]	--	--	--	--	--	--	--	--	1.081	0.229	0.632	1.531
Treatment												
Mow	-0.190	0.262	-0.704	0.324	--	--	--	--	--	--	--	--
Tebuthiuron	-1.326	0.438	-2.184	-0.468	--	--	--	--	--	--	--	--
Distance (km)	--	--	--	--	-0.019	0.026	-0.071	0.033	0.013	0.016	-0.018	0.043
Time[b]	0.129	0.171	-0.206	0.465	0.100	0.407	-0.698	0.898	-0.188	0.280	-0.736	0.360
Mow × Time	-0.130	0.307	-0.731	0.471	--	--	--	--	--	--	--	--
Spike × Time	0.841	0.470	-0.080	1.763	--	--	--	--	--	--	--	--
Distance[c] × Time	--	--	--	--	0.026	0.031	-0.034	0.087	-0.013	0.022	-0.056	0.029

[a]Females equipped with necklace transmitters serve as reference.

[b]Pre- and post-treatment.

[c]Distance to nearest treatment regardless of type.

Table 3.4. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) from models comparing greater sage-grouse nest survival between mowing and tebuthiuron treatments in central Wyoming, USA, 2011–2017.

Parameter	Estimate	SE	LCL	UCL
Environmental				
Precipitation (1 d)	0.040	0.013	0.014	0.066
Treatment				
Mow[a]	1.133	0.459	0.234	2.032
Time[b]	0.952	0.439	0.091	1.813
Mow[a] × Time	-0.946	0.506	-1.937	0.045

[a]Tebuthiuron treatment individuals serve as reference.

[b]Pre- and post-treatment.

Table 3.5. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) from models comparing greater sage-grouse brood survival between mowing and tebuthiuron treatments in central Wyoming, USA, 2011–2017.

	Mow				**Tebuthiuron**			
Parameter	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**
Distance (km)	-0.033	0.032	-0.097	0.030	0.006	0.048	-0.088	0.101
Time[a]	-0.284	0.531	-1.325	0.756	0.461	0.555	-0.628	1.550
Distance × Time	0.048	0.038	-0.027	0.123	-0.007	0.059	-0.123	0.109

[a]Pre- and post-treatment.

Table 3.6. Variable coefficients, standard errors (SE), and 95% confidence intervals (LCL and UCL) from models comparing greater sage-grouse adult female survival between mowing and tebuthiuron treatments in central Wyoming, USA, 2011–2017.

	Mow				Tebuthiuron			
Parameter	**Estimate**	**SE**	**LCL**	**UCL**	**Estimate**	**SE**	**LCL**	**UCL**
Transmitter Type[a]	1.265	0.275	0.727	1.804	0.913	0.444	0.041	1.784
Distance (km)	-0.004	0.018	-0.040	0.031	0.027	0.036	-0.043	0.098
Time[b]	-0.367	0.346	-1.046	0.311	0.160	0.665	-1.143	1.463
Distance × Time	-0.004	0.025	-0.053	0.046	-0.034	0.047	-0.127	0.058

[a]Females equipped with necklace transmitters serve as reference.

[b]Pre- and post-treatment.

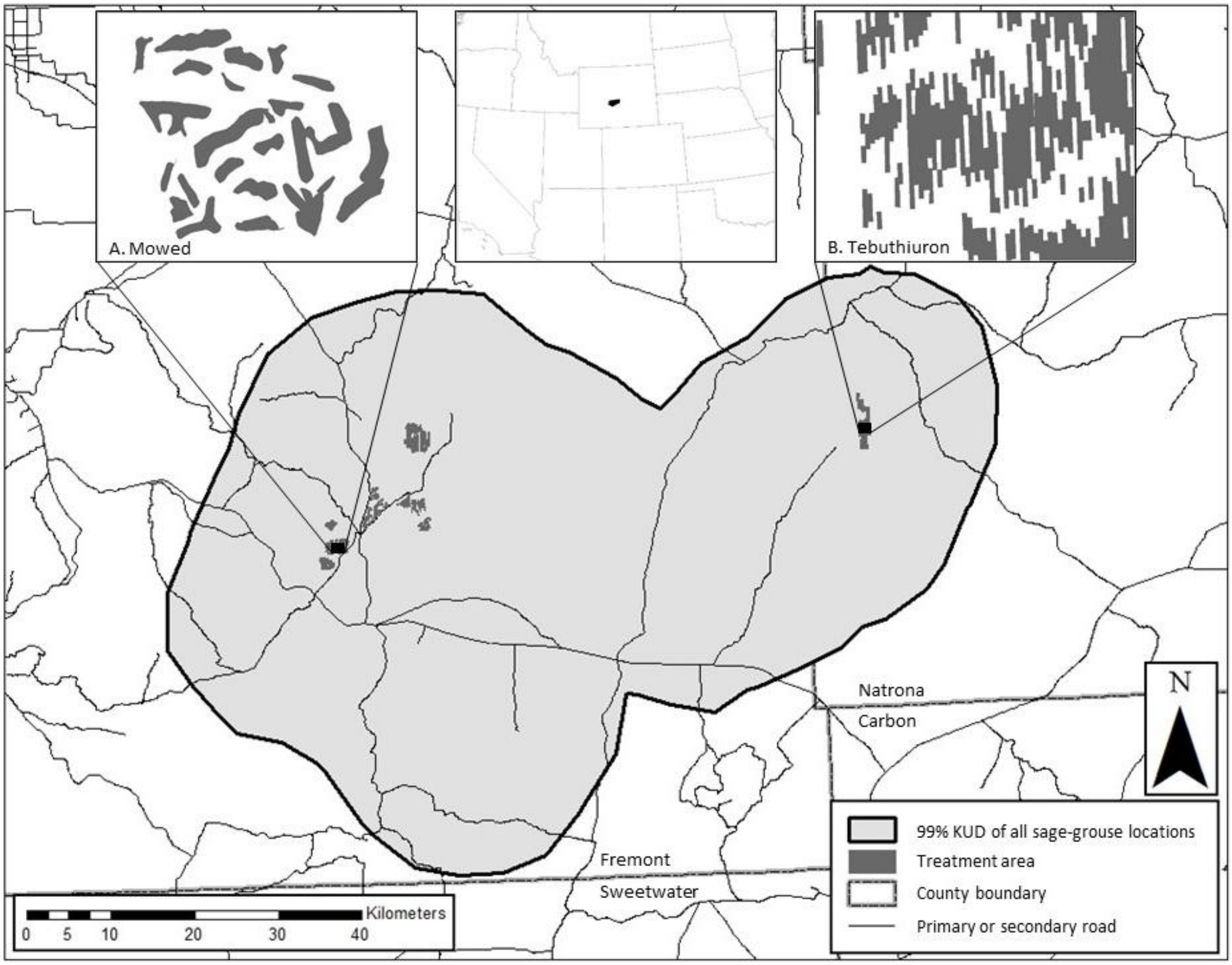

Figure 3.1. Study area defined by a 99% kernel utilization distribution (KUD) of greater sage-grouse nesting, brood-rearing, and adult use locations encompassing ~4,595 km^2 in central Wyoming from 2011−2017. Two mowed (A) and 2 tebuthiuron (B) treatments were implemented in 2014 and occurred across 4.9 and 6.1 km^2 of the study area, respectively, central Wyoming, USA, 2011–2017.

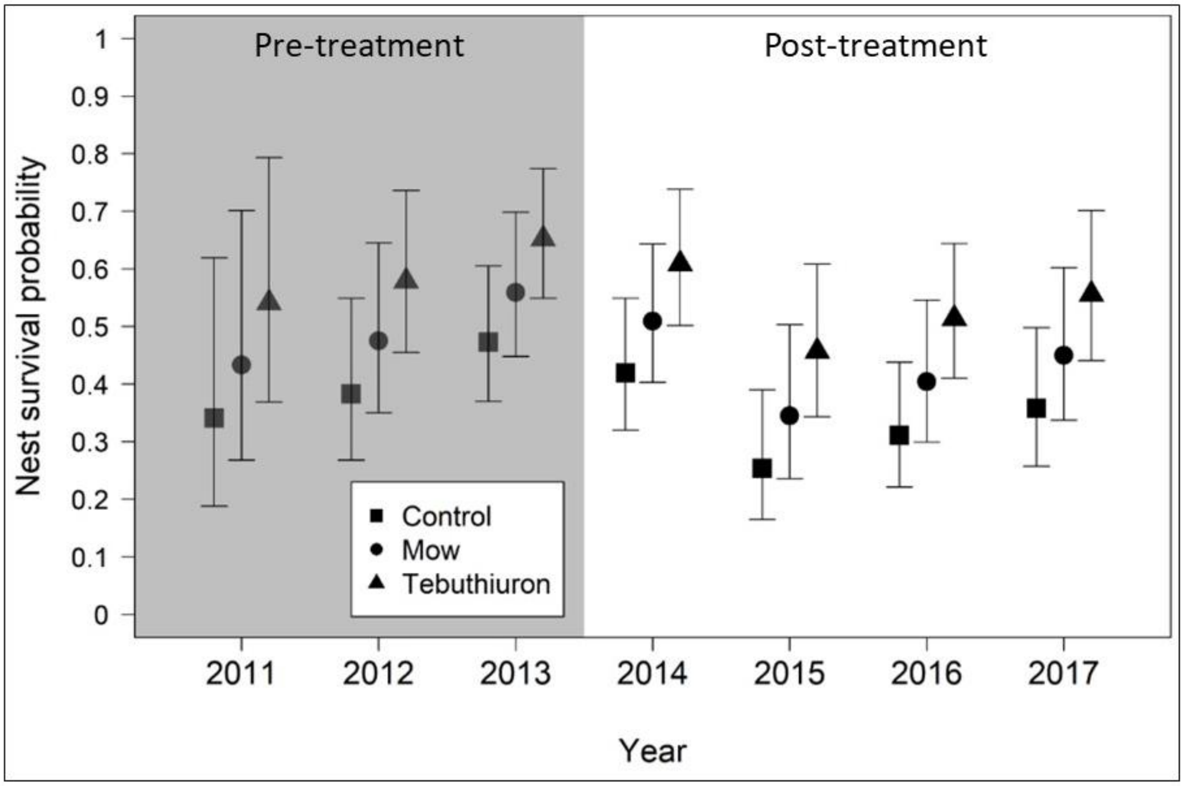

Figure 3.2. Probability of greater sage-grouse nest survival and 95% confidence intervals separated by year and treatment type during pre-treatment (gray) and post-treatment (white) time periods, central Wyoming, USA, 2011–2017.

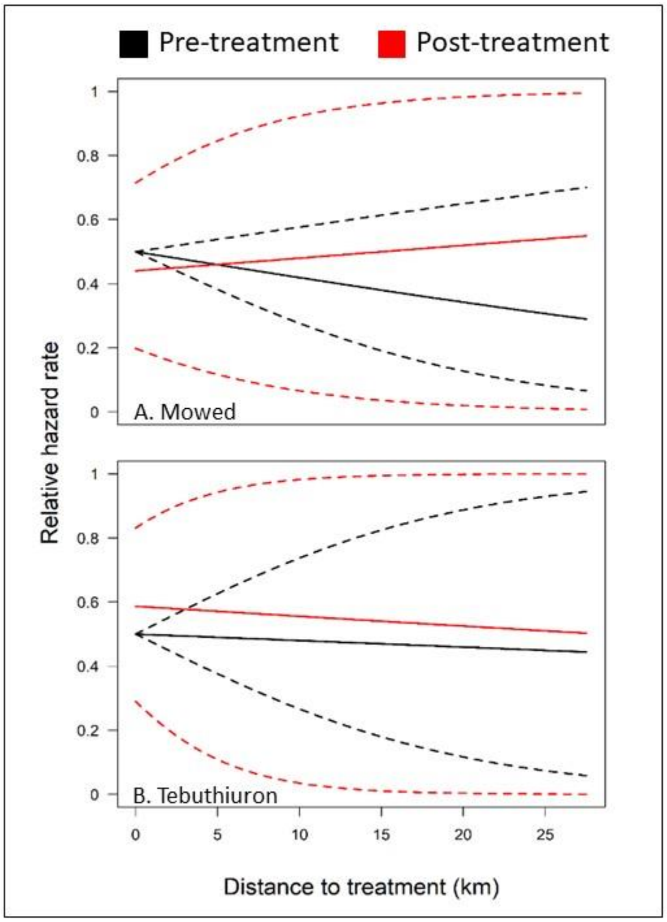

Figure 3.3. Relative hazard rate curves (± 95% CIs) of greater sage-grouse brood survival during pre-treatment (2011−2013; black lines) and post-treatment (2014−2017; red lines) time periods in relation to distance (km) to nearest mowed (A) or tebuthiuron (B) treatment, central Wyoming, USA, 2011–2017.

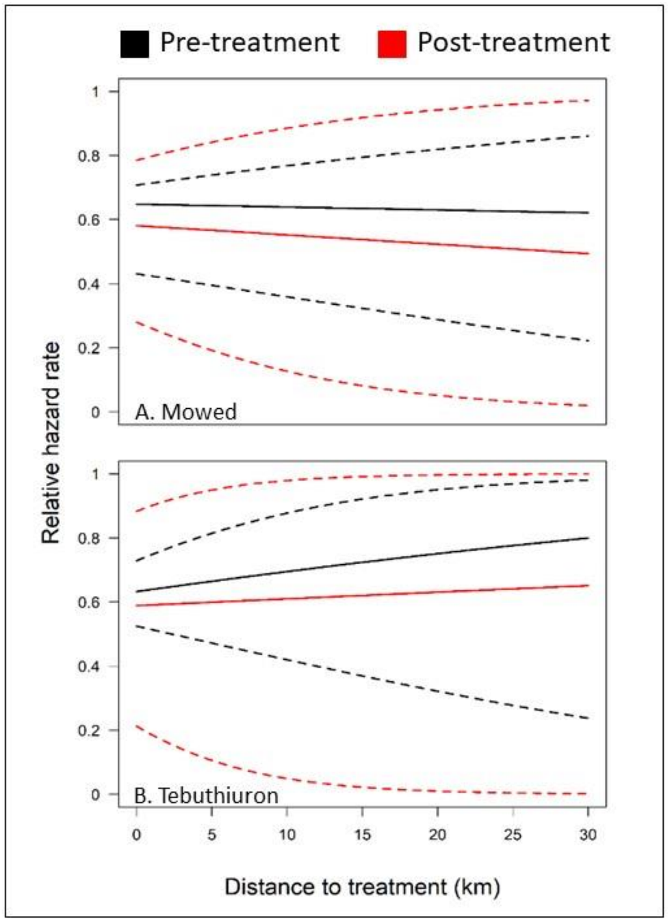

Figure 3.4. Relative hazard rate curves (± 95% CIs) of adult female greater sage-grouse survival during pre-treatment (2011−2013; black lines) and post-treatment (2014−2017; red lines) time periods in relation to distance (km) to nearest mowed (A) or tebuthiuron (B) treatment, central Wyoming, USA, 2011–2017.